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Abiotic Factors Related to Accrual of Common Filamentous Macroalgae in California's Central Coast Streams

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ABIOTIC FACTORS RELATED TO ACCRUAL OF COMMON FILAMENTOUS MACROALGAE IN CALIFORNIA'S CENTRAL COAST STREAMS

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by

Lisa Dillon

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ABSTRACT

Abiotic Factors Related to Accrual of Common Filamentous
Macroalgae in California's Central Coast Streams
by
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Master of Science in Coastal and Watershed Science and Policy
California State University Monterey Bay, 2009

In an effort to develop regional autecological information on nuisance-prone filamentous macroalgae in the Mediterranean climate of California's Central Coast, I explored relationships between stream conditions and presence and abundance of 4 common macroalgal taxa. Algae samples and stream data were taken from a regional bioassessment study conducted during the dry seasons of 2006 and 2007 at 199 low-gradient streams. I developed a priori hypotheses based on a review of algal ecology literature. Within a two-part conditional model framework, I used an information theoretic approach to compare algal presence and abundance (biovolume per area of substrate) response to cover of riparian canopy, total nitrogen (TN) and total phosphorus (TP) concentrations, flow velocity, substrate size, pH, conductivity, and season. Model comparison and multi-model inference results supported two main findings for each of three target taxa: *Cladophora* spp. presence and abundance increased with a higher percentage of stable substrata in the stream reach and a lower percentage of riparian canopy cover; *Spirogyra* spp. presence increased with a lower canopy cover and lower TP concentrations; and *Ulva* spp. presence increased with lower canopy cover of and higher conductivity. Post hoc analyses showed dissolved oxygen saturation to be higher in the presence of *Cladophora* spp. and *Ulva* spp. These results highlight the role of riparian canopy in regulating filamentous macroalgal accrual and maintaining stream health in the region.

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DOCUMENT ORGANIZATION

This thesis is organized into three main sections. Chapter one is a discussion of the policy background and policy implications of the study. Chapter two is a manuscript written for publication in a peer-reviewed science journal. The appendix contains extra material included to compliment chapter two.

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CHAPTER 1

THESIS INTRODUCTION

NUISANCE ALGAE: TOO MUCH OF A GOOD THING

Prolific growth of benthic algae in freshwater streams can create conditions that interfere with human uses and ecosystem function. While such prolific growth can result from anthropogenic stressors, these algae are often a natural periodic component of healthy stream ecosystems. As primary producers, algae sustain the nutrient demands of higher trophic organisms and provide valuable aquatic habitat. In healthy systems, algal growth and accrual is limited by a number of ecological factors including nutrient and light availability, algivory, and hydrologic disturbance (Horner et al. 1990, Hill at al. 1995, Feminella and Hawkins 1995, Borchardt 1996). But given significant changes in the factors that regulate growth, such as significant loss of riparian canopy or cultural eutrophication, algae may proliferate to excessive levels (Biggs 2000a, Dodds and Welch 2000). These proliferations, also known as nuisance algae, affect the stream environment by reducing water clarity, creating harmful diel fluctuations in pH and dissolved oxygen concentrations, reducing habitat quality for macroinvertebrates and spawning fish, and increasing probability of fish kills (Carpenter et al. 1998; Smith et al. 1999; Dodds and Welch 2000). In addition, nuisance blooms can impede recreational, industrial, agricultural, and municipal uses, leading to economic losses (Carpenter et al. 1998, Dodds and Welch 2000, Biggs 2000a). Biggs (2000a) suggests that algal biomass levels >150-200 mg/m^2 chlorophyll *a* can interfere with contact recreation and sport fishing, are very noticeable, and are likely to be unnaturally high.

Nuisance blooms manifest in different forms depending on the dominant algal functional group. Blooms can appear as phytoplankton-rich green water, carpets of short-stalked benthic diatoms, floating gelatinous colonies, and filamentous mats. The latter are made up of benthic filamentous green algae that tend to dominate the climax community in eutrophic waters (Chetelat et al. 1999, Biggs 2000b). Filamentous algal proliferations can lead to higher biomass accrual than other functional groups (Dodds 1991) and are

more nuisance-prone in lotic ecosystems (Horner et al. 1983, Welch et al. 1989). In the western U.S., filamentous nuisance blooms are dominated by *Cladophora glomerata*, *Rhizoclonium* spp., *Oedogonium* spp., *Spirogyra* spp., *Stigeoclonium* spp., *Ulothrix* spp., and *Ulva* spp. (Figure 1; Biggs and Price 1987, Welch et al. 1998, Lembi 2003, Busse et al. 2006).

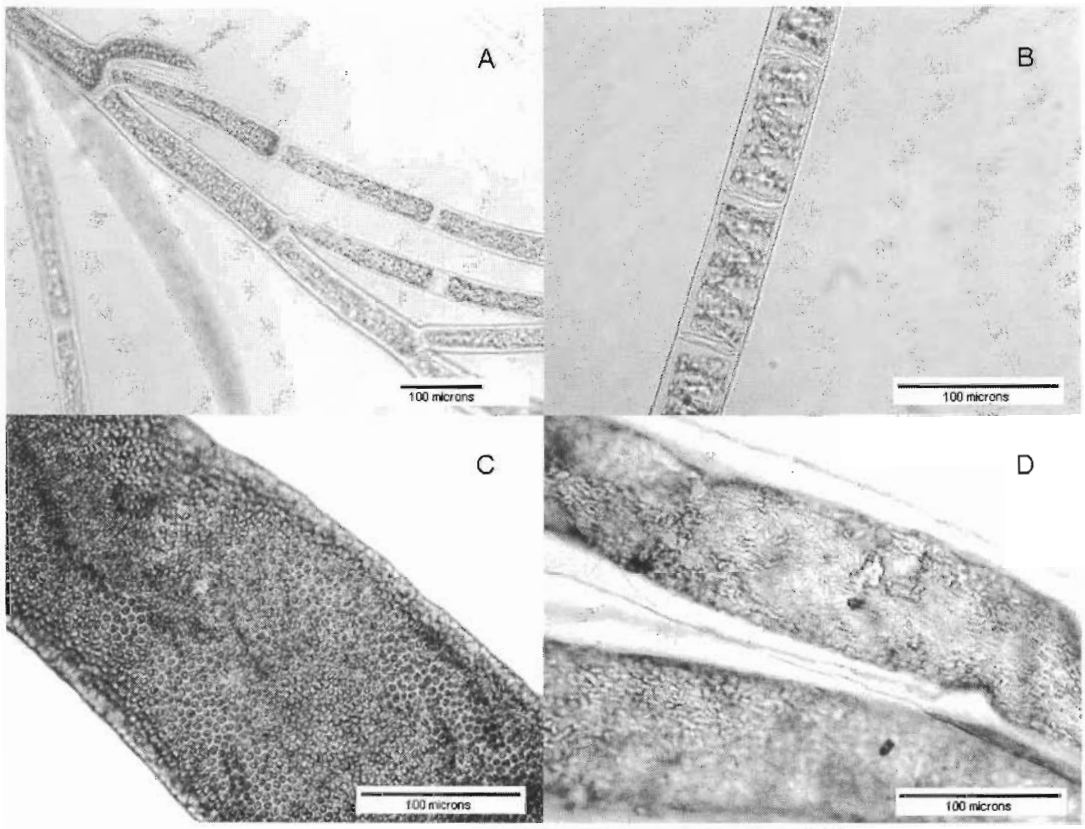

Figure 1.1 Four nuisance-potential macroalgae common to Central Coast streams: A) *Cladophora* sp., B) *Spirogyra* sp., C) *Ulva* sp., and D) *Vaucheria* sp. Photo: Lisa Dillon.

Nuisance algal blooms were first reported from the U.S. in lakes of densely populated areas of the Midwest around the early 1900s (Prescott 1948). In the 1930s and 40s the full scope of ecological and human use issues associated with prolific algal growth, such as fish kills and livestock poisoning, were brought to light (Fitch and Bishop 1934, Prescott 1948). Prescott (1948) identified high nitrogen and phosphorus content in these lakes as a leading cause of nuisance algal blooms. Although algal production in streams requires higher nutrient concentrations than in lakes, increases in

stream algal biomass, as well, can be found following eutrophication (Smith et al. 1999). In 1970, Whitton (1970) found an increasing number of reports of nuisance growth in streams. By the 1980s, several steam researchers were investigating nutrient influence on algal proliferations (Horner et al. 1983, Biggs 1985, Welch et al. 1988). But study results differ, perhaps due to environmental factors that vary regionally, such as density of riparian canopy, grazing pressure, algal community composition, and frequency of high velocity flows (Dodds 1991, Peterson and Stevenson 1992, Taulbee et al. 2005). Thus, study results from one region may not be applicable in another.

Whether or not algal blooms proliferate to nuisance levels on the Central Coast is challenging to determine. Freshwater researchers (Biggs and Price 1987, Dodds et al. 1998) have suggested that, in general, filamentous algae exceeding 30 – 40% cover adversely impacts recreational and aesthetic uses, but few regulatory agencies have assigned numeric thresholds for prolific growth in streams. Florida proposed stream listing for nutrient impairment if annual mean chlorophyll *a* concentrations exceed 20 $\mu g\ l^{-1}$ or if data indicate annual mean chlorophyll *a* values increased by more than 50% over historical values for at least two consecutive years (Florida DEP 2007). A Montana watershed stakeholder group that included local governments developed an EPA-approved threshold of an annual average not to exceed 100 mg/m^2 chlorophyll *a* or a maximum of 150 mg/m^2 (Watson et al. 1999). While these proliferations are often thought to be associated with high nutrient concentrations, many factors play a role in the accrual of benthic filamentous algae. Although the aforementioned taxa have been documented at nuisance levels elsewhere, few studies exist for California's Central Coast region (RWQCB 2005). Consequently, policy makers may lack sufficient published autecological algal research to support scientifically sound decision making in the region.

LINKAGES TO CALIFORNIA'S CENTRAL COAST REGION

While the potential for nuisance proliferation remains relatively unstudied in California's Central Coast region, studies conducted elsewhere indicate that agricultural and urban activity may set the stage for nuisance blooms and subsequent negative effects on water quality, such as low levels of dissolved oxygen, through elevated nutrient loading (Sharpley et al. 1994, Howarth et al. 1996, Busse et al. 2006, Morgan et al.

2006). In the Central Coast region, cultivated lands have been heavily fertilized, resulting in substantially increased nitrogen (N) and phosphorus (P) concentrations in soil, surface water, and ground water (Anderson et al. 2003, Hartz et al. 2003, Jones et al. 2006, Los Huertos et al. 2006). Irrigation practices alter timing and volume of groundwater and surface water flows (Thompson and Reynolds 2002). Riparian canopy in the region has been diminished by livestock grazing and vegetation removal practices associated with fruit and vegetable production (Roberts et al. 1981, Larsen et al. 1998, FDA 1998, Newman et al. 2003). Urban activities as well, may contribute to nuisance generating conditions (Walsh et al. 2005, Catford et al. 2007). Sewage input and failed septic systems can lead to high nutrient input to surface and groundwater (Sabater et al. 2000). Impervious surfaces can carry nutrient rich urban runoff to local receiving waters (Taylor et al. 2004). Urban development too has caused the loss of riparian ecosystems and altered stream flow (Beighley et al. 2003, Catford et al. 2007). Natural sources in the regions, such as soil, rocks, and organic debris, also supply nutrients to surface waters (Mueller and Helsel 1996).

Streams of Mediterranean climates, such as California's Southern and the Central Coasts, are characterized by long periods of low flow during dry summer months. The absence of periodic high flows allows for accumulation of algae and stabilized nutrient concentrations (Busse et al. 2006). Periphyton communities of nutrient enriched summer low flow streams in New Zealand contained more filamentous algae than non-enriched summer low flow streams (Suren et al. 2003). More frequent algal proliferations were observed in streams where nutrient concentrations exceeded 0.02 mg l^{-1} soluble inorganic nitrogen and 0.002 mg l^{-1} soluble reactive phosphorus and accrual periods exceeded 50 days (Biggs 2000a). Nutrients may thus have a more influential role in streams that experience long periods of low flow such as in Mediterranean climates. Indeed, percent cover of filamentous algae in Southern California streams exceeded Biggs' (2000b) recommended cover levels of less than 30% (Busse et al. 2006). Nutrient levels were found to be higher in these streams than in more commonly studied temperate streams (Dodds et al. 1998, Busse et al. 2006), and Busse et al. (2006) determined that total nitrogen (TN) and total phosphorus (TP) were related to algal biomass (chlorophyll *a* concentration) in this region.

IMPAIRED WATERS AND BIOSTIMULATORY SUBSTANCES

The 1972 Federal Clean Water Act (CWA) was passed to address growing water pollution issues and to restore the health of impaired water bodies of the United States. Today, this includes protecting the designated uses (e.g., drinking water supply, recreation, aquatic habitat) assigned to particular water bodies. Section 303(d) of the CWA requires that states list impaired water bodies (i.e., those that do not meet the criteria of the designated use) and establish pollutant load standards for each listing. These standards, called total maximum daily loads (TMDL), establish limits for pollutant loads in water bodies according to pollutant tolerance limits of designated uses.

The 1969 California Porter-Cologne Water Quality Control Act created water pollution legislation and state and regional boards (SWRCB and RWQCB) to oversee water quality policy. The regional boards establish and enforce Basin Plans for water quality regulation. These plans include beneficial use designations (i.e., designated uses) and water quality objectives (Sunding and Zilberman 2006).

Under the Central Coast Basin Plan (SWRCB 1994), there are 2 types of objectives for water quality: numeric and narrative. A numeric objective determines the amount of pollutant allowed in a given water body so as not to impinge upon its beneficial uses. A narrative objective, however, is qualitative and may not articulate numeric concentration limits. While such statements are subject to interpretation, they were frequently used as grounds for 303(d) listing (Painter 2005). For listed waterbodies, these objectives present general descriptions of water quality that must be attained. Narrative water quality objectives can include descriptive standards for biostimulatory substances, color, dissolved oxygen, taste and odor, and turbidity. Algal proliferations affect all of these objectives, but are most commonly cited in association with the biostimulatory objective.

The biostimulatory objective states that waters "shall not contain biostimulatory substances in concentrations that promote aquatic growths to the extent that such growths cause nuisance or adversely affect beneficial uses (SWRCB 1994)." Thus, prolific algal growth caused by excess N or P in the waterway violates the biostimulatory objective if the proliferation interferes with a beneficial use. While this objective guards against biostimulatory conditions, it fails to identify both a numeric standard at which algal

accrual is considered a nuisance and numeric criteria for pollutants that cause nuisance growth. The only numeric objective regulating any biostimulatory substance, albeit indirectly, is the California drinking water standard for nitrate. In fact, as of 2005, most states had no standards for N and P (Painter 2005). On the other hand, assigning such numeric objectives is not a simple task. Each waterbody must be individually evaluated as each has a unique suite of designated uses, algal species, and environmental conditions.

In California's Central Coast region, numerous streams have been found in violation of water quality regulations and added to the CWA 303(d) impaired water body list. Twenty-two of these are listed for nutrient impairment and 10 have TMDL requirements for N or P (EPA 2009). In the case of the Pajaro River and Llagas Creek, however, original 1998 listings due to nutrient impairment did not specify which water quality objective the impairment was attributed to (RWQCB 2005). Listings were based on information gathered from academic, consulting, and agency reports, but none documented a violation of the narrative objective for biostimulatory substances. The U.S. EPA provided states with ecoregional recommendations for nutrient criteria (TN and TP), but on the Central Coast, the standards were found to be unattainably low and impractical (EPA 2000). In the end, RWQCB staff recommended a TMDL be developed due to a documented nitrate violation of the municipal and domestic supply numeric objective. The objective follows the drinking water standard (10 mg l^{-1} as nitrogen) from the California Safe Drinking Water Act. The 2005 TMDL for nitrate in the Pajaro River addresses the municipal use violation while further research is conducted to determine whether or not the TMDL should be altered to address nuisance algal conditions (RWQCB 2005). Findings could result in further nutrient restrictions as well as requirements for the increased assimilative capacity of the water bodies.

The next steps in preventing nuisance proliferations are to (1) set quantifiable standards for nuisance growth and (2) develop numeric objectives for biostimulatory substances or conditions that cause nuisance growth. Improving knowledge of the region's algal ecology will aid policy makers in identifying the main factors regulating algal accrual. This understanding will, in turn, help formulate a picture of potential

biostimulatory stream conditions in this region of concentrated agricultural activity (RWQCB 2004).

MANAGING STREAM HABITAT

In the present investigation, I began to address the uncertainties associated with the Central Coast's biostimulatory objective in a region-wide field study of the effects of stream characteristics and known biostimulatory substances on algal growth. I examined the response of potential nuisance filamentous algae to in situ conditions in low gradient streams. This evaluation considers the role of water chemistry, riparian canopy, flow velocity, substrate size, and season in the presence and abundance of four potential nuisance taxa. Additionally, I took a preliminary look at associations between algal taxa, riparian canopy, and dissolved oxygen concentrations. The results regarding biostimulatory substances, TN and TP, were inconclusive. Instead, riparian canopy was the strongest predictor of filamentous algal accrual.

Since the 2006 Central Coast spinach *E. coli* outbreak, the debate over the function of riparian canopy in the human landscape has escalated. Historically, agriculture and urban development have reduced riparian habitat, and the consequent impacts to riparian ecosystem functions have been a concern of environmentalists. As a result of the recent food safety scare, increased attention is being paid to 1998 FDA recommendations (FDA 1998) to remove all vegetation, including riparian, growing near crops due to its potential to harbor pathogen vectors (Lieberman 2008). The Western Growers Association is advocating stricter standards and grower-wide compliance with vegetation removal recommendations.

Riparian buffer zones, however, are recommended for the protection of water quality under the Central Coast's Conditional Waiver of Waste Discharge Requirements for Discharges from Irrigated Lands program (RWQCB 2006). Buffers can filter runoff through naturally occurring physical and biological processes by reducing, converting, or storing pollutants on land rather than allowing them to enter aquatic systems (Basnyat et al. 2000). Given well dispersed surface water flow and sufficient vegetation, buffer zones have proven efficient at removing sediment and sediment-adhering phosphorus. Riparian rooting zones can reduce nitrate concentrations in lateral ground water flows through

denitrification and uptake by plants (Correll 1996, Anbumozhi et al. 2005). Under favorable conditions, intact riparian buffers can substantially reduce concentrations of biostimulatory substances in receiving waters (Fennessy and Cronk 1997). A cost-benefit model has shown that restored riparian zones have greater benefits through water quality improvements than the same land under crop production (Fennessy and Cronk 1997). But, water quality mandates that require growers to maintain riparian zones are costly in a competitive market concerned with food safety. However, local taxpayers may support funding to ensure the integrity of these ecosystems (Fennessy and Cronk 1997).

For management of nuisance algae in streams, the results of this study indicate that biostimulatory conditions, in addition to the biostimulatory substances already regulated, should be addressed. As light conditions are attenuated by riparian canopy, it would be prudent to sustain this aspect of the stream habitat for the control of nuisance growth. However under current California policy, the SWRCB and the majority of regional water boards, including the Central Coast, have not consistently managed riparian canopy due in part to the lack of a formal definition of riparian areas (SWRCB 2008). Analysis of the local data presented here bolsters both the adoption of a definition of riparian areas by the Central Coast RWQCB and Phase 3 of the SWRCB's proposed Wetlands and Riparian Area Protection Policy. During Phase 3, the SWRCB will consider new beneficial uses definitions, water quality objectives, and an implementation program to achieve the objectives to protect riparian area-related functions (SWRCB 2008).

As the biological integrity of these streams appears to be strongly linked to the riparian zone, the RWQCB should at minimum recommend the maintenance of riparian vegetation to land use planning agencies and include riparian protection in best management practice recommendations. The Central Coast RWQCB may coordinate with the Wildlife Conservation Board, created through the California Fish and Game Code, to identify areas needing protection via the California Riparian Habitat Conservation Program (WCB 2007). Of course management strategies involving habitat manipulation will need to consider appropriateness of the application, both ecologically and socio-economically, but riparian revegetation may prove highly successful in protecting the designated uses of streams. Not only does shade-providing riparian

vegetation maintain lower stream temperatures, filter nutrients and sediment from runoff, and provide streams with a source of carbon and large woody debris (Vought et al. 1994, Correll 1996, Anbumozhi et al. 2005), this study suggests Central Coast water quality can benefit from the riparian zone by reducing the potential for nuisance algal growth. Here, I explored characteristics of stream environments in the Central Coast that could turn generally beneficial primary producers into too much of a good thing.

CHAPTER 2

ABIOTIC FACTORS RELATED TO ACCRUAL OF COMMON FILAMENTOUS MACROALGAE IN CENTRAL COAST STREAMS

INTRODUCTION

Algal proliferations become a water quality management concern when they interfere with the designated use of a water body (e.g., drinking water supply, recreational use, and functional aquatic habitat). These problem proliferations, or nuisance algae, can alter water characteristics and prohibit fishing and swimming, directly affecting human uses (Dodds and Gudder 1992, Dodds and Welch 2000). They can also lead to harmful diel fluctuations of dissolved oxygen in the water column, affecting macroinvertebrate and fish species intolerant of anoxic conditions (Nebeker 1972, Richardson et al. 2001, Connolly et al. 2004). Prolific growth and accrual can vary at the regional scale due to a wide range of environmental factors (Biggs 1996, Stevenson 1997). Thus regional scale knowledge of algal response to local conditions can greatly aid the development of appropriate local management strategies where proliferations are a concern.

To understand the causes of prolific growth, and algal ecology in general, previous studies have examined relationships between algal productivity and environmental factors. Field studies, however, are fraught with contradictory results (see reviews in Borchardt 1996, Hill 1996, and Stevenson 1996). Inconsistencies likely derive from regional differences in lotic ecosystem structure and function, as well as the general complexity of physical and biological interactions that influence accrual of algal biomass (Biggs 1996, Stevenson 1997). A body of scientific literature has amassed, nonetheless, in favor of several rudimentary factors that may influence algal growth.

Algae respond to a number of stream chemistry variables. Nutrients, particularly nitrogen (N) and phosphorus (P), are essential to productivity and can be limited in the

stream environment (Borchardt 1996). Increases in N and P concentrations have been linked to high algal production and resulting stream impairment (Horner 1983, Dodds et al. 1997). Algal species vary in their ability to tolerate dissolved ions (Potapova and Charles 2003). For example, Biggs and Price (1987) found Spirogyra biomass to be associated with low conductivity, while Cladophora biomass was associated with high conductivity. In a study spanning North America, Cladophora glomerata was also found to have found a positive correlation with pH and temperature (Sheath and Cole 1992).

Stream habitat factors can also influence the distribution and abundance of macroalgae. In the stream environment, canopy cover has the greatest effect on light availability. Dense canopy can intercept over 95% of incoming solar irradiance, and this reduction in light reduces photosynthetic activity (Hill et al. 1995). Stream flow rate and substrate size can control accrual of filamentous algal biomass at attachment sites. Stream currents enhance algal production rates by stimulating nutrient uptake and metabolism (Stevenson 1996). High current velocities, however, cause sloughing of attached filaments due to sheer stress and scour (Horner et al. 1990, Stevenson 1996). Filamentous green algae were found to achieve peak biomass at velocities ranging from 20 – 70 cm/s (Biggs and Stoketh 1996, Biggs et al. 1998). Stream substrates that are relatively large in size (e.g., cobble, boulder) are less susceptible to tumbling and subsequent filament loss at high current velocities allowing greater algal accrual (Power and Stewart 1987). Also, growth and senescence, of filamentous algae may be a function of seasonal cycling in biotic, abiotic, and autogenic factors (Biggs 1996, Francoeur et al. 1999). Therefore, changes in biomass or taxon presence may be observed over the course of inter-seasonal sampling.

This investigation aimed to explore the primary abiotic factors related to benthic filamentous algal distribution and abundance in California's Central Coast region. To accomplish this, I postulated that the aforementioned environmental factors (nitrogen, phosphorus, conductivity, pH, temperature, canopy cover, current velocity, substrate size, and season), may each influence algae distribution and abundance. I built hypotheses in the form of linear regression models and compared them using an information theoretic approach (Burnham and Anderson 2002). The environmental data and benthic algal samples examined in this study were obtained from a concurrent Central Coast stream

bioassessment study. The variables I included in the hypotheses were chosen from the bioassessment dataset and were supported by findings reported in the literature. Additionally, I explored associations between filamentous algal taxa and daytime water column dissolved oxygen concentrations. Few investigations have focused on macroalgae in this region, and little is known about their autecology or the conditions that could lead to nuisance blooms in this area.

METHODS

Study area

The study area covers 17,945 km^2 of coastal central California from the Santa Cruz Mountains south to the Santa Ynez Mountains and east through the Salinas Valley (Figure 2). This area is mainly defined by the Central Coast Regional Water Quality Control Board Region 3, but also includes 23 sites in adjacent watersheds to the north with similar ecosystem structure. Soils and alluvium of the region chiefly derive from shale, sandstone, and granodiorite parent material (Schoenherr 1992). Elevation ranges from sea level to 2078 m. The climate of the region is characterized by mild dry summers and cool moist winters, though coastal portions of this region experience fog. Average temperatures range from a high of 85°F in the summer to a low of 35°F in the winter (PRISM 2006). Mean annual precipitation is spatially heterogeneous, ranging from less than 25 cm in the Salinas Valley to over 170 cm in the Santa Cruz Mountains (PRISM 2006). Rainfall occurs primarily from October through May with heaviest rain events typically occurring in January and February. Grasslands, chaparral, and oak woodlands make up most of the region's natural vegetation, while coniferous forests are found in localized coastal and montane zones. Major watersheds of the region include the Salinas, Pajaro, Cuyama, Santa Ynez, Estrella, and Sisquoc.

Undeveloped natural areas and grazing lands dominate the foothills and mountains of the Central Coast landscape, while irrigated crops and urban development occupy the valley floors (Newman et al. 2003). As of 2001, land cover in the study area included forest/shrubland (57.4%), grassland and rangeland (28.9%), cultivated crops (6.2%), light urban (4.5%), barrens (1.6%), urban (1.1%), and water (0.3%) (MRLC 2001). Agricultural and urban activities, such as irrigation, municipal water use,

fertilization, urban development, livestock grazing, and gravel mining, affect stream nutrient and sediment concentrations, stream flow, and riparian habitat in the region (Newman et al. 2003).

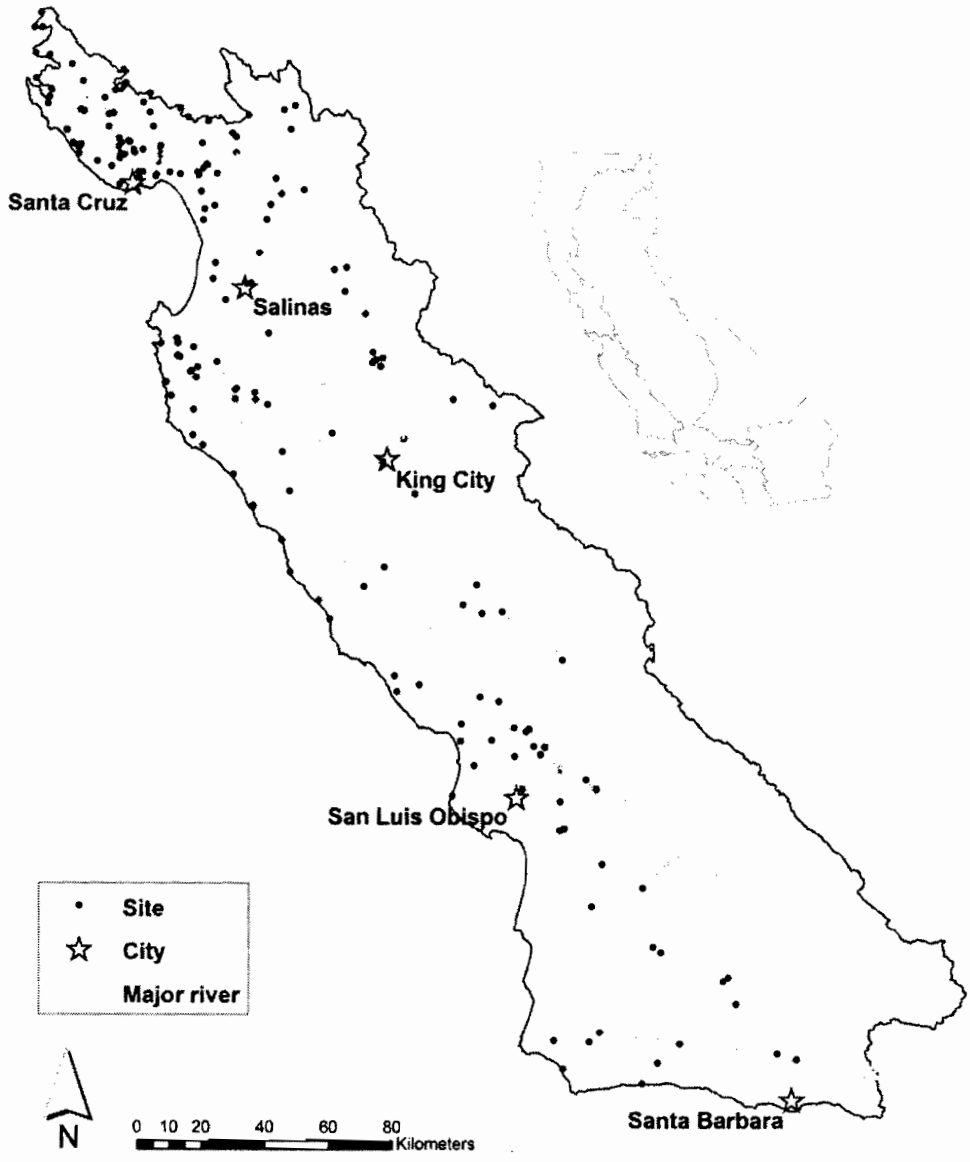

Figure 2. Location of sampling sites within Central Coast Region 3 study area.

Dataset and study design

Site characteristics and algal samples were acquired from a regional stream bioassessment study designed for the development of multimetric and multivariate assessment tools using benthic diatoms (Los Huertos and Rollins in progress). Sites were selected in an effort to capture both least-impaired and highly impaired low-gradient (i.e., slope ≤ 2%) stream conditions representative of the Central Coast region. In the field, site selection was further constrained by access and flow conditions. As a result, sites reflect a range of stream impairment within the region. Sites were distributed among the Southern and Central California Chaparral and Oak Woodlands Ecoregion (102), the Coast Range Ecoregion (55), and the Southern California Mountains Ecoregion (42) (Omernik 1987).. Catchments above the sites ranged in size from 1 to 10,884 km^2, draining to both ephemeral and perennial streams.

Water samples and physical habitat data were collected by field teams of 3-5 technicians following methods described in Ode (2007) and Stevenson and Rollins (2006). Benthic algae sampling protocols were modified from Peck et al. (2006). Two-hundred seventy-three site visits were conducted during the dry season of 2 dry years, June-October 2007 and April-August 2008, at a total of 214 sites. I analyzed data from 199 sites, excluding those with incomplete data and high salinity due to tidal influence. In 2007, field teams noted clumping of algal filaments in the composite sample which may have led to unequal distribution of filaments in the aliquots. In 2008, clumps of filamentous algae were manually shredded prior to depositing into the composite sample. Where repeat site visits occurred, I chose samples from 2008 over 2007 due to the improved sampling protocol and minimized algae sample holding times. Although the change in protocol may have affected cell counts between years, I chose to keep 2007 samples in an effort to maintain a large sample size and maximize usage of available information. Thus, an assumption of this work is that 2007 and 2008 data are comparable. And, while a difference between years may be difficult to detect due to a high amount of variance in the data, a Wilcoxan rank sum test showed no difference in abundance between 2007 and 2008 samples ($p > 0.1$).

Water chemistry

Water samples and in situ measurements were collected at the stream thalweg. Temperature, pH, dissolved oxygen (DO) and specific conductance were measured using a Hydrolab DSX water quality multiprobe (Hach Company, Loveland, CO). Field teams collected total N (TN) and total P (TP) samples from the water column in acid-washed polyethylene bottles and placed them on ice during transport. Following acid/oxidant digestion, TN and TP concentrations were determined colorimetrically using a Flow Injection Analyzer (Lachat Instruments, Inc. QuikChem 8000 Series, Hach Company, Loveland, CO; APHA 1998, Wendt 2000, Diamond 2007). Method detection limits were 0.01 mg N l^{-1} and 0.009 mg P l^{-1}.

Physical habitat

Physical habitat data were collected from 11 transects and 10 inter-transects (i.e., an additional transect equally spaced between each main transect) oriented perpendicular to stream flow and spaced every 7.5 m within a 150 m reach of the stream. At each transect, field teams measured wetted width and estimated canopy cover using a Strickler-modified 17-point spherical densiometer (Strickler 1959). Points were counted facing four directions (upstream, left bank, downstream, and right bank) one foot above the water surface at the center of each transect (44 readings). Reach slope was measured using an auto level or clinometer and a stadia rod held at the water surface at each transect. Slope was calculated as the average of the measurements. Site latitudinal and longitudinal coordinates were recorded using a Trimble Geo Explorer 3 GPS (70% of sites) or were estimated using Google Maps (http://maps.google.com/) when satellite signals were blocked by steep terrain (30% of sites).

Substrate size class (e.g., cobble, gravel, sand) and stream depth were measured at five equidistant points along each transect and inter-transect. Stevenson et al. (2006) determined substrata suitable for algal accrual to be > 2 cm. For this study, I re-classified substrate from 8 size classes to 2, hard (> 16 mm diameter) and soft (< 16 mm diameter), in order to attain a single continuous substrate variable (% hard) with a cutoff as close to 2 cm as possible. Field teams measured current velocity at five equidistant points along each transect using a FlowTracker Acoustic Doppler Velocimeter (Son Tek, San Diego,

CA) positioned at 0.6-depth to capture mean velocity in the vertical of the water column (USGS 1983). Mean current velocity was calculated for each of the 11 transects using wetted width, depth, and velocity measurements. Means velocities were averaged to characterize the reach.

Benthic algae

A composite periphyton sample was collected from the reach substrate at 11 transects. At each transect, field teams alternated substrate collection from the right, middle, or left region and sampled from the substrate type that best represented the entire transect. Rocks were removed by hand and placed in a collection bin while maintaining their up facing orientation. A rubber washer and sampling strap delineated a 12 cm^2 area of the up-facing rock surface. Periphyton was dislodged from this area using a plastic spatula and toothbrush followed by a rinse with stream water. Depositional substrate, composed of fine gravel, sand, or silt, was delimited using a 12 cm^2 PVC pipe placed at 1 cm depth and transported to the collection bin using a spatula. The periphyton slurry and any depositional substratum were placed in a plastic bottle and gently shaken to dislodge algae from sand and gravel particles. The composite sample was then decanted into a graduated cylinder in order to record volume. Next, the sample was homogenized in a large plastic bottle by manual shaking. Homogenized sample was divided into 45-mL aliquots and preserved with 2.5% glutaraldahyde. Samples were stored at approximately 4°C until analyzed. To assist with identification of filamentous algal fragments during enumeration, a grab sample of macroalgae was collected from each reach. This sample included any visible macroalgae seen during the survey. The macroalgae grab samples were also preserved with 2.5% glutaraldahyde.

A pilot study identified the most common filamentous taxa in the samples: *Cladophora*, *Spirogyra*, *Ulva* (a filamentous-like colonial species), *Vaucheria*, *Mougeotia,* and *Zygnema*. Each of these taxa occurred at $\geq$ 18 sites. Species within genera could not be distinguished due to a lack of reproductive structures which, for many soft algae, are necessary for species level identification (Stevenson and Pan 1999). Although John (2003) asserts that *Ulva flexuosa* is the only freshwater species of the genus *Ulva* in North America, several other authors have found additional species in

North American freshwaters (Kamer and Fong 2001, Lougheed and Stevenson 2004, McAvoy and Klug 2005). *U. flexuosa* was identified in the pilot samples, but due to uncertain taxonomy, I limited identification to the genus level. Through further examination, I found *Ulva* spp. and *Vaucheria* spp. to be difficult to identify from composite sample fragments. While *Mougeotia* and *Zygnema* were not listed in the literature as potential nuisance algae, these genera did occur frequently in the samples and were included in the study to advance knowledge of macroalgae of the region. *Zygnema* was excluded from analyses but included in a distribution map due to a low proportion of detection at sampling sites. Thus, abundance data were collected on *Cladophora* and *Spirogyra* while the remaining taxa were recorded as either present or absent from the composite and macroalgae grab samples. The following taxonomic keys were used for identification: Prescott (1970), John (2003), Gerrath (2003), Ott and Oldham-Ott (2003), and Skinner and Entwisle (2004).

Abundance (biovolume per unit area) of filamentous algae was determined microscopically by enumerating taxa over a fixed area of substrate (76.8 mm^2). The fixed area method equalizes the enumeration effort between composite samples of unequal volume and was accomplished by adjusting the concentration of a subsample of homogenized composite. In 15-mL centrifuge tubes, subsamples were twice rinsed with DI water and centrifuged to remove preservative and to concentrate algal cells. Prior to microscopy, 14.5 mL of supernatant were removed and the remaining 0.5 mL of sample homogenized by stirring. Eighty microliters of this homogenized sample were placed on each slide. The number of slides enumerated was determined by the concentration of the subsample. In some cases, subsamples contained large amounts of sediment and thus required further dilution. As a result, I used conversion factors to make abundance estimations comparable with undiluted samples.

To prepare for enumeration, 80 µL of sample plus 1-2 drops of DI were placed onto a standard microscope slide and covered with a large cover slip (24 x 40 mm). Target algae were identified and individual cells counted at 100-200x magnification using a Nikon Labophot-2 compound light microscope. Enumeration transects covered the entire area of the cover slip so that all 80 uL of sample were examined. Using a Micrometrics digital camera and software, I calculated the median length and width from

15 cells of each target taxon in the sample. Cell volume was calculated as the volume (V) of a cylinder (Hillebrand et al. 1999):

$$V = \frac{\pi}{4} h d^2$$

where h is median height and d is median diameter. If fewer than 15 cells were found in a sample, additional measurements were taken from the macroalgae grab sample. Abundance was calculated as density multiplied by cell volume.

Analyses

I used an information theoretic approach (Burnham and Anderson 2002) to make inferences about the relationship between the macroalgal taxa and stream characteristics commonly attributed to algal presence and abundance in freshwater streams. From my postulates, I derived 32 a priori hypotheses about macroalgae presence-absence and 25 hypotheses about macroalgae abundance (see Appendix A). Each hypothesis was represented by a linear regression model. I used Akaike's Information Criterion, corrected for small sample size (AIC_c), to determine the likelihood of each model given the data and the set of models (Burnham and Anderson 2002). I inferred that the best supported hypotheses were those whose corresponding regression models received the most support in the AIC analysis. More specifically, a given predictor variable was inferred to be related to the algal response if 95% confidence limits for model-averaged coefficient estimates did not include zero. The models were evaluated based on support given by their delta AIC_c values, Akaike weights (w_i), and evidence ratios (refer to Table 1 for description of terms). If no single model received $w_i \geq 0.90$, a 90% confidence set was averaged to determine parameter coefficients, standard errors, and coefficient confidence intervals. The 90% confidence set of models is the subset of models in a suite that has a probability of 0.9 of including the best model (i.e., the model that loses the least amount of information when used to approximate reality) given the suite of models (Burnham and Anderson 2002). The use of multi-model inference (i.e., model averaging) allows the information from more than one model to be considered when there is uncertainty regarding the best model.

Table 1. Description of terms used to evaluate models when applying an information theoretic approach (Burnham and Anderson 2002; after Croyle 2009).

Term	Definition	Use in evaluation of model comparison results
AIC_c	A measure of the goodness of fit of a model given the data. Competing models are ranked based on AICc score.	Lowest AIC_c = Best model: model that is estimated to be closest to full reality given the set of models
Delta AIC_c (Δ_i)	Difference in AIC value between the model with the lowest score and every other competing model in the set.	$\Delta_i \leq 2$ = substantial support $4 \leq \Delta_i \leq 7$ = considerably less support $\Delta_i > 10$ = essentially no support
Akaike weight (w_i)	The probability of being the best model given the set of models and the data.	w_i = .90: 90% probability of being the best model among the competing models $w_i \geq .90$ = appropriate for single-model inference
90% confidence set	A subset of models that have a probability of .90 of containing the best model. Determined by summing w_i from highest to lowest until ≥ .90 (or other desired level of confidence).	$\sum w_i = .90$ = appropriate for multi-model inference
Evidence Ratio (ER)	The ratio of one model's w_i relative to another in the set ($ER = w_i/w_j$). Ratio definitions are based on Bayes Factors (Jeffreys 1961 in Stauffer 2008).	If $ER = w_i/w_j$ then, $ER < \sqrt{10}$ = minimal evidence for w_i over w_j $ER \geq \sqrt{10}$ = minimal evidence for w_i over w_j $ER > 10$ = substantial evidence for w_i over w_j $ER > 100$ = strong evidence for w_i over w_j $ER > 100$ = decisive evidence for w_i over w_j

I developed the set of competing hypotheses and corresponding models using results from the algal literature and personal knowledge of the stream systems under investigation (Appendix A). These linear regression models contained a combination of seven predictor variables: canopy cover (%), mean current velocity (cm/s), hard substrate (%), TN (mg l^{-1}), TP (µg l^{-1}), day of year (a proxy for season), specific conductance (µS/cm) and pH. Canopy cover is a measure of light availability and was included in the majority of models to account for the hypothesized importance of this variable. Nutrients, particularly TP, were also included in a large percentage of the models due to support from the literature regarding algal response to stream nutrient concentration. To model the hypothesis that macroalgae are light limited in the presence of high nutrient concentrations (Hill and Knight 1988, Rosemond 1993, Taulbee et al. 2005), I included interaction terms between canopy cover and nutrients in the abundance model suite. Although current velocity and day of year could have been included in the models as quadratic terms, I modeled them with a monotonic response due to the limited range of

stream conditions in which sampling occurred. Lastly, I included a null model in the set to represent a constant response.

Prior to model fitting, I calculated Moran's I using ArcGIS v. 9.2 to check for spatial autocorrelation among algae samples, and used Spearman rank correlation to check for collinearity among predictor variables. Moran's I values indicated no spatial autocorrelation in occurrence or abundance of taxa between sites, with the exception of *Mougeotia* which was further examined for ecoregion preferences using Pearson's Chi-squared test. Due to the lack of independence in the data, *Mougeotia* was excluded from the modeling analyses. Spearman rank correlation coefficient (r_s) showed moderate correlation between riparian canopy cover and stream temperature ($r_s = -0.50, p < 0.001$). Temperature was, therefore, removed from all models suites. Several predictor variables failed to demonstrate uniform distribution. In particular, values for TN and TP concentrations, current velocity, and conductivity were more frequent in the low end of their ranges.

Due to the occurrence of many zeroes in the abundance data, I used AIC_c within the framework of a two-part conditional model (Stefansson 1996, Fletcher et al. 2005). I first created 2 data sets: one containing presence-absence data for all sites and the other containing abundance data for only those sites where *Cladophora* or *Spirogyra* were present. If these taxa were present in the macroalgae grab sample but not the composite sample, I imputed an abundance value for them that was greater than 0 but less than the lowest recorded abundance value. Hence, to estimate imputed values, I averaged 4 replicates from the lowest abundance site and divided by 2. Thirty-eight and 19 values were imputed for *Cladophora* and *Spirogyra* respectively. I fit models to both sets of data using the generalized linear model (glm) procedure in R version 2.7.2 (R Development Core Team 2005). From presence-absence data, I estimated the probability of taxon occurrence using logistic regression, and from abundance data I predicted taxon abundance given presence using multiple linear regression. Due to the positive skew of abundance data, I log-transformed the response and assumed a normal distribution of the errors, although the data were still somewhat positively skewed (Fletcher et al. 2005). The 90% confidence set of models from each of the 2 parts were combined to predict taxon abundance in the Central Coast region. When predicting taxon abundance in a 2-

part model, let *Z(x)* represent a binary variable indicating presence or absence (i.e. one equals present, zero equals absent) where *x* is the vector of predictor variables, and *Y(w)* represent the abundance of a taxon where *w* is the vector of predictor variables. The expected value of *Y* is then given by:

$$E(Y) = \Pr(Z = 1)\,E(Y \mid Z = 1) + \Pr(Z = 0)E(Y \mid Z = 0),$$
$$E(Y) = \Pr(Z = 1)\,E(Y \mid Z = 1),$$
$$E(Y) = \pi\mu,$$

where $\pi = \Pr(Z = 1)$ and $\mu = E(Y \mid Z = 1)$. Thus algal abundance can be estimated as the product of the estimated probability of occurrence ($\hat{\pi}$) and the estimated abundance given presence ($\hat{\mu}$) calculated as follows (Stefansson 1996):

$$\hat{\pi} = \frac{\exp(x'\hat{\beta})}{1 + \exp(x'\hat{\beta})}$$

and

$$\hat{\mu} = \exp(w'\hat{\theta} + \frac{\hat{\sigma}^2}{2}),$$

where x' and $\hat{\beta}$ are the vectors of predictor variables and their coefficients from the averaged 90% confidence set of logistic regression models. Similarly, w' and $\hat{\theta}$ are the vectors of predictor variables and their coefficients and $\hat{\sigma}^2$ is the residual mean square from the averaged 90% confidence set of log-normal regression models. It should be noted that the predictors in the logistic and log-normal regression models need not be identical.

I used global models containing all predictor variables to check model fit. The global presence-absence model had a total of 10 parameters, while the global abundance model had 11 parameters. Although not included in the model suites, I checked the fit of the global logistic regression models using the Le Cessie-van Houwelingen goodness-of-fit test (le Cessie and van Houwelingen 1991) and the model-averaged logistic models using Receiver Operating Characteristic Curves (ROC; Fielding and Bell 1997). ROC curves evaluate model accuracy. The greater the area under the curve (AUC), the better a

model is expected to perform. I assessed the fit of the global log-normal regression model using the adjusted coefficient of multiple determination (R^2_{adj}) and of the combined model using mean absolute error.

Following a priori model comparison, I examined post hoc the potential effects of filamentous macroalgae on water column dissolved oxygen (DO) concentration. I conducted a Wilcoxon rank sum test to test for differences in DO saturation (%) in the presence and absence of the macroalgal taxa. Along these lines, I also conducted Spearman rank correlation on percent cover of canopy and DO saturation.

RESULTS

Large-scale single-event sampling captured the range of environmental variables for streams of the Central Coast (Table 2). During the time of sampling, highest mean current velocities (~55–70 cm/s) were found in the Salinas, San Antonio, Sisquoc, and San Benito Rivers. Currents at most sites however were much slower (median mean velocity = 7 cm/s); 31 sites had mean velocities < 1 cm/s. Many sampling sites were well shaded (median canopy cover = 73.8%), particularly smaller streams located in the Santa Cruz Mountains. The percentage of hard substrate at sites was well distributed over the range. Highest TN concentrations occurred in the Pajaro and Salinas Rivers and tributaries of the Monterey Bay area (~10–40 mg l^{-1}), followed by mid-range concentrations in Santa Margarita Creek (4.43 mg l^{-1}) and Chorro Creek (3.10 mg mg l^{-1}) of the San Luis Obispo area. However, most sites had concentrations below 1 mg l^{-1}. TP concentrations were also mostly low (< 10 µg l^{-1}), but surprisingly, high concentrations were found at several sites within the relatively remote Pinnacles National Monument (431–2610 µg l^{-1}). Groupings of high concentrations also occurred in the San Lorenzo River and Soquel Creeks within the Santa Cruz region (40–513 µg l^{-1}). Twenty-two inland streams exceeded the specific conductance freshwater limit (1300 µS/cm; Russell and Kane 1993). Specific conductance was highest in upper Soquel Creek above Santa Cruz (5077 µS/cm) and in San Lorenzo Creek upstream of King City (6000 µS/cm). Throughout the region pH was slightly basic (mean = 8.02) with little variation.

Table 2. Descriptive statistics on environmental variables measured at 199 sites.

Variable	Mean	Median	Minimum	Maximum
Canopy cover (%)	62	74	0	99
Specific conductance ($\mu S\ cm^{-1}$)	740.2	575.1	97.6	5999.6
Mean current velocity ($cm\ s^{-1}$)	10	7	0	71
Day of year	186	184	98	282
pH	8.02	8.09	6.92	8.77
Hard substrate (%)	56	60	0	98
Total nitrogen ($mg\ l^{-1}$)	1.45	0.34	0.01	39.60
Total phosphorus ($\mu g\ l^{-1}$)	153	80	< 10	2610

The target taxa were found at a total of 152 out of 199 sampled sites (Figure 3). There was some variation in the total number of sites examined for different taxa due to late additions to the target group. *Cladophora* was the most commonly detected macroalgae in the region, occurring at 64% of sites, while *Zygnema* was the least common of the macroalgae examined and detected at 10% of sites. A Pearson's Chi-squared test conducted to investigate the spatial autocorrelation exhibited by *Mougeotia*, detected at 45 out of 188 sites, indicated a preference for the Southern California Mountains Ecoregion ($X^2 = 9.59$, df = 2, $p = 0.008$). Anecdotally, sites that had no macroalgae were usually highly shaded or appeared to contain high sediment loads with little to no hard substrate. Filamentous macroalgae generally appeared to occur on rocks or stream banks under open canopy. *Vaucheria* was detected at 45 out of 198 sites. A comparison of *Vaucheria* spp. presence-absence models was inconclusive as the null model had substantial support ($\Delta_i < 2$), indicating no trend in occurrence (Appendix A). Model comparisons concerning the remaining taxa presented no single best model from which to make inferences. Thus, multi-model inference was derived from a 90% confidence set for each model suite.

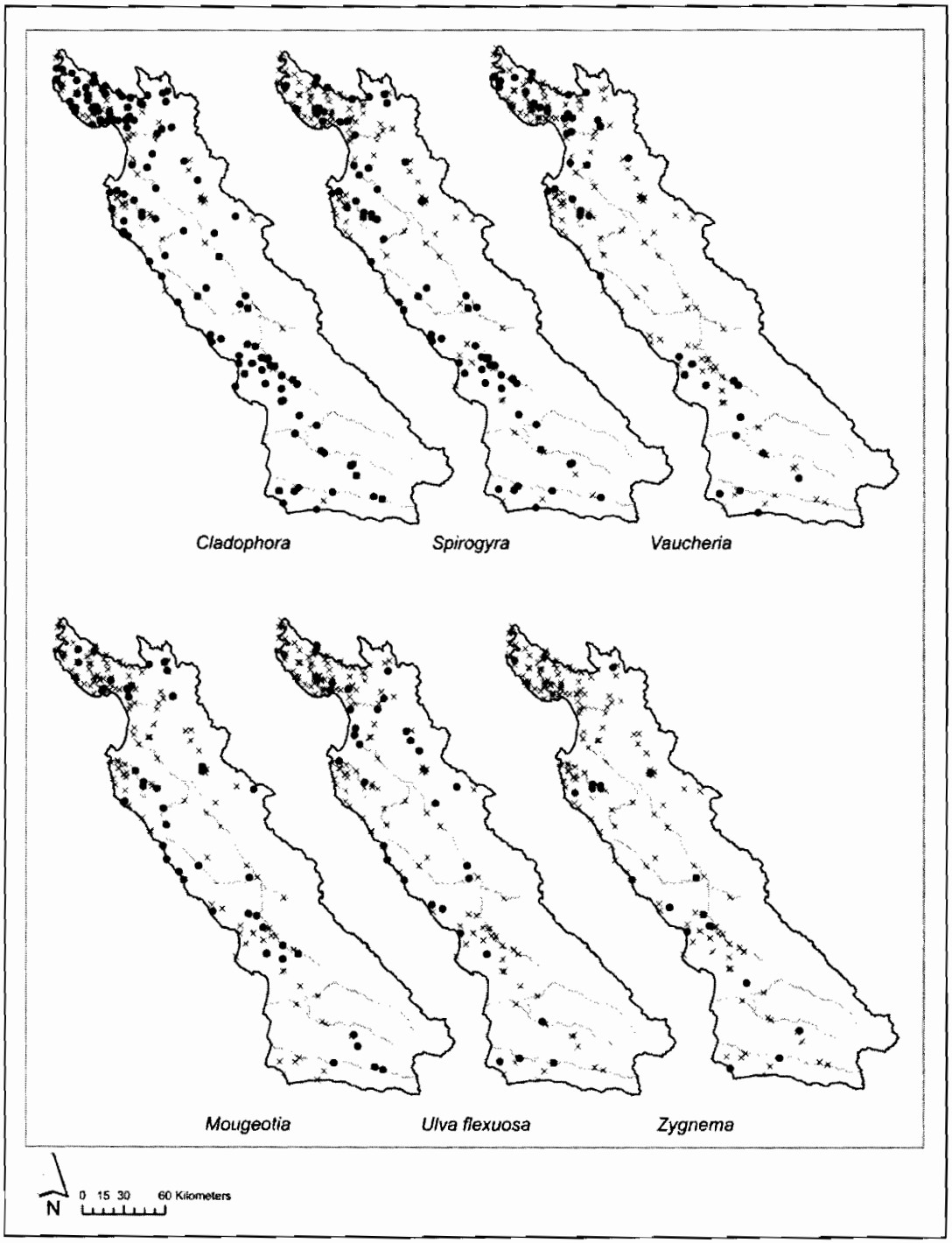

Figure 3. Locations of six filamentous macroalgae found in the Central Coast study area during 199 single sampling events from Jun. 2007 to Aug. 2008 (• = detected, x = not detected).

Cladophora spp.

Cladophora was the most prolific of filamentous macroalgae in the region, detected at 128 of the 199 sites. Abundance (biovolume/area) ranged from a minimum of 6.02×10^3 $\mu m^3/mm^2$, for imputed values, to 1.28×10^7 $\mu m^3/mm^2$ with four outliers in the range of 2.47×10^7 to 9.68×10^7 $\mu m^3/mm^2$. Cell width ranged from 18.38–138.42 μm and cell length ranged from 79.10–500.34 μm.

Substrate and canopy cover occurred in all presence-absence models of the 90% confidence set. These were the only two predictors whose model-averaged coefficient confidence intervals did not include zero (Table 3). Standardized estimates showed percent hard substrate to have 1.2 times greater effect on probability of presence than canopy cover. Presence of *Cladophora* spp. can be estimated as a function of these two parameters and has a negative relationship with canopy cover and a positive relationship with hard substrate (Figure 4). All presence-absence models of the 90% confidence set had substantial support and additionally included TP, current, day of year, and conductivity (Table 4). The le Cessie-van Houwelingen goodness of fit test of the global model indicated good fit ($p = 0.60$). The ROC showed moderate accuracy of the averaged presence-absence model (AUC = 0.73).

Table 3. Model-averaged coefficient estimates and their upper and lower confidence limits (95%) derived from the 90% confidence set of *Cladophora* spp. presence-absence models. Standardized estimates are included for comparison of the relative influence of each variable on estimated probability of presence. Values in bold indicate coefficient intervals that do not include zero; all other 95% confidence intervals around coefficient estimates include zero, thus the data do not support an affect of these variables on *Cladophora* spp. probability of presence.

Variable	Estimate	L.CI	U.CI	Standardized estimate
Hard substrate	**2.65×10^{-2}**	**1.24×10^{-2}**	**4.06×10^{-2}**	6.75×10^{-1}
Canopy cover	**-1.72×10^{-2}**	**-2.86×10^{-2}**	**-5.84×10^{-3}**	-5.65×10^{-1}
Total phosphorus	-9.87×10^{-4}	-2.43×10^{-3}	4.59×10^{-4}	-2.45×10^{-1}
Current velocity	1.15×10^{-2}	-7.57×10^{-3}	3.06×10^{-2}	1.38×10^{-1}
Day of year	-8.18×10^{-4}	-2.51×10^{-3}	8.77×10^{-4}	-3.62×10^{-2}
Sp. conductance	4.77×10^{-5}	-6.76×10^{-5}	1.63×10^{-4}	3.24×10^{-2}

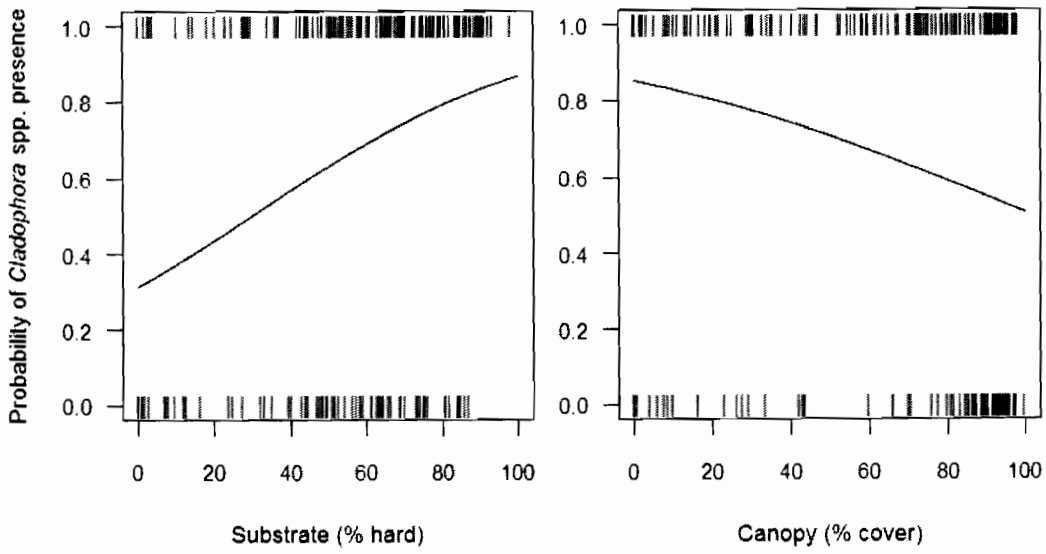

Figure 4. Estimates of probability of presence of *Cladophora* spp. plotted against percent hard substrate and percent cover of riparian canopy. Predictions use model averaged coefficients with all other environmental variables held at their means (Vincenzi et al. 2006). Tick marks show distribution of the data.

Table 4. Model selection results showing 90% confidence set on a priori models for probability of *Cladophora* spp. presence. Evidence ratios are relative to the best model in the set. These models were used for multi-model inference.

Model	k	Δ_i	w_i	ER
Substrate + canopy + TP + current	6	0.00	0.27	1.00
Substrate + canopy + TP	5	0.60	0.20	1.35
Substrate + canopy + current	5	1.12	0.16	1.75
Substrate + canopy + TP + conduct	6	1.33	0.14	1.95
Substrate + canopy + DOY	5	1.45	0.13	2.07
Substrate + canopy	4	2.16	0.09	2.95

Abbreviations: Substrate, hard substrate; canopy, canopy cover; TP, total phosphorus; current, current velocity; conduct, specific conductance; DOY, day of year; k, no. of parameters; Δ_i, delta AIC; w_i, Akaike weights; ER, evidence ratio

Comparison of abundance given presence models showed that the null model (i.e. the model representing the hypothesis that presence-absence did not depend on any of the predictor variables) had a probability of less than 0.01 of being the best model in the set of models. There was strong evidence (evidence ratio (ER) = 27) in favor of the top model as compared to the null. However, the global model for this suite had a poor fit to

the data (R^2_{adj} = 0.07, n = 128). Canopy cover was the only variable in the 90% confidence set of models whose coefficient confidence interval did not include zero; all others variables may not contribute to abundance (Table 5). Although this model lacks the ability to make accurate predictions, a general trend of decreasing abundance with increasing canopy cover can be seen (Figure 5). All models of the 90% confidence set included canopy, and all had substantial support (Table 6).

Table 5. Model-averaged coefficient estimates and their upper and lower confidence limits (95%) derived from the 90% confidence set of *Cladophora* spp. abundance models. Standardized estimates are included for comparison of the relative influence of each variable on estimated probability of presence. Values in bold indicate coefficient intervals that do not include zero; all other 95% confidence intervals around coefficient estimates include zero, thus the data do not support an affect of these variables on *Cladophora* spp. abundance given presence.

Variable	Estimate	L.CI	U.CI	Standardized estimate
Canopy cover	**-1.92×10^{-2}**	**-3.23×10^{-2}**	**-6.12×10^{-3}**	-6.23×10^{-1}
Hard substrate	5.46×10^{-3}	-4.08×10^{-3}	1.50×10^{-2}	1.26×10^{-1}
Day of year	-1.50×10^{-3}	-4.71×10^{-3}	1.72×10^{-3}	-6.33×10^{-2}
Total nitrogen	-1.46×10^{-2}	-4.85×10^{-2}	1.93×10^{-2}	-3.64×10^{-2}
Sp. conductance	5.12×10^{-5}	-6.54×10^{-5}	1.68×10^{-4}	3.29×10^{-2}
Total phosphorus	2.37×10^{-4}	-5.05×10^{-4}	9.80×10^{-4}	2.84×10^{-2}
Current velocity	-4.18×10^{-5}	-1.63×10^{-3}	1.55×10^{-3}	-5.46×10^{-4}

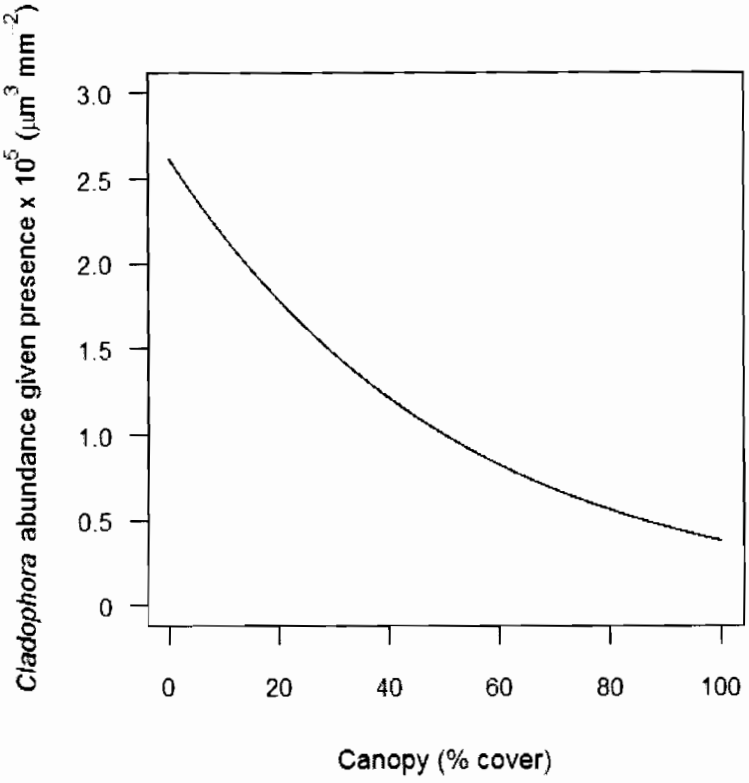

Figure 5. Estimates of *Cladophora* spp. abundance given presence plotted against percent cover of riparian canopy. Predictions use model averaged coefficients with all other environmental variables held at their means (Vincenzi et al. 2006).

Table 6. Model selection results showing 90% confidence set on a priori models for abundance of *Cladophora* spp. given presence. Evidence ratios are relative to the best model in the set. These models were used for multi-model inference.

Model	k	Δ_i	w_i	ER
Canopy + substrate	4	0.00	0.17	1.00
Canopy	3	0.40	0.14	1.22
Canopy + substrate + DOY	5	0.66	0.12	1.39
Canopy + conduct	4	0.75	0.12	1.46
Canopy + DOY	4	0.75	0.12	1.46
Canopy + TN	4	1.09	0.10	1.72
Canopy + substrate + TP	5	1.45	0.08	2.07
Canopy + TP	4	2.19	0.06	2.99
Canopy + current	4	2.53	0.05	3.54
Canopy + TN + TP	5	2.69	0.04	3.83

Abbreviations: Canopy, canopy cover; substrate, hard substrate; DOY, day of year; conduct, specific conductance; TN, total nitrogen; TP, total phosphorus; current, current velocity; k, no. of parameters; Δ_i, delta AIC; w_i, Akaike weights; ER, evidence ratio

The combined presence and abundance given presence models yielded a weak predictive model of *Cladophora* spp. abundance with a high mean absolute error (MAE = 2 x 10^6; Figure 6). Removal of imputed values, used when *Cladophora* spp. was undetected in the composite sample but observed in the macroalgae grab sample, made no improvements, so they were retained in the dataset. Derived from these data, the two-part conditional model has minimal predictive utility.

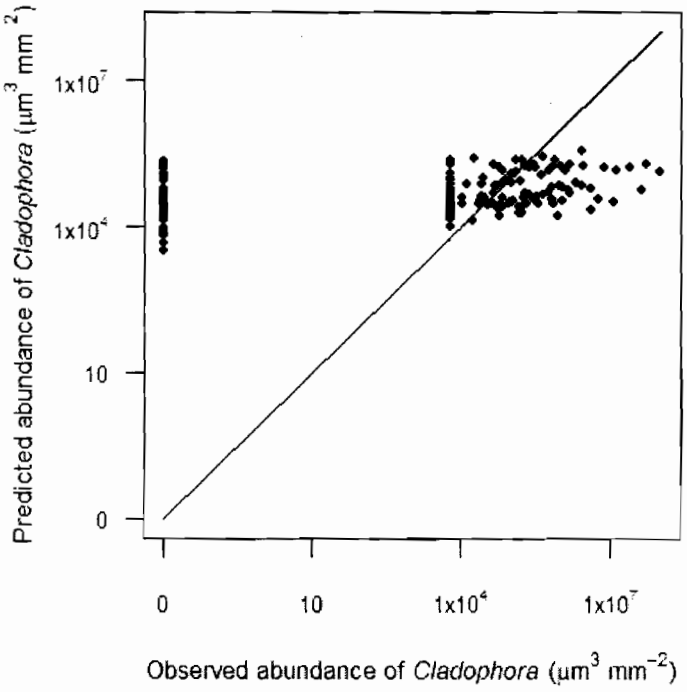

Figure 6. Plot of predicted vs. expected abundance of *Cladophora* spp. on a log-log scale with one-to-one line shows weakness of predictions of the two-part model. The vertical line of points at 0 $\mu m^3/mm^2$ is due to the large number of zero observations, while the vertical line of points at 9000 $\mu m^3/mm^2$ is due to the large number of imputed values.

Spirogyra spp.

Spirogyra spp. was detected at 70 of 199 Central Coast samplings sites. Abundance ranged from a minimum of 1.07 x 10^3 $\mu m^3/mm^2$, for imputed values, to 3.05 x 10^6 $\mu m^3/mm^2$ with one outlier near 3.92 x 10^6 $\mu m^3/mm^2$. Cell width and length ranged from 22.05-109.76 μm and 24.91-239.21 μm respectively.

Of all predictor variables included in the 90% confidence set of *Spirogyra* spp. presence-absence models only canopy cover and TP had model-averaged coefficients whose confidence intervals did not include zero (Table 7). Presence of *Spirogyra* spp. can be estimated as a function of these two parameters, both of which have a negative effect on presence (Figure 7). Standardized estimates showed percent canopy cover to have 1.3 times greater effect on probability of presence than TP concentration. Other variables included in the 90% confidence set of presence-absence models had substantial support, including current, TN, substrate, conductivity, and day of year (Table 8). However, without reliable coefficient estimates (i.e., estimates whose C.I.s do not include zero), the remaining variables were considered unrelated to occurrence of *Spirogyra* spp. The le Cessie-van Houwelingen goodness of fit test of the global model indicated good fit ($p = 0.24$). An ROC showed good predictive power from the model-averaged 90% confidence set (AUC = 0.77).

Table 7. Model-averaged coefficient estimates and their upper and lower confidence limits (95%) derived from the 90% confidence set of *Spirogyra* spp. presence-absence models. Standardized estimates are included for comparison of the relative influence of each variable on estimated probability of presence. Values in bold indicate coefficient intervals that do not include zero; all other 95% confidence intervals around coefficient estimates include zero, thus the data do not support an affect of these variables on *Spirogyra* spp. probability of presence.

Variable	Estimate	L.CI	U.CI	Standardized estimate
Canopy cover	**-2.74×10^{-2}**	**-3.84×10^{-2}**	**-1.64×10^{-2}**	-9.01×10^{-1}
Total phosphorus	**-2.74×10^{-3}**	**-5.36×10^{-3}**	**-1.24×10^{-4}**	-6.82×10^{-1}
Current velocity	-1.23×10^{-2}	-3.08×10^{-2}	6.30×10^{-3}	-1.47×10^{-1}
Total nitrogen	-1.71×10^{-2}	-5.12×10^{-2}	1.71×10^{-2}	-8.13×10^{-2}
Hard substrate	2.32×10^{-3}	-2.73×10^{-3}	7.36×10^{-3}	5.91×10^{-2}
Sp. conductance	-6.21×10^{-5}	-2.03×10^{-4}	7.87×10^{-5}	-4.22×10^{-2}
Day of year	-8.64×10^{-4}	-2.57×10^{-3}	8.43×10^{-4}	-3.83×10^{-2}

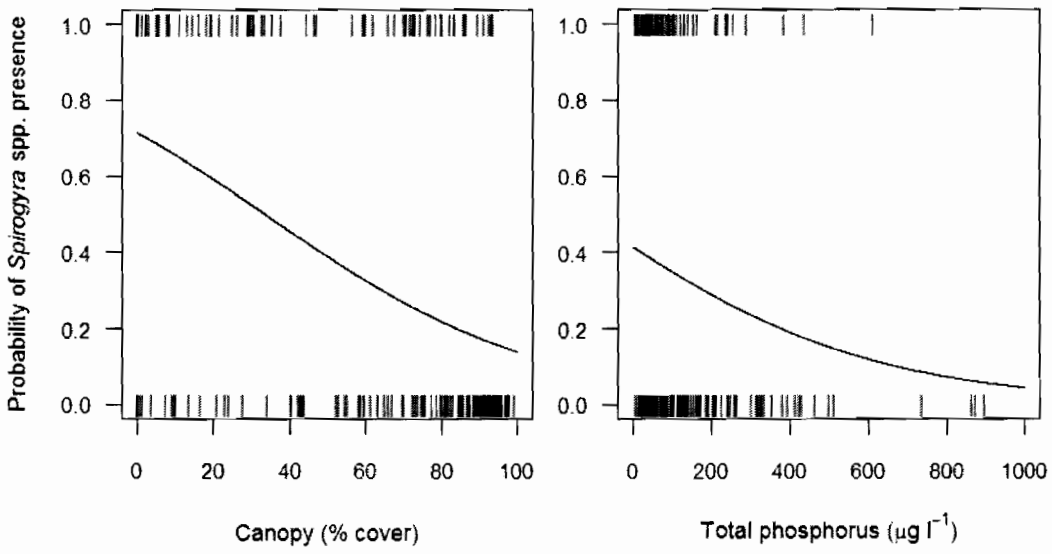

Figure 7. Estimates of probability of presence of *Spirogyra* spp. plotted against percent cover of riparian canopy and total phosphorus. Predictions use model averaged coefficients with all other environmental variables held at their means (Vincenzi et al. 2006). Tick marks show distribution of the data.

Table 8. Model selection results showing 90% confidence set on a priori models for probability of *Spirogyra* spp. presence. Evidence ratios are relative to the best model in the set. These models were used for multi-model inference.

Model	k	Δ_i	w_i	ER
Canopy + TP + current + TN	6	0.00	0.17	1.00
Canopy + TP + current	5	0.41	0.14	1.23
Canopy + TP + current + conduct	6	0.46	0.13	1.26
Canopy + TP	4	0.62	0.12	1.36
Canopy + TP + TN	5	0.94	0.11	1.60
Canopy + TP + current + substrate	6	1.25	0.09	1.87
Canopy + TP + substrate	5	1.38	0.09	1.99
Canopy + substrate + DOY	5	2.02	0.06	2.75
Canopy + DOY	4	2.51	0.05	3.52
Canopy + TP + substrate + conduct	6	2.81	0.04	4.09

Abbreviations: Canopy, canopy cover; TP, total phosphorus; current, current velocity; TN, total nitrogen; conduct, specifi conductance; substrate, hard substrate; DOY, day of year; k, no. of parameters; Δ_i, delta AIC; w_i, Akaike weights; ER, evidence ratio

Comparison of abundance given presence models proved inconclusive for *Spirogyra* spp. Although the no trend model (i.e., null) had zero probability of being the best model in the set ($w_i = 0$), the analysis did not identify any accurate predictors of trend in abundance (Table 9). The most probable model of those considered ($w_i = 0.19$) includes TP and TN (Table 10). In addition the global model lacked good fit ($R^2_{adj} = 0.07$, n = 70). Because no accurate predictors of abundance were identified, calculating a two-part model prediction was unwarranted.

Table 9. Model-averaged coefficient estimates and their upper and lower confidence limits (95%) derived from the 90% confidence set of *Spirogyra* spp. abundance models. Standardized estimates are included for comparison of the relative influence of each variable on estimated probability of presence. Values in bold indicate coefficient intervals that do not include zero; all other 95% confidence intervals around coefficient estimates include zero, thus the data do not support an affect of these variables on *Spirogyra* spp. abundance given presence.

Variable	Estimate	L.CI	U.CI	Standardized estimate
Total phosphorus	-3.50×10^{-3}	-7.86×10^{-3}	8.50×10^{-4}	-3.73×10^{-1}
Total nitrogen	-8.95×10^{-2}	-2.09×10^{-1}	3.04×10^{-2}	-3.24×10^{-1}
Current velocity	-6.68×10^{-3}	-2.28×10^{-2}	9.43×10^{-3}	-7.35×10^{-2}
Day of year	-1.19×10^{-3}	-3.66×10^{-3}	1.28×10^{-3}	-5.93×10^{-2}
Canopy cover	8.62×10^{-4}	-2.82×10^{-3}	4.55×10^{-3}	2.71×10^{-2}
Sp. conductance	4.84×10^{-5}	-8.39×10^{-5}	1.81×10^{-4}	2.39×10^{-2}
Hard substrate	-1.49×10^{-4}	-1.83×10^{-3}	1.53×10^{-3}	-3.79×10^{-3}

Table 10. Model selection results showing 90% confidence set on a priori models for abundance of *Spirogyra* spp. given presence. Evidence ratios are relative to the best model in the set.

Model	k	Δ_i	w_i	ER
TP + TN	4	0.00	0.19	1.00
TP + TN + current	5	1.07	0.11	1.71
TN	3	1.14	0.11	1.77
TP	3	1.31	0.10	1.93
DOY	3	1.74	0.08	2.39
TP + TN + canopy	5	2.05	0.07	2.78
TP + conduct	4	2.54	0.05	3.56
TP + current	4	2.66	0.05	3.79
TP + canopy	4	3.14	0.04	4.81
TP + TN + current + substrate	6	3.17	0.04	4.88
TN + canopy	4	3.29	0.04	5.18
TP + canopy + substrate	5	3.72	0.03	6.41
Conduct	3	3.97	0.03	7.27
Current	3	3.99	0.03	7.34
Substrate	3	4.51	0.02	9.54

Abbreviations: TP, total phosphorus; TN, total nitrogen; current, current velocity; DOY, day of year; canopy, canopy cove conduct, specific conductance; substrate, hard substrate; k, no. of parameters; Δ_i, delta AIC; w_i, Akaike weights; ER, evidence ratio

Ulva spp.

Ulva spp. was detected at 31 of 198 sites and was not included in the two-part conditional modeling. Accurate biovolume measurements were problematic because *Ulva* spp. composite sample fragments were difficult to identify. Therefore, only occurrence data were collected for this taxon. Canopy cover and specific conductance occurred in the top three models with substantial support. Only these two parameters had model-averaged coefficients whose confidence intervals did not include zero (Table 11). Coefficient estimates indicated a negative relationship between *Ulva* spp. and canopy cover and a positive relationship with specific conductance (Figure 8). Standardized estimates showed percent canopy cover to have 1.5 times greater effect on probability of presence than specific conductance. The 90% confidence set of models also included TP, TN, current, and substrate (Table 12), but given the uncertainty of their coefficient estimates, these variables cannot be used to predict probability of *Ulva* spp. presence. The le Cessie-van Houwelingen goodness of fit test of the global model indicated good fit ($p = 0.19$). ROC showed good predictive power from the model-averaged 90% confidence set (AUC = 0.84).

Table 11. Model-averaged coefficient estimates and their upper and lower confidence limits (95%) derived from the 90% confidence set of *Ulva* spp. presence-absence models. Standardized estimates are included for comparison of the relative influence of each variable on estimated probability of presence. Values in bold indicate coefficient intervals that do not include zero; all other 95% confidence intervals around coefficient estimates include zero, thus the data do not support an affect of these variables on *Ulva* spp. probability of presence.

Variable	Estimate	L.CI	U.CI	Standardized estimate
Canopy cover	**-2.95×10^{-2}**	**-4.34×10^{-2}**	**-1.55×10^{-2}**	-9.66×10^{-1}
Sp. conductance	**9.30×10^{-4}**	**2.90×10^{-4}**	**1.57×10^{-3}**	6.34×10^{-1}
Total phosphorus	-1.72×10^{-3}	-4.50×10^{-3}	1.06×10^{-3}	-4.27×10^{-1}
Total nitrogen	1.98×10^{-2}	-1.61×10^{-2}	5.56×10^{-2}	9.44×10^{-2}
Current velocity	1.69×10^{-3}	-5.70×10^{-3}	9.08×10^{-3}	1.93×10^{-2}
Hard substrate	-3.92×10^{-4}	-4.08×10^{-3}	3.30×10^{-3}	-1.00×10^{-2}

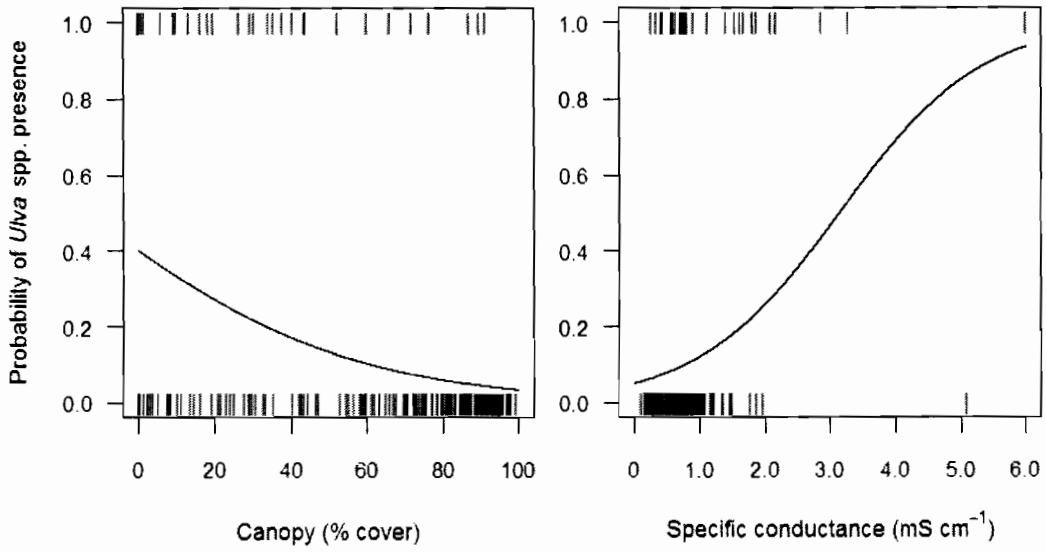

Figure 8. Estimates of probability of presence of *Ulva* spp. plotted against percent cover of riparian canopy and specific conductance. Predictions use model averaged coefficients with all other environmental variables held at their means (Vincenzi et al. 2006). Tick marks show distribution of the data.

Table 12. Model selection results showing 90% confidence set on a priori models for probability of *Ulva* spp. presence. Evidence ratios are relative to the best model in the set. These models were used for multi-model inference.

Model	k	Δ_i	w_i	ER
Canopy + conduct	4	0.00	0.43	1.00
Canopy + conduct + TP + current	6	1.37	0.22	1.98
Canopy + conduct + TP + substrate	6	1.55	0.20	2.17
Canopy + TP + TN	5	2.73	0.11	3.92
Canopy + TN	4	4.76	0.04	10.83

Abbreviations: Canopy, canopy cover; conduct, specific conductance; TP, total phosphorus; current, current velocity; substrate, hard substrate; TN, total nitrogen; k, no. of parameters; Δ_i, delta AIC; w_i, Akaike weights; ER, evidence ratio

Post hoc analysis

In the interest of water quality management, post modeling analyses were conducted to explore the effect of canopy cover on DO concentrations via macroalgal presence. Spearman rank correlation indicated a weak but definite negative relationship between DO and percent cover of canopy ($r_s = -0.32$, $p < 0.0001$). A Wilcoxon rank sum test showed an increase in DO saturation in the presence of *Cladophora* spp. ($p = 0.0001$), and *Ulva* spp. ($p < 0.0001$) (Figure 9).

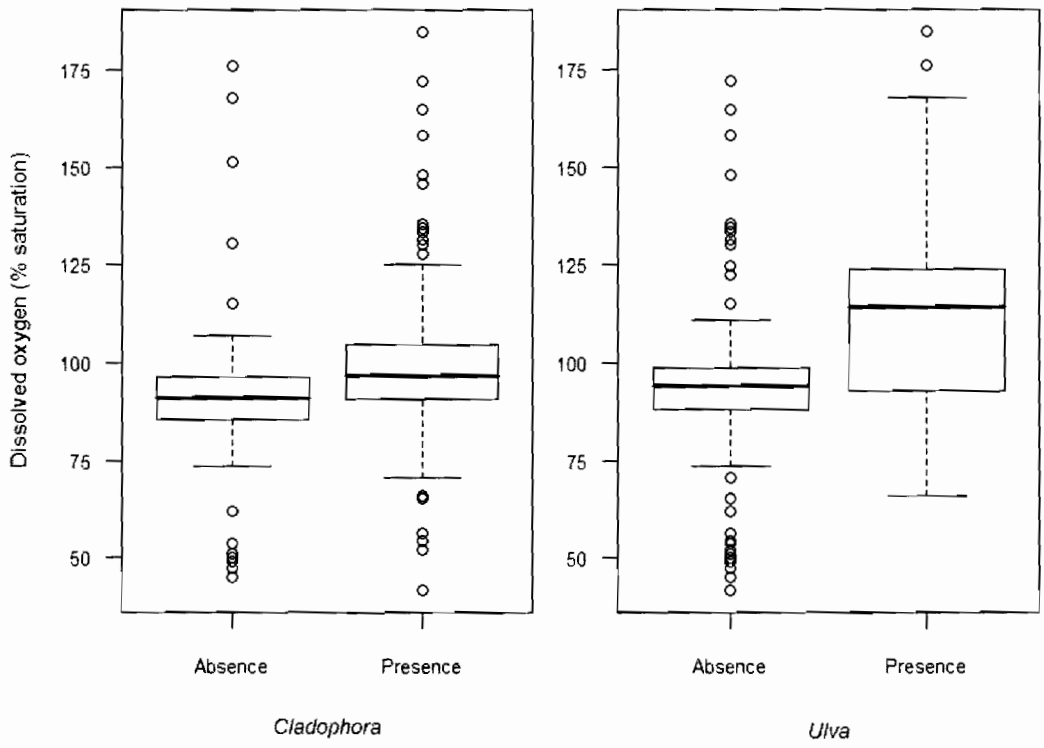

Figure 9. Dissolved oxygen concentrations in presence and absence of *Cladophora* spp. and *Ulva* spp. Higher concentrations occurred in the presence of these two macroalgae.

DISCUSSION

Cladophora spp.

Cladophora was the most commonly found macroalgae during the sampling period indicating widespread distribution throughout the Central Coast. Indeed, it is thought to be the most ubiquitous macroalgae of freshwaters worldwide (Dodds 1991), though it continues to thwart attempts to understand the factors influencing its distribution and abundance (Westlake 1981, Morgan et al. 2006). Of the model predictors evaluated in this study, *Cladophora* spp. presence was most strongly associated with high percent cover of hard substrate and low percent cover of canopy. Canopy cover was also negatively related to *Cladophora* spp. abundance, but poor fit diminished the model's predictive utility.

In accordance with Dodds and Gudder (1992) and Ensminger et al. (2005), I found *Cladophora* spp. probability of presence to be higher in streams with a higher

percentage of stable substrate. Large substrates such as cobble are typically more stable attachment sites at higher flows than smaller-sized grains such as sand. A higher percentage of hard substrate in a reach may also indicate reduced bed load movement and subsequent disturbance due to sediment scour (Biggs and Close 1989, Horner et al. 1990, Power 2001). *Cladophora glomerata* growths tend to be most abundant in riffle habitats (Stevenson et al. 2006), again indicating the importance of stable attachment sites to *Cladophora* presence. Larger substrates also elevate filaments in the water column thereby increasing access to light. However, *Cladophora* is not dependent on attachment for survival. It can detach, drift, and be caught by other structures, such as a rocks or branches, and continue to photosynthesize (Dodds and Gudder 1992).

Percent cover of canopy determined both *Cladophora* spp. occurrence and abundance, likely indicating the importance of light to its growth habit. Likewise, Robinson and Hawkes (1986), Sabater et al. (1998), Morgan et al. (2006), found increases in *Cladophora* accrual with higher irradiance. This taxon, however, is also tolerant of low light conditions (Dudley and D'Antonio 1991, Ensminger et al. 2005), which may contribute to its ubiquity. In this study it was detected under a wide range of riparian coverage (0-98%). Although *Cladophora* spp. was present in highly shaded streams, it was more abundant in full sun. In addition, *Cladophora* demonstrates photosynthetic plasticity under changing environmental conditions and is capable of high productivity rates at high levels of irradiance (Necchi 2004, Ensminger et al. 2005).

Over the course of the study, I observed excessive macroalgal proliferations at several sites. Whether or not algal proliferations were a nuisance in these locations is unknown. In some cases, proliferations were only localized, coinciding with open canopy in an otherwise shaded stream. Such circumstances may have confounded model predictive ability. Given the preference of *Cladophora* spp. for sunlight and stable substrate, streams with sparse riparian vegetation and ample stable attachment sites in regions of infrequent hydrologic disturbance may be prone to natural ephemeral algal proliferations.

Spirogyra spp.

Model selection results indicated increased probability of *Spirogyra* spp. presence with decreased canopy cover and TP. While the negative response of *Spirogyra* spp. to higher canopy cover was expected (Lowe et al. 1986, Steinman et al. 1991, Graham et al. 1995), a negative relationship with TP was not. Several studies report a positive effect of phosphorus on *Spirogyra* (Borchardt et al. 1994, McCormick and O'Dell 1996, Townsend and Padovan 2005). McCormick and Stevenson (1998) even noted its potential as an indicator of high phosphorus concentration. Conversely, no studies were found to support the result reported here. Where Ensminger et al. (2000) found a negative correlation between soluble reactive phosphorus (SRP) and percent coverage of *Cladophora glomerata*, they speculated that increased SRP uptake by highly productive photoautotrophs resulted in lowered water column concentrations. If grazer densities increase in nutrient enriched streams (Elwood et al 1981), herbivory could mask effects of high TP concentration on *Spirogyra* productivity as it has on other benthic algae (Rosemond 1994, Hillebrand 2002, Liess and Kahlert 2009). Alternatively, algae or macrophytes better equipped to acquire and allocate phosphorus for growth may outcompete *Spirogyra* in highly productive streams (Borchardt 1996, Suren et al 2003).

Members of this genus demonstrated a diversity of cell sizes and chloroplast arrangements, which indicate detection of more than one species. At least 16 species were found in a similar bioassessment study of coastal southern California streams (Stancheva et al. 2009). It is thus likely that numerous species were not differentiated during the analysis thereby convoluting results where species have unique responses to ecological factors.

Ulva spp.

Ulva (formerly *Enteromorpha* (Hayden et al. 2003)) is a common estuarine macroalgal genus. Although found primarily in saline waters, this genus appears to be increasingly detected in freshwater systems of the United Kingdom and Great Lakes region (Whitton 2000, Lougheed and Stevenson 2004). The current study reveals its presence in partially shaded to open canopy freshwater streams up to 68 km from the ocean with specific conductance ranging from 250-3000 µS/cm. McAvoy and Klug

(2005) suggests that *Ulva* proliferations found in freshwaters are likely due to elevated nutrient concentrations. Several studies of *Ulva intestinalis* support the hypothesis that some species of this genus may be able to tolerate fresh water environments when nutrient concentrations are high (Kamer and Fong 2001, McAvoy and Klug 2005). Nutrient concentrations in the Central Coast stream reaches where *Ulva* spp. were found ranged from low to high (0.01 - 40 mg l^{-1} TN and 6 - 736 µg l^{-1} TP), but model selection results showed no evidence of a relationship between *Ulva* spp. and TN or TP. While *Ulva* has a wide distribution in saline, fresh, and brackish waters, Shimada et al. (2008) suggested that *U. flexuosa* survival in low salinity environments in Japan was temporary and thus the species was not adapted to freshwater. Further research would be necessary to determine the persistence of this genus in freshwater streams of the Central Coast.

Environmental factors

The overarching result of the study shows the importance of light to the distribution of all three taxa and its association with *Cladophora* spp. abundance (Figure 10). These results are not unexpected as aquatic photoautotrophs respond directly to changes in the amount of light energy reaching a stream (Ensminger et al. 2005). Responses include changes in algal community composition and biomass. Light was found to be a key limiting factor in the distribution and abundance of *Cladophora* in an oligotrophic Mediterranean stream (Sabater et al. 1998) as well as in other systems (Morgan et al. 2006). Streams that lost canopy cover to logging in northeast Spain experienced chlorophyll *a* concentrations 10 times greater than forested areas (Sabater et al. 1998).

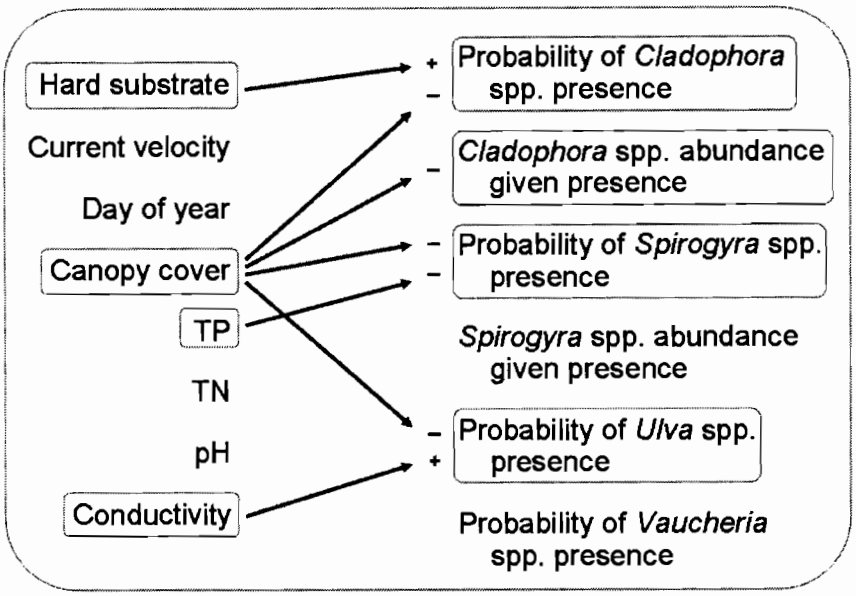

Figure 10. Arrow diagram summarizing relationships between predictor and response variables arrived at using an information theoretic approach.

Other stream variables produced less certain results in this study. Contrary to previous work and the expectation of the author, this study did not find a positive relationship between nutrients and macroalgal abundance. This finding could be due to a number of potential reasons: temporal fluctuations in nutrient concentrations and the delayed response of algal biomass, clumped spatial distribution of filamentous algae, right-skewed nutrient data, or community interactions. Nutrient concentrations were, however, both above and below growth saturating levels for benthic algae (35-60 $\mu g\ l^{-1}$ TP and 0.35-0.5 $mg\ l^{-1}$ TN; Wong and Clark 1976, Dodds et al. and Dodds et al. 1997, respectively).

Establishing algal-nutrient relationships is made difficult by temporally variable nutrient concentrations and patchy algal distribution. Oscillations in stream nutrient concentration can be caused by diurnal, daily, and seasonal factors such as microbial activity, assimilation by photoautotrophs, and stormwater runoff (Meyer et al. 1988). Algal growth response to these fluctuations is not immediately evident (Collos 1986), and single event sampling may fail to capture nutrient-stimulated accrual (Hillebrand 2002). Benthic filamentous algae exhibit patchy distribution at the reach scale (Stevenson et al.

2006). Such heterogeneous macroalgal growth was observed during this study. At each site a total of 132 cm^2 was sampled from 11 points within a 150 m reach. The location of these points in relation to algal patches may have altered abundance estimates, possibly masking subtle relationships within the noise of the data. Stevenson et al. (2006) recommend an extensive and frequent sampling method in order to account for both spatial heterogeneity and temporal fluctuations in nutrient concentrations and algal biomass.

Some environmental variables lacked uniformly distributed data, which may have affected model comparison results. Many of the sites sampled exhibited nutrient concentrations on the low end of the scale while a smaller proportion of sites exhibited high concentrations (Figure 11). This type of skewed condition makes it difficult to estimate reliable regression parameters over the entire range of values.

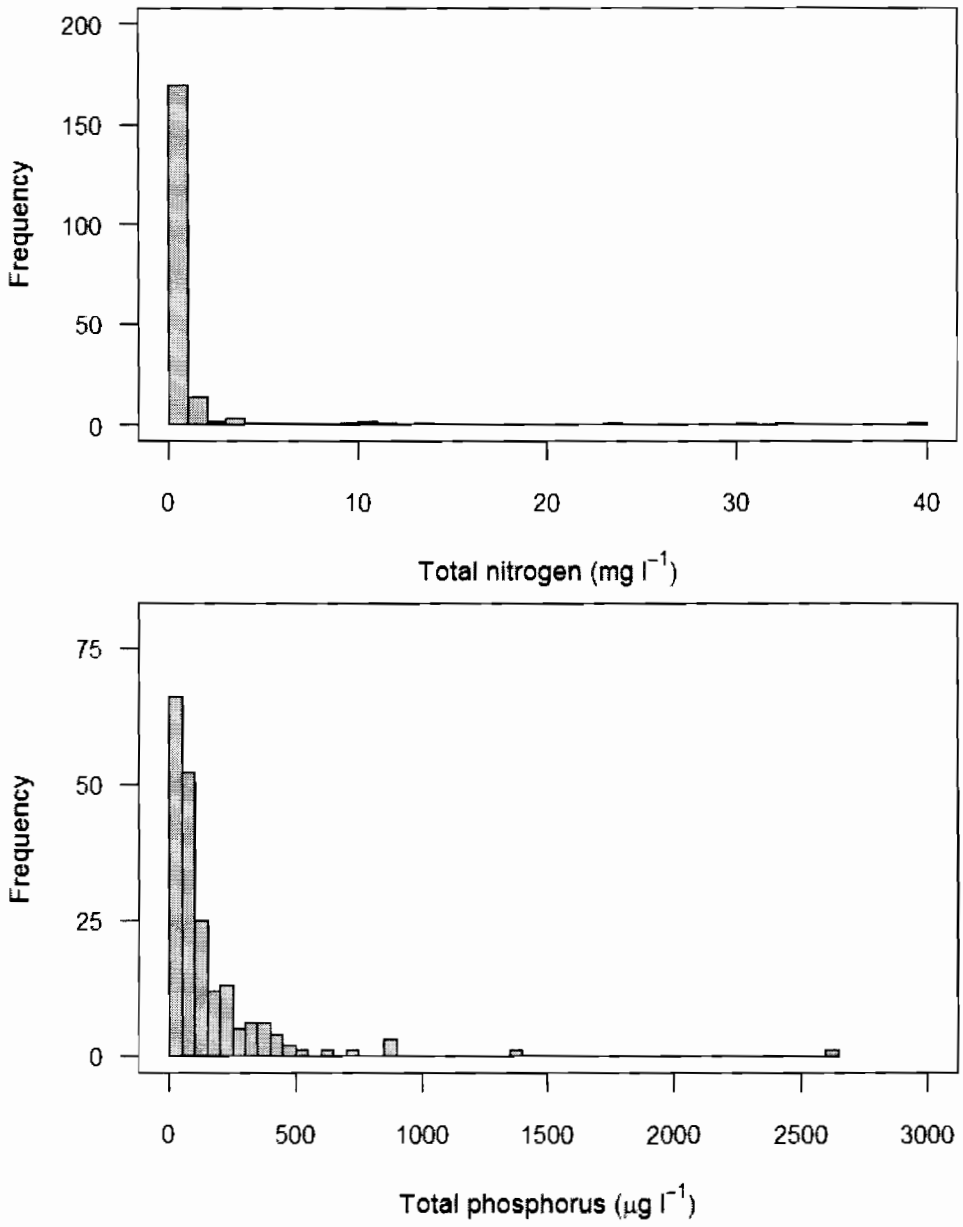

Figure 11. Distribution of TN and TP water column concentrations over the entire range of values. Nutrient concentrations do not exhibit uniform distribution.

Community interactions, such as herbivory and competition, were not examined in this study, however they may be integral in controlling algal biomass and could account for a lack of strong patterns in the data. Benthic algae are strongly regulated by stream herbivory (Feminella and Hawkins 1995). Filamentous macroalgae occupy

multiple feeding zones and thus may be susceptible to grazing by numerous feeding groups (Steinman 1996). In addition some filamentous macroalgae, such as *Cladophora* and *Vaucheria*, provide attachment sites for epiphytes. In the case of *Cladophora*, the alga itself is not always the preferred food source, but is damaged in the process of epiphyte grazing (Dodds and Gudder 1992). On the other hand, Roll et al. (2005) found that rapid growth of filamentous macroalgae under high nutrient conditions produced increasing biomass even in the presence of high grazer density. The chances for such a response increase when the initial algal growth period precedes the recovery or immigration of the grazer community (Power 1992). Algal communities are also affected by competition between algal species or with macrophytes (McCormick and Stevenson 1991, Everitt and Burkholder 2001). Following disturbance events, colonization by competitively similar species may occur stochastically, and early immigrants can dominate the substrate to the exclusion of other species (Yodzis 1986, Townsend 1989). Under high light, shallow, nutrient-enriched conditions, macrophytes outcompete benthic macroalgae for space (Sand-Jensen and Borum 1991). Epiphyte load can also affect host productivity through shading and competition for nutrients (Jansson 1969). These community interactions, in part, dictate species abundance and can make it difficult to identify taxon response patterns to nutrients or other environmental factors (Rosemond 1994, Hillebrand 2002).

Dissolved oxygen

Analyses of dissolved oxygen coupled with a priori model comparison results support the hypothesis that riparian cover is also important in the prevention of extreme fluctuations in DO and occurrence of nighttime anoxia. When percent cover of riparian canopy is low, solar irradiance is more available in the water column. The probability of presence of 3 common filamentous macroalgae increased under these conditions. Presence of the 2 more prolific taxa, *Cladophora* spp. and *Ulva* spp., was related to higher daytime DO concentrations. Morgan et al. (2006) found that when present, *Cladophora glomerata* biomass explained 64% of the variation in the diel ranges of DO saturation in agricultural streams of Illinois. Daytime levels of DO > 125% saturation (found at 16 sites) have been linked to anoxic conditions at night in the Pajaro River

watershed as algae continue to use oxygen for respiration but cease oxygen production (Los Huertos et al. 2004).

Management implications

The Central Coast Basin Plan outlines water quality directives to be upheld by regional resource managers. Among the directives, the biostimulatory objective requires control of nuisance algal proliferations that interfere with the designated uses of streams. This study took an exploratory approach to garnering autecological information about nuisance-prone macroalgae by utilizing a large regional dataset.

While the study found no indication of a stimulatory effect of nutrients on potential nuisance taxa, overwhelming evidence from the literature indicate that a relationship does exist (Borchardt 1996). Future research should further test the algal-nutrient relationship in the Central Coast. Refinements to the approach taken here may include stratification by canopy cover, flow, and substrate in a longitudinal study (i.e., multiple sampling events). Biotic factors as well may be too important to exclude from future work.

This study suggests that higher cover of canopy may reduce dissolved oxygen fluctuations through its regulation of macroalgae. Because aquatic fauna rely on high and stable dissolved oxygen concentrations for health and survival (Nebeker 1972, Richardson et al. 2001, Connolly et al. 2004), it is imperative that water quality managers understand the factors that can cause and mediate potentially harmful fluctuations. A confirmatory study could evaluate the interaction between riparian canopy and macroalgae in influencing extreme fluctuations in stream dissolved oxygen concentrations in Mediterranean climates.

Model comparison results suggest that riparian revegetation is an important tool with which managers (e.g., RWQCB, California Department of Fish and Game) can control nuisance proliferations and improve biotic integrity. When implemented appropriately, riparian vegetation is thought to provide a multitude of other water quality benefits as well (e.g., reduced instream temperature, filtration of nutrient and sediment from runoff, source of carbon for heterotrophs, and source of large woody debris for

habitat structure; Vought et al. 1994, Correll 1996, Anbumozhi et al. 2005), and so may be an obvious choice for water quality improvement measures.

CONCLUSIONS

This is the first regional assessment of filamentous macroalgae in Central Coast streams. The main objective of the study was to explore the ecological relationships between filamentous macroalgal taxa and abiotic stream conditions using model comparison methods. *Cladophora* spp., found at 64% of sites, was the most commonly detected macroalgae. The estuarine alga *Ulva* spp. was detected in inland streams up to 68 km from the coastline. The strongest evidence supports canopy cover as the primary abiotic factor responsible for the probability of *Cladophora* spp., *Spirogyra* spp., and *Ulva* spp. presence. These taxa responded negatively to increases in percent cover of canopy over a reach. Canopy cover was also negatively related to *Cladophora* spp. abundance, but the degree of the relationship is unknown. These data did not support a biostimulatory effect of nutrients on the target taxa. On the contrary, increases in TP concentration appeared to decrease probability of *Spirogyra* spp. presence. A positive relationship with nutrients may have been obscured by overriding physical habitat characteristics and several confounding factors. Additional findings showed evidence in support of a positive influence of large substrate on *Cladophora* spp. presence and a positive influence of conductivity on *Ulva* spp. presence. Finally, presence of *Cladophora* spp. and *Ulva* spp. was correlated with higher dissolved oxygen concentrations. These findings support the use of shade-providing riparian vegetation to limit nuisance algae proliferations and thereby protect the designated uses of streams in the Central Coast.

To avoid the confounding factors that may have influenced the results of the present study, future work should be conducted through a longitudinal study. In this way, the data will capture temporal fluctuations in nutrient concentrations and algal biomass and potential patterns may be observed. Due to the clumped spatial distribution of filamentous algae, abundance may be best estimated using in situ percent cover measurements within a stratified sampling design. Care should be taken to attain

uniformly distributed data for all independent variables and consideration given to biotic factors that can strongly influence algal accrual.

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APPENDICES

APPENDIX A

A PRIORI MODELS

Table A.1. Complete model suite used in logistic regression analysis to evaluate factors influencing probability of *Cladophora spp.* presence in Central Coast streams. Models are ranked by AIC_c results.

Model	k	AIC_c	Δ_i	w_i
Canopy + current + substrate + TP	6	236.9	0.00	0.27
Canopy + substrate+ TP	5	237.5	0.60	0.20
Canopy + current + substrate	5	238.0	1.12	0.15
Canopy + conduct + substrate + TP	6	238.2	1.33	0.14
Canopy + DOY + substrate	5	238.3	1.45	0.13
Canopy + substrate	4	239.0	2.16	0.09
Current + substrate + TN + TP	6	244.6	7.68	0.01
Substrate + TP	4	246.4	9.57	< 0.01
Canopy + TN + TP	5	246.5	9.64	< 0.01
Canopy + current + TN + TP	6	246.7	9.84	< 0.01
Canopy + current + TP	5	248.2	11.30	< 0.01
Canopy + TP	4	248.8	11.88	< 0.01
Current + TN + TP	5	249.3	12.47	< 0.01
Current + TP	4	249.5	12.60	< 0.01
DOY + TN + TP	5	250.0	13.09	< 0.01
Canopy + conduct + current + TP	6	250.1	13.27	< 0.01
Substrate	3	251.0	14.11	< 0.01
TN + TP	4	251.3	14.39	< 0.01
Canopy + TN	4	251.9	15.02	< 0.01
TP	3	251.9	15.02	< 0.01
Canopy + DOY	4	253.1	16.24	< 0.01
Conduct + TP	4	253.6	16.77	< 0.01
Canopy + current	4	254.9	18.03	< 0.01
Canopy	3	256.3	19.45	< 0.01
Current	3	257.5	20.64	< 0.01
DOY	3	257.7	20.83	< 0.01
Canopy + conduct	4	258.4	21.48	< 0.01
pH	3	258.6	21.75	< 0.01
TN	3	258.7	21.87	< 0.01
Conduct + current	4	259.1	22.24	< 0.01
Null	2	261.3	24.46	< 0.01
Conduct	3	263.2	26.35	< 0.01

Abbreviations: canopy, canopy cover; conduct, specific conductance; current, current velocity; DOY, day of year; substrate, hard substrate; TN, total nitrogen; TP, total phosphorus; k, no. of parameters; Δi, delta AIC; w_i, Akaike weights

Table A.2. Complete model suite used in logistic regression analysis to evaluate factors influencing probability of *Spirogyra spp.* presence in Central Coast streams. Models are ranked by AIC_c results.

Model	k	AIC_c	Δ_i	w_i
Canopy + current + TN + TP	6	226.1	0.00	0.16
Canopy + current + TP	5	226.5	0.41	0.13
Canopy + conduct + current + TP	6	226.5	0.46	0.12
Canopy + TP	4	226.7	0.62	0.11
Canopy + TN + TP	5	227.0	0.94	0.10
Canopy + current + substrate + TP	6	227.3	1.25	0.08
Canopy + substrate+ TP	5	227.5	1.38	0.08
Canopy + DOY + substrate	5	228.1	2.02	0.06
Canopy + DOY	4	228.6	2.51	0.04
Canopy + conduct + substrate + TP	6	228.9	2.81	0.04
Canopy + substrate	4	230.2	4.08	0.02
Canopy + current + substrate	5	230.2	4.15	0.02
Canopy + TN	4	231.1	5.02	0.01
Canopy	3	231.8	5.73	0.01
Canopy + current	4	231.9	5.80	0.01
Canopy + conduct	4	232.5	6.38	0.01
DOY + TN + TP	5	249.5	23.41	< 0.01
TP	3	251.7	25.62	< 0.01
TN + TP	4	253.6	27.50	< 0.01
Substrate + TP	4	253.6	27.55	< 0.01
Conduct + TP	4	253.7	27.57	< 0.01
Current + TP	4	253.8	27.67	< 0.01
DOY	3	255.5	29.43	< 0.01
Current + TN + TP	5	255.7	29.57	< 0.01
Current + substrate + TN + TP	6	257.5	31.38	< 0.01
pH	3	258.3	32.23	< 0.01
Null	2	260.1	34.05	< 0.01
TN	3	261.3	35.22	< 0.01
Substrate	3	261.9	35.83	< 0.01
Current	3	262.1	36.06	< 0.01
Conduct	3	262.2	36.08	< 0.01
Conduct + current	4	264.2	38.10	< 0.01

Abbreviations: canopy, canopy cover; conduct, specific conductance; current, current velocity; DOY, day of year; substrate, hard substrate; TN, total nitrogen; TP, total phosphorus; k, no. of parameters; Δi, delta AIC; w_i, Akaike weights

Table A.3. Complete model suite used in logistic regression analysis to evaluate factors influencing probability of *Ulva* spp. presence in Central Coast streams. Models are ranked by AIC_c results.

Model	k	AIC_c	Δ_i	w_i
Canopy + conduct	4	137.4	0.00	0.40
Canopy + conduct + current + TP	6	138.8	1.37	0.20
Canopy + conduct + substrate + TP	6	139.0	1.55	0.18
Canopy + TN + TP	5	140.2	2.73	0.10
Canopy + TN	4	142.2	4.76	0.04
Canopy + current + TN + TP	6	142.3	4.84	0.04
Canopy + DOY	4	143.4	5.95	0.02
Canopy + DOY + substrate	5	145.3	7.89	0.01
Canopy	3	147.7	10.24	< 0.01
Canopy + TP	4	148.8	11.37	< 0.01
Canopy + substrate	4	148.9	11.49	< 0.01
Canopy + substrate+ TP	5	149.1	11.69	< 0.01
Canopy + current	4	149.7	12.26	< 0.01
Canopy + current + TP	5	150.8	13.38	< 0.01
Canopy + current + substrate	5	150.9	13.49	< 0.01
Canopy + current + substrate + TP	6	151.0	13.61	< 0.01
Conduct + TP	4	153.9	16.45	< 0.01
Conduct + current	4	156.4	18.97	< 0.01
Conduct	3	157.5	20.09	< 0.01
TN + TP	4	160.5	23.08	< 0.01
DOY + TN + TP	5	161.0	23.55	< 0.01
Current + substrate + TN + TP	6	161.3	23.83	< 0.01
Current + TN + TP	5	161.3	23.91	< 0.01
TN	3	166.0	28.60	< 0.01
pH	3	166.7	29.29	< 0.01
Substrate + TP	4	167.4	30.00	< 0.01
DOY	3	170.7	33.29	< 0.01
Substrate	3	171.2	33.76	< 0.01
TP	3	172.9	35.46	< 0.01
Null	2	173.9	36.42	< 0.01
Current + TP	4	174.1	36.71	< 0.01
Current	3	174.6	37.19	< 0.01

Abbreviations: canopy, canopy cover; conduct, specific conductance; current, current velocity; DOY, day of year; substrate, hard substrate; TN, total nitrogen; TP, total phosphorus; k, no. of parameters; Δi, delta AIC; w_i, Akaike weights

Table A.4. Complete model suite used in logistic regression analysis to evaluate factors influencing probability of *Vaucheria spp.* presence in Central Coast streams. Models are ranked by AIC_c results.

Model	k	AIC_c	Δ_i	w_i
Conduct	3	214.1	0.00	0.13
Null	2	214.3	0.11	0.12
Conduct + TP	4	215.6	1.43	0.06
TP	3	215.8	1.62	0.06
pH	3	215.9	1.73	0.05
DOY	3	215.9	1.79	0.05
Conduct + current	4	216.0	1.88	0.05
Substrate	3	216.1	1.99	0.05
Canopy + conduct	4	216.2	2.01	0.05
Current	3	216.2	2.09	0.05
Canopy	3	216.3	2.15	0.04
TN	3	216.3	2.15	0.04
Substrate + TP	4	217.5	3.32	0.02
Current + TP	4	217.8	3.66	0.02
TN + TP	4	217.8	3.68	0.02
Canopy + TP	4	217.8	3.68	0.02
Canopy + DOY	4	218.0	3.85	0.02
Canopy + substrate	4	218.2	4.06	0.02
Canopy + current	4	218.3	4.15	0.02
Canopy + TN	4	218.4	4.21	0.02
Canopy + conduct + current + TP	6	219.4	5.29	0.01
Canopy + substrate+ TP	5	219.5	5.37	0.01
DOY + TN + TP	5	219.5	5.39	0.01
Canopy + conduct + substrate + TP	6	219.5	5.40	0.01
Canopy + DOY + substrate	5	219.8	5.69	0.01
Current + TN + TP	5	219.9	5.73	0.01
Canopy + current + TP	5	219.9	5.74	0.01
Canopy + TN + TP	5	219.9	5.76	0.01
Canopy + current + substrate	5	220.2	6.08	0.01
Canopy + current + substrate + TP	6	221.6	7.46	< 0.01
Current + substrate + TN + TP	6	221.6	7.49	< 0.01
Canopy + current + TN + TP	6	222.0	7.83	< 0.01

Abbreviations: canopy, canopy cover; conduct, specific conductance; current, current velocity; DOY, day of year; substrate, hard substrate; TN, total nitrogen; TP, total phosphorus; k, no. of parameters; Δi, delta AIC; w_i, Akaike weights

Table A.5. Complete model suite used in linear regression analysis to evaluate factors influencing *Cladophora spp.* abundance given presence in Central Coast streams. Models are ranked by AIC_c results.

Model	k	AIC_c	Δ_i	w_i
Canopy + substrate	4	585.3	0.00	0.16
Canopy	3	585.7	0.40	0.13
Canopy + DOY + substrate	5	586.0	0.66	0.11
Canopy + conduct	4	586.0	0.75	0.11
Canopy + DOY	4	586.0	0.75	0.11
Canopy + TN	4	586.4	1.09	0.09
Canopy + substrate + TP	5	586.7	1.45	0.08
Canopy + TP	4	587.5	2.19	0.05
Canopy + current	4	587.8	2.53	0.04
Canopy + current + TP	5	588.0	2.69	0.04
Canopy + current + substrate + TP	6	588.9	3.66	0.02
Canopy + current + TP	5	589.6	4.35	0.02
Conduct	3	590.6	5.29	0.01
DOY	3	591.5	6.19	0.01
Null	2	591.9	6.61	0.01
TN	3	592.5	7.20	< 0.01
Conduct + TP	4	592.6	7.29	< 0.01
Canopy + current + TN + TP + canopy*TN + canopy*TP	8	593.3	7.97	< 0.01
Substrate	3	593.3	7.99	< 0.01
Current	3	593.4	8.09	< 0.01
TP	3	593.9	8.63	< 0.01
TN + TP	4	594.4	9.14	< 0.01
Current + TP	4	595.5	10.16	< 0.01
Current + TN + TP	5	595.8	10.55	< 0.01
Current + substrate + TN + TP	6	597.3	12.06	< 0.01

Abbreviation: canopy, canopy cover; conduct, specific conductance; current, current velocity; DOY, day of year; substrate, hard substrate; TN, total nitrogen; TP, total phosphorus; k, no. of parameters; Δi, delta AIC; w_i, Akaike weights

Table A.6. Complete model suite used in linear regression analysis to evaluate factors influencing *Spirogyra spp.* abundance given presence in Central Coast streams. Models are ranked by AIC_c results.

Model	k	AIC_c	Δ_i	w_i
TN + TP	4	331.6	0.00	0.18
Current + TN + TP	5	332.7	1.07	0.10
TN	3	332.7	1.14	0.10
TP	3	332.9	1.31	0.09
DOY	3	333.3	1.74	0.07
Canopy + current + TP	5	333.6	2.05	0.06
Conduct + TP	4	334.1	2.54	0.05
Current + TP	4	334.3	2.66	0.05
Canopy + TP	4	334.7	3.14	0.04
Current + substrate + TN + TP	6	334.8	3.17	0.04
Canopy + TN	4	334.9	3.29	0.03
Canopy + DOY	4	335.3	3.72	0.03
Conduct	3	335.6	3.97	0.02
Current	3	335.6	3.99	0.02
Substrate	3	336.1	4.51	0.02
Canopy	3	336.2	4.55	0.02
Canopy + current + TP	5	336.3	4.73	0.02
Canopy + substrate + TP	5	337.0	5.43	0.01
Canopy + DOY + substrate	5	337.2	5.61	0.01
Canopy + conduct	4	337.5	5.95	0.01
Canopy + current	4	337.7	6.15	0.01
Canopy + substrate	4	338.2	6.63	0.01
Canopy + current + substrate + TP	6	338.7	7.13	0.01
Canopy + current + TN + TP + canopy*TN + canopy*TP	8	339.2	7.65	< 0.01
Null	2	2110.5	1778.92	0.00

Abbreviations: canopy, canopy cover; conduct, specific conductance; current, current velocity; DOY, day of year; substrate, hard substrate; TN, total nitrogen; TP, total phosphorus; k, no. of parameters; Δi, delta AIC; w_i, Akaike weights

APPENDIX B

R CODE FOR STATISTICAL ANALYSES

```
#Two-part Conditional Modeling and Model Comparison
library(Design)
library(verification)

# Part 1: Logistic regression on presence-absence for Cladophora
#Import data into R
clad.spir.pres<-read.csv(file.choose())
attach(clad.spir.pres)

#Conduct Spearman's rho correlation test on matrix of predictor variables
cor(clad.spir.pres, method="spearman", use="complete.obs")

# Fred's function for AICtable
function(aic,n){
K<-aic$df
AICc<-aic$AIC+2*K*(K+1)/(n-K-1)
delAIC<-AICc-min(AICc)
AICw<-exp(-0.5*delAIC)/sum(exp(-0.5*delAIC))
#AIC table ready to publish
data.frame(aic,AICc,delAIC,AICw)
}

######GENERIC FUNCTIONS FOR MODEL COMPARISON DATA OUPUT####
# Marc developed generic functions to condense the code I used for each algal taxa. These
      #functions are only for part of the analysis.
#Function to check fit of logistic regression models using LeCessie-VanHouwelingen goodness
      # of fit test
global <- function(dependent){
#global logistic regression model
pres.global<-lrm(dependent~TP+canopy+substrate+conduct+TN+current+doy+pH,
  data=clad.spir.pres,x=TRUE,y=TRUE)
resid(pres.global,type="gof")
}
```

```
global(clad.pres)

# Model Comparison Function for logistic regression models
        # Outputs AIC table and individual summary results of coefficients and standard errors
model_comp <- function(dependent){
# Fit models
p.constant<-glm(dependent~1,family=binomial(link=logit),data=clad.spir.pres) #constant model
p1<-glm(dependent~canopy,family=binomial(link=logit),data=clad.spir.pres)
p2<-glm(dependent~substrate,family=binomial(link=logit),data=clad.spir.pres)
p3<-glm(dependent~TP,family=binomial(link=logit),data=clad.spir.pres)
p4<-glm(dependent~TN,family=binomial(link=logit),data=clad.spir.pres)
p5<-glm(dependent~current,family=binomial(link=logit),data=clad.spir.pres)
p6<-glm(dependent~doy,family=binomial(link=logit),data=clad.spir.pres)
p7<-glm(dependent~conduct,family=binomial(link=logit),data=clad.spir.pres)
p8<-glm(dependent~pH,family=binomial(link=logit),data=clad.spir.pres)
p10<-glm(dependent~canopy+TN,family=binomial(link=logit),data=clad.spir.pres)
p11<-glm(dependent~canopy+TP,family=binomial(link=logit),data=clad.spir.pres)
p12<-glm(dependent~canopy+substrate,family=binomial(link=logit),data=clad.spir.pres)
p13<-glm(dependent~canopy+current,family=binomial(link=logit),data=clad.spir.pres)
p14<-glm(dependent~canopy+doy,family=binomial(link=logit),data=clad.spir.pres)
p15<-glm(dependent~canopy+conduct,family=binomial(link=logit),data=clad.spir.pres)
p16<-glm(dependent~TP+substrate,family=binomial(link=logit),data=clad.spir.pres)
p17<-glm(dependent~TP+conduct,family=binomial(link=logit),data=clad.spir.pres)
p18<-glm(dependent~TP+current,family=binomial(link=logit),data=clad.spir.pres)
p19<-glm(dependent~TP+TN,family=binomial(link=logit),data=clad.spir.pres)
p20<-glm(dependent~current+conduct,family=binomial(link=logit),data=clad.spir.pres)

p21<-glm(dependent~canopy+substrate+current,family=binomial(link=logit),
        data=clad.spir.pres)
p22<-glm(dependent~canopy+TP+TN,family=binomial(link=logit),data=clad.spir.pres)
p23<-glm(dependent~canopy+TP+current,family=binomial(link=logit),data=clad.spir.pres)
p24<-glm(dependent~canopy+TP+substrate,family=binomial(link=logit),data=clad.spir.pres)
```

```
p25<-glm(dependent~canopy+substrate+doy,family=binomial(link=logit),data=clad.spir.pres)
p26<-glm(dependent~TP+TN+current,family=binomial(link=logit),data=clad.spir.pres)
p27<-glm(dependent~TP+TN+doy,family=binomial(link=logit),data=clad.spir.pres)
p28<-glm(dependent~TP+TN+current+substrate,family=binomial(link=logit),
        data=clad.spir.pres)
p29<-glm(dependent~canopy+TP+current+substrate,family=binomial(link=logit),
        data=clad.spir.pres)
p37<-glm(dependent~TP+canopy+substrate+conduct,family=binomial(link=logit),
        data=clad.spir.pres)
p39<-glm(dependent~TP+canopy+current+conduct,family=binomial(link=logit),
        data=clad.spir.pres)
p41<-glm(dependent~TN+canopy+TP+current,family=binomial(link=logit),data=clad.spir.pres)

#build AIC table using 199 as n, because there are 199 entries in the vector (199 samples)
print(AICtable(AIC(p.constant,p1,p2,p3,p4,p5,p6,p7,p8,p10,
p11,p12,p13,p14,p15,p16,p17,p18,p19,p20,
p21,p22,p23,p24,p25,p26,p27,p28,p29,p37,p39,p41),199))

# For multi-model inference, generate coefficient estimates and standard errors
print("Model Constant");print(summary(p.constant)$call);
        print(summary(p.constant)$coef[1,1:2])
print("p1");print(summary(p1)$call); print(summary(p1)$coef[1:2,1:2])
print("p2");print(summary(p2)$call); print(summary(p2)$coef[1:2,1:2])
print("p3");print(summary(p3)$call); print(summary(p3)$coef[1:2,1:2])
print("p4");print(summary(p4)$call); print(summary(p4)$coef[1:2,1:2])
print("p5");print(summary(p5)$call); print(summary(p5)$coef[1:2,1:2])
print("p6");print(summary(p6)$call); print(summary(p6)$coef[1:2,1:2])
print("p7");print(summary(p7)$call); print(summary(p7)$coef[1:2,1:2])
print("p8");print(summary(p8)$call); print(summary(p8)$coef[1:2,1:2])
print("p10");print(summary(p10)$call); print(summary(p10)$coef[1:2,1:2])
print("p11");print(summary(p11)$call); print(summary(p11)$coef[1:2,1:2])
print("p12");print(summary(p12)$call); print(summary(p12)$coef[1:2,1:2])
```

```
print("p13");print(summary(p13)$call); print(summary(p13)$coef[1:2,1:2])
print("p14");print(summary(p14)$call); print(summary(p14)$coef[1:2,1:2])
print("p15");print(summary(p15)$call); print(summary(p15)$coef[1:2,1:2])
print("p16");print(summary(p16)$call); print(summary(p16)$coef[1:2,1:2])
print("p17");print(summary(p17)$call); print(summary(p17)$coef[1:2,1:2])
print("p18");print(summary(p18)$call); print(summary(p18)$coef[1:2,1:2])
print("p19");print(summary(p19)$call); print(summary(p19)$coef[1:2,1:2])
print("p20");print(summary(p20)$call); print(summary(p20)$coef[1:2,1:2])
print("p21");print(summary(p21)$call); print(summary(p21)$coef[1:2,1:2])
print("p22");print(summary(p22)$call); print(summary(p22)$coef[1:2,1:2])
print("p23");print(summary(p23)$call); print(summary(p23)$coef[1:2,1:2])
print("p24");print(summary(p24)$call); print(summary(p24)$coef[1:2,1:2])
print("p25");print(summary(p25)$call); print(summary(p25)$coef[1:2,1:2])
print("p26");print(summary(p26)$call); print(summary(p26)$coef[1:2,1:2])
print("p27");print(summary(p27)$call); print(summary(p27)$coef[1:2,1:2])
print("p28");print(summary(p28)$call); print(summary(p28)$coef[1:2,1:2])
print("p29");print(summary(p29)$call); print(summary(p29)$coef[1:2,1:2])
print("p37");print(summary(p37)$call); print(summary(p37)$coef[1:2,1:2])
print("p39");print(summary(p39)$call); print(summary(p39)$coef[,1:2])
print("p41");print(summary(p41)$call); print(summary(p41)$coef[,1])
}
model_comp(clad.pres)
########################END OF GENERIC FUNCTIONS#########################
```

#The following is the code I used for *Cladophora* sp. (clad). It was repeated for every taxon. To save space I omitted duplicate code for the other taxa from the appendices.

```
#Check logistic regression global model fit using Le Cessie-van Houwelingen goodness-of-fit
    #test
clad.pres.global<-lrm(clad.pres~TP+canopy+substrate+conduct+TN+current+doy+pH,
    data=clad.spir.pres,x=TRUE,y=TRUE)
resid(clad.pres.global,type="gof")
```

```
# Fit logistic regression models using glm (32 models)
clad.p.constant<-glm(clad.pres~1,family=binomial(link=logit),data=clad.spir.pres)
clad.p1<-glm(clad.pres~canopy,family=binomial(link=logit),data=clad.spir.pres)
clad.p2<-glm(clad.pres~substrate,family=binomial(link=logit),data=clad.spir.pres)
clad.p3<-glm(clad.pres~TP,family=binomial(link=logit),data=clad.spir.pres)
clad.p4<-glm(clad.pres~TN,family=binomial(link=logit),data=clad.spir.pres)
clad.p5<-glm(clad.pres~current,family=binomial(link=logit),data=clad.spir.pres)
clad.p6<-glm(clad.pres~doy,family=binomial(link=logit),data=clad.spir.pres)
clad.p7<-glm(clad.pres~conduct,family=binomial(link=logit),data=clad.spir.pres)
clad.p8<-glm(clad.pres~pH,family=binomial(link=logit),data=clad.spir.pres)
clad.p10<-glm(clad.pres~canopy+TN,family=binomial(link=logit),data=clad.spir.pres)
clad.p11<-glm(clad.pres~canopy+TP,family=binomial(link=logit),data=clad.spir.pres)
clad.p12<-glm(clad.pres~canopy+substrate,family=binomial(link=logit),data=clad.spir.pres)
clad.p13<-glm(clad.pres~canopy+current,family=binomial(link=logit),data=clad.spir.pres)
clad.p14<-glm(clad.pres~canopy+doy,family=binomial(link=logit),data=clad.spir.pres)
clad.p15<-glm(clad.pres~canopy+conduct,family=binomial(link=logit),data=clad.spir.pres)
clad.p16<-glm(clad.pres~TP+substrate,family=binomial(link=logit),data=clad.spir.pres)
clad.p17<-glm(clad.pres~TP+conduct,family=binomial(link=logit),data=clad.spir.pres)
clad.p18<-glm(clad.pres~TP+current,family=binomial(link=logit),data=clad.spir.pres)
clad.p19<-glm(clad.pres~TP+TN,family=binomial(link=logit),data=clad.spir.pres)
clad.p20<-glm(clad.pres~current+conduct,family=binomial(link=logit),data=clad.spir.pres)
clad.p21<-glm(clad.pres~canopy+substrate+current,family=binomial(link=logit),
      data=clad.spir.pres)
clad.p22<-glm(clad.pres~canopy+TP+TN,family=binomial(link=logit),data=clad.spir.pres)
clad.p23<-glm(clad.pres~canopy+TP+current,family=binomial(link=logit),data=clad.spir.pres)
clad.p24<-glm(clad.pres~canopy+TP+substrate,family=binomial(link=logit),data=clad.spir.pres)
clad.p25<-glm(clad.pres~canopy+substrate+doy,family=binomial(link=logit),
      data=clad.spir.pres)
clad.p26<-glm(clad.pres~TP+TN+current,family=binomial(link=logit),data=clad.spir.pres)
clad.p27<-glm(clad.pres~TP+TN+doy,family=binomial(link=logit),data=clad.spir.pres)
clad.p28<-glm(clad.pres~TP+TN+current+substrate,family=binomial(link=logit),
      data=clad.spir.pres)
```

```
clad.p29<-glm(clad.pres~canopy+TP+current+substrate,family=binomial(link=logit),
        data=clad.spir.pres)
clad.p37<-glm(clad.pres~TP+canopy+substrate+conduct,family=binomial(link=logit),
        data=clad.spir.pres)
clad.p39<-glm(clad.pres~TP+canopy+current+conduct,family=binomial(link=logit),
        data=clad.spir.pres)
clad.p41<-glm(clad.pres~TN+canopy+TP+current,family=binomial(link=logit),
        data=clad.spir.pres)

#Model comparison using AIC
AICtable(AIC(clad.p.constant,clad.p1,clad.p2,clad.p3,clad.p4,clad.p5,clad.p6,clad.p7,clad.p8,
        clad.p10,clad.p11,clad.p12,clad.p13,clad.p14,clad.p15,clad.p16,clad.p17,clad.p18,
        clad.p19,clad.p20,clad.p21,clad.p22,clad.p23,clad.p24,clad.p25,clad.p26,clad.p27,
        clad.p28,clad.p29,clad.p37,clad.p39,clad.p41),199)

# Recalculate AIC table for 90% confidence set on models
AICtable(AIC(clad.p12,clad.p21,clad.p24,clad.p25,clad.p29,clad.p37),199)

# Generate coefficient estimates for multi-model inference (computed in Excel) using 90%
        #confidence set
summary(clad.p12)
summary(clad.p21)
summary(clad.p24)
summary(clad.p25)
summary(clad.p29)
summary(clad.p37)

# Standardize variables in order to compare them
std<-function(x){
(x-mean(x))/sd(x)
}
#Standardize the predictors
```

```
canopys<-std(canopy)
TPs<-std(TP)
currents<-std(current)
substrates<-std(substrate)
doys<-std(doy)
TNs<-std(TN)
conducts<-std(conduct)
pHs<-std(pH)

# Run 90% confidence set models with standardized variables
clad.p12s<-glm(clad.pres~canopys+substrates,family=binomial(link=logit),data=clad.spir.pres)
clad.p21s<-glm(clad.pres~canopys+substrates+currents,family=binomial(link=logit),
        data=clad.spir.pres)
clad.p24s<-glm(clad.pres~canopys+TPs+substrates,family=binomial(link=logit),
        data=clad.spir.pres)
clad.p25s<-glm(clad.pres~canopys+substrates+doys,family=binomial(link=logit),
        data=clad.spir.pres)
clad.p29s<-glm(clad.pres~canopys+TPs+currents+substrates,family=binomial(link=logit),
        data=clad.spir.pres)
clad.p37s<-glm(clad.pres~TPs+canopys+substrates+conducts,family=binomial(link=logit),
        data=clad.spir.pres)

#Generate standardized coefficients
summary(clad.p12s)
summary(clad.p21s)
summary(clad.p24s)
summary(clad.p25s)
summary(clad.p29s)
summary(clad.p37s)

# Calculate ROC and AUC for model-averaged logistic model
clad.p.predict<-1/(1+exp(-(0.422104277311041+(-0.017205506657328)*canopy+
```

```
        (-0.000986857940783)*TP+(0.000047650482698)*conduct+(0.026471044226824)*
        substrate+(0.0115082554485)*current+(-0.00081811866024)*doy)))
roc.area(clad.pres,clad.p.predict)

# Logistic regression figure
# Plot single predictor holding everything else at mean
windows(7,3.75)
par(mfrow=c(1,2))  #sets graphics window  c(rows,columns)
substratex<-seq(0,100,.1)
clad.substrate<-1/(1+exp(-(0.422104277311041+(0.026471044226824)*substratex+
        (-0.017205506657328)*mean(canopy)+(-0.000986857940783)*mean(TP)+
        (0.000047650482698)*mean(conduct)+(0.0115082554485)*mean(current)+
        (-0.00081811866024)*mean(doy))))

canopyx<-seq(0,100,.1)
clad.canopy<-1/(1+exp(-(0.422104277311041+(-0.017205506657328)*canopyx+
        (-0.000986857940783)*mean(TP)+(0.000047650482698)*mean(conduct)+
        (0.026471044226824)*mean(substrate)+(0.0115082554485)*mean(current)+
        (-0.00081811866024)*mean(doy))))

par(mar=c(4.5,4.1,1,0))
plot(substratex,clad.substrate,type="l",ylim=c(0,1.0),axes=FALSE,cex.lab=.9,
        xlab="Substrate (% hard)",
        ylab=expression(paste("Probability of"," ",italic("Cladophora")," spp. ","presence")))
points(substrate,clad.pres,pch="|",cex=.9)
axis(1,at=c(0,20,40,60,80,100),lab=c("0","20","40","60","80","100"),cex.axis=.8)
axis(2,las=1,at=c(0,0.2,0.4,0.6,0.8,1.0),lab=expression("0.0","0.2","0.4","0.6","0.8","1.0"),
        cex.axis=.8)
box()

par(mar=c(4.5,2.8,1,1))
plot(canopyx,clad.canopy,type="l",ylim=c(0,1.0),axes=FALSE,cex.lab=.9,
```

```
        xlab="Canopy (% cover)",
        ylab="")
points(canopy,clad.pres,pch="|",cex=.9)
axis(1,at=c(0,20,40,60,80,100),lab=c("0","20","40","60","80","100"),cex.axis=.8)
axis(2,las=1,at=c(0,0.2,0.4,0.6,0.8,1.0),lab=expression("0.0","0.2","0.4","0.6","0.8","1.0"),
        cex.axis=.8)
box()

#############################################################################
# Part 2: Linear regression on abundance given presence of Cladophora
#Import data
clad.abundance<-read.csv(file.choose())
attach(clad.abundance)

#Log transformation of response variable
clad.abunl<-log(clad.abun)
#Check fit of global log-normal regression model using r-squared value
clad.a.global<-lm(clad.abunl~TP+canopy+TP*canopy+substrate+conduct+TN+TN*canopy+
        current+doy,data=clad.abundance)
summary(clad.a.global)

# Fit log-normal models using glm (25 models)
clad.a.constant<-glm(clad.abunl~1,family=gaussian,data=clad.abundance)
clad.a1<-glm(clad.abunl~canopy,family=gaussian,data=clad.abundance)
clad.a2<-glm(clad.abunl~substrate,family=gaussian,data=clad.abundance)
clad.a3<-glm(clad.abunl~TP,family=gaussian,data=clad.abundance)
clad.a4<-glm(clad.abunl~TN,family=gaussian,data=clad.abundance)
clad.a5<-glm(clad.abunl~current,family=gaussian,data=clad.abundance)
clad.a6<-glm(clad.abunl~doy,family=gaussian,data=clad.abundance)
clad.a7<-glm(clad.abunl~conduct,family=gaussian,data=clad.abundance)
clad.a10<-glm(clad.abunl~canopy+TN,family=gaussian,data=clad.abundance)
clad.a11<-glm(clad.abunl~canopy+TP,family=gaussian,data=clad.abundance)
```

```
clad.a12<-glm(clad.abunl~canopy+substrate,family=gaussian,data=clad.abundance)
clad.a13<-glm(clad.abunl~canopy+current,family=gaussian,data=clad.abundance)
clad.a14<-glm(clad.abunl~canopy+doy,family=gaussian,data=clad.abundance)
clad.a15<-glm(clad.abunl~canopy+conduct,family=gaussian,data=clad.abundance)
clad.a16<-glm(clad.abunl~TP+conduct,family=gaussian,data=clad.abundance)
clad.a17<-glm(clad.abunl~TP+current,family=gaussian,data=clad.abundance)
clad.a18<-glm(clad.abunl~TP+TN,family=gaussian,data=clad.abundance)
clad.a21<-glm(clad.abunl~canopy+TP+TN,family=gaussian,data=clad.abundance)
clad.a22<-glm(clad.abunl~canopy+TP+current,family=gaussian,data=clad.abundance)
clad.a23<-glm(clad.abunl~canopy+TP+substrate,family=gaussian,data=clad.abundance)
clad.a24<-glm(clad.abunl~canopy+substrate+doy,family=gaussian,data=clad.abundance)
clad.a25<-glm(clad.abunl~TP+TN+current,family=gaussian,data=clad.abundance)
clad.a27<-glm(clad.abunl~TP+TN+current+substrate,family=gaussian,data=clad.abundance)
clad.a28<-glm(clad.abunl~canopy+TP+current+substrate,family=gaussian,data=clad.abundance)
clad.a40<-glm(clad.abunl~TN+canopy+TN*canopy+TP+TP*canopy+current,
        family=gaussian,data=clad.abundance)

#Model comparison using AIC
AICtable(AIC(clad.a.constant,clad.a1,clad.a2,clad.a3,clad.a4,clad.a5,clad.a6,clad.a7,clad.a10,
        clad.a11,clad.a12,clad.a13,clad.a14,clad.a15,clad.a16,clad.a17,clad.a18,clad.a21,
        clad.a22,clad.a23,clad.a24,clad.a25,clad.a27,clad.a28,clad.a40),128)

# Recalculate AIC table for 90% confidence set on models
AICtable(AIC(clad.a1,clad.a10,clad.a11,clad.a12,clad.a13,clad.a14,clad.a15, clad.a21,
        clad.a23,clad.a24),128)

# Generate coefficient estimates for multi-model inference (computed in Excel) using 90%
        #confidence set
summary(clad.a1)
summary(clad.a10)
summary(clad.a11)
summary(clad.a12)
```

```
summary(clad.a13)
summary(clad.a14)
summary(clad.a15)
summary(clad.a21)
summary(clad.a23)
summary(clad.a24)

# Run 90% confidence set models with standardized variables
clad.a1s<-glm(clad.abunl~canopys,family=gaussian,data=clad.abundance)
clad.a10s<-glm(clad.abunl~canopys+TNs,family=gaussian,data=clad.abundance)
clad.a11s<-glm(clad.abunl~canopys+TPs,family=gaussian,data=clad.abundance)
clad.a12s<-glm(clad.pres~canopys+substrates,family=gaussian,data=clad.abundance)
clad.a13s<-glm(clad.pres~canopys+currents,family=gaussian,data=clad.abundance)
clad.a14s<-glm(clad.pres~canopys+doys,family=gaussian,data=clad.abundance)
clad.a15s<-glm(clad.pres~canopys+conducts,family=gaussian,data=clad.abundance)
clad.a21s<-glm(clad.abunl~canopys+TPs+TNs,family=gaussian,data=clad.abundance)
clad.a23s<-glm(clad.abunl~canopys+TPs+substrates,family=gaussian,data=clad.abundance)
clad.a24s<-glm(clad.abunl~canopys+substrates+doys,family=gaussian,data=clad.abundance)

#Generate standardized coefficients
summary(clad.a1s)
summary(clad.a10s)
summary(clad.a11s)
summary(clad.a12s)
summary(clad.a13s)
summary(clad.a14s)
summary(clad.a15s)
summary(clad.a21s)
summary(clad.a23s)
summary(clad.a24s)

# Log-normal regression figure
```

```
# Plot single predictor holding everything else at mean
windows(4.75,4.5)
par(mar=c(4.5,4,2.1,2.1),oma=c(0,1,0,0))
canopyx<-seq(0,100,.1)
clad.canopy<-exp(12.3638467778668+(-0.019217412857278)*canopyx+
        (0.00023714638007)*mean(TP)+(-0.01456629536505)*mean(TN)+
        (0.00546490693841)*mean(substrate)+(-0.000041822682345)*
        mean(current)+(-0.00149531719361)*mean(doy)+(0.000051201279694)*
        mean(conduct))
plot(canopyx,clad.canopy,type="l",ylim=c(0,300000),axes=FALSE,cex.lab=.9,xlab="Canopy
        (% cover)",
ylab=expression(paste(italic("Cladophora")," abundance given presence x 10"^{5},"
        (",mu,"m"^{3}," mm"^{-2},")")))
axis(1,at=c(0,20,40,60,80,100),lab=c("0","20","40","60","80","100"),cex.axis=.8)
axis(2,las=1,at=c(0,50000,100000,150000,200000,250000,300000),lab=expression("0","0.5","1.
        0","1.5","2.0","2.5","3.0"),cex.axis=.8)
box()
##########################################################################
# Two-part conditional model prediction of Cladophora abundance
clad.pres.abun<-read.csv(file.choose())
attach(clad.pres.abun)
str(clad.pres.abun)

#Model-averaged presence-absence model
clad.p.predict<-1/(1+exp(-(0.422104277311041+(-0.017205506657328)*canopy+
        (-0.000986857940783)*TP+(0.000047650482698)*conduct+(0.026471044226824)*
        substrate+(0.0115082554485)*current+(-0.00081811866024)*doy)))

#Model-averaged abundance given presence model
clad.a.predict<-exp(12.3638467778668+(-0.019217412857278)*canopy+
        (0.00023714638007)*TP+(-0.01456629536505)*TN+(0.00546490693841)*substrate+
        (-0.000041822682345)*current+(-0.00149531719361)*doy+
        (0.000051201279694)*conduct)
```

```
#Combined model
clad.predict<-clad.p.predict*clad.a.predict

# Mean absolute error of combined model
mae<-mean(abs(clad.predict-clad.abun))

# One-to-one plot of predicted vs. observed
windows(4.25,4.75)
plot(clad.abun+.01, clad.predict+.01,
     ylim=c(.01,100000000),xlim=c(.01,100000000),log="xy",axes=FALSE,pch=20,cex.lab=
     .8,xlab=expression(paste("Observed abundance of"," ",italic("Cladophora"),"
     ","(",mu,"m"^{3},"  mm"^{-2},")")),
ylab=expression(paste("Predicted abundance of"," ",italic("Cladophora")," ","(",mu,"m"^{3},"
     mm"^{-2},")")))
axis(1,at=c(.01,10,10000,10000000),lab=expression("0","10","1x10"^"4","1x10"^"7"),cex.axis=.
     75)
axis(2,las=1,at=c(.01,10,10000,10000000),lab=expression("0","10","1x10"^"4","1x10"^"7"),cex.
     axis=.75)
x<-seq(.01,100000000,500)
y<-seq(.01,100000000,500)
lines(x,y)
box()
##########################################################################
# SPIROGYRA
# see Cladophora for logistic and linear model comparison code

# Calculate ROC and AUC for model-averaged model
spir.p.predict<-1/(1+exp(-(1.56949500465139+(-0.02741796228227)*canopy+
     (-0.002744303208259)*TP+(-0.01706527496334)*TN+(0.002315035574074)*
     substrate+(-0.01226763273631)*current+(-0.00086352140142)*doy+
     (-0.000062119914244)*conduct)))
roc.area(spir.pres,spir.p.predict)
```

```
# Logistic regression figure
# Plot single predictors holding everything else at mean
windows(7,3.75)
par(mfrow=c(1,2))
canopyx<-seq(0,100,.1)
spir.canopy<-1/(1+exp(-(1.56949500465139+(-0.02741796228227)*canopyx+
        (-0.002744303208259)*mean(TP)+(-0.01706527496334)*mean(TN)+
        (0.002315035574074)*mean(substrate)+(-0.01226763273631)*mean(current)+
        (-0.00086352140142)*mean(doy)+(-0.000062119914244)*mean(conduct))))
par(mar=c(4.5,4.1,1,0))
plot(canopyx,spir.canopy,type="l",ylim=c(0,1.0),axes=FALSE,cex.lab=.9,xlab="Canopy (%
        cover)",
ylab=expression(paste("Probability of"," ",italic("Spirogyra")," spp. ","presence"))) #italicize
        name only
points(canopy,spir.pres,pch="|",cex=.9)
axis(1,at=c(0,20,40,60,80,100),lab=c("0","20","40","60","80","100"),cex.axis=.8)
axis(2,las=1,at=c(0,0.2,0.4,0.6,0.8,1.0),lab=expression("0.0","0.2","0.4","0.6","0.8","1.0"),cex.ax
        is=.8) #make axis label horizontally oriented
box()


TPx<-seq(0,1000,1)
spir.TP<-1/(1+exp(-(1.56949500465139+(-0.02741796228227)*mean(canopy)+
        (-0.002744303208259)*TPx+(-0.01706527496334)*mean(TN)+(0.002315035574074)*
        mean(substrate)+(-0.01226763273631)*mean(current)+
        (-0.00086352140142)*mean(doy)+(-0.000062119914244)*mean(conduct))))
par(mar=c(4.5,2.8,1,1))
plot(TPx,spir.TP,type="l",ylim=c(0,1.0),axes=FALSE,cex.lab=.9, xlab=expression(paste("Total
        phosphorus (",mu,"g"," l"^{-1},")")),
ylab="")
points(TP,spir.pres,pch="|",cex=.9)
axis(1,at=c(0,100,200,300,400,500,600),lab=c("0","100","200","300","400","500","600"),cex.ax
        is=.8)
axis(2,las=1,at=c(0,0.2,0.4,0.6,0.8,1.0),lab=expression("0.0","0.2","0.4","0.6","0.8","1.0"),cex.ax
        is=.8) #make axis label horizontally oriented
```

```
box()

axis(1,at=c(0,200,400,600,800,1000),lab=c("0","200","400","600","800","1000"),cex.axis=.8)
axis(2,las=1,at=c(0,0.2,0.4,0.6,0.8,1.0),lab=expression("0.0","0.2","0.4","0.6","0.8","1.0"),cex.ax
        is=.8) #make axis label horizontally oriented
box()
#############################################################################
# ULVA
# see Cladophora for logistic model comparison code

# Calculate ROC and AUC for model averaged model
ulva.p.predict<-1/(1+exp(-(-0.853482823188888+(-0.02948766276049)*canopy+
        (0.00093030442531)*conduct+(-0.00172361467391)*TP+(0.01976228314314)*TN+
        (-0.00039184840596)*substrate+(0.00168990249961)*current)))
roc.area(ulva.pres,ulva.p.predict)

# Logistic regression figure
# Plot single predictors holding everything else at mean
windows(7,3.75)
par(mfrow=c(1,2))
canopyx<-seq(0,100,.1)
ulva.canopy<-1/(1+exp(-(-0.853482823188888+
        (-0.02948766276049)*canopyx+(0.00093030442531)*mean(conduct)+
        (-0.00172361467391)*mean(TP)+(0.01976228314314)*mean(TN)+
        (-0.00039184840596)*mean(substrate)+(0.00168990249961)*mean(current))))
par(mar=c(4.5,4.1,1,0))
plot(canopyx,ulva.canopy,type="l",ylim=c(0,1.0),axes=FALSE,cex.lab=.9,xlab="Canopy (%
        cover)",
ylab=expression(paste("Probability of"," ",italic("Ulva")," spp. ","presence")))    #italicize name
points(canopy,ulva.pres,pch="|",cex=.9)
axis(1,at=c(0,20,40,60,80,100),lab=c("0","20","40","60","80","100"),cex.axis=.8)
axis(2,las=1,at=c(0,0.2,0.4,0.6,0.8,1.0),lab=expression("0.0","0.2","0.4","0.6","0.8","1.0"),cex.ax
        is=.8)
```

```
box()

conductx<-seq(0,6000,.1)
ulva.conduct<-1/(1+exp(-(-0.853482823188888+(0.00093030442531)*conductx+
        (-0.02948766276049)*mean(canopy)+(-0.00172361467391)*mean(TP)+
        (0.01976228314314)*mean(TN)+(-0.00039184840596)*mean(substrate)+
        (0.00168990249961)*mean(current))))
par(mar=c(4.5,2.8,1,1))
plot(conductx,ulva.conduct,type="l",ylim=c(0,1.0),axes=FALSE,cex.lab=.9,
        xlab=expression(paste("Specific conductance (mS","/" cm"^{-1},")")),
        ylab="")
points(conduct,ulva.pres,pch="|",cex=.9)
axis(1,at=c(0,1000,2000,3000,4000,5000,6000),lab=c("0","1.0","2.0","3.0","4.0","5.0","6.0"),ce
        x.axis=.8)
axis(2,las=1,at=c(0,0.2,0.4,0.6,0.8,1.0),lab=expression("0.0","0.2","0.4","0.6","0.8","1.0"),cex.ax
        is=.8) #make axis label horizontally oriented
box()

#############################################################################
# VAUCHERIA
# see Cladophora for logistic model comparison code

#############################################################################
# Wilcox nonparametric test for Dissolved Oxygen analysis
clad.spir.pres<-read.csv(file.choose())
attach(clad.spir.pres)
wilcox.test(do~clad.pres,data=clad.spir.pres)
wilcox.test(do~spir.pres,data=clad.spir.pres)

vauc.ulva.pres<-read.csv(file.choose())
attach(vauc.ulva.pres)
wilcox.test(do~ulva.pres,data=vauc.ulva.pres)
wilcox.test(do~vauc.pres,data=vauc.ulva.pres)
```

```
# Boxplot of Cladophora and Ulva presence and DO
windows(7,5)
par(mfrow=c(1,2))
par(mar=c(4.5,4.1,1,0))
boxplot(do~clad.pres,data=clad.pres.do,names=c("Absence","Presence"),axes=F,cex.axis=.75,
        cex.lab=.8,xlab=expression(paste(italic("Cladophora"))),ylab="Dissolved oxygen
        (% saturation)")
axis(1,at=c(1,2),lab=c("Absence","Presence"),cex.axis=.75,cex.lab=.8)
axis(2,las=1,at=c(0,25,50,75,100,125,150,175),lab=c("0","25","50","75","100","125","150","175
        "),cex.axis=.75 )
box()
par(mar=c(4.5,2.8,1,1))
boxplot(do~ulva.pres,data=ulva.pres.do,names=c("Absence","Presence"),axes=F,cex.axis=.75,ce
        x.lab=.8,xlab=expression(paste(italic("Ulva"))))
axis(1,at=c(1,2),lab=c("Absence","Presence"),cex.axis=.75,cex.lab=.8)
axis(2,las=1,at=c(0,25,50,75,100,125,150,175),lab=c("0","25","50","75","100","125","150","175
        "),cex.axis=.75 )
box()


#Correlation test on DO and canopy cover
clad.spir.pres<-read.csv(file.choose())
attach(clad.spir.pres)
cor.test(do,canopy,method="spearman",use="complete.obs",data=clad.spir.pres)
##############################################################################
# Figure
# histograms showing distribution of nutrient concentrations
windows(5.5,7)
par(mfrow=c(2,1))
par(mar=c(4.5,4.1,1,.5))
hist(TN,nclass=40,xlab=expression(paste("Total nitrogen (mg"," l"^{-
        1},")")),xlim=c(0,40),main=c(""),col="grey",ylim=c(0,200),axes=FALSE,cex.lab=.9)
axis(1,at=c(0,10,20,30,40),lab=c("0","10","20","30","40"),cex.axis=.8)
```

```
axis(2,las=1,at=c(0,50,100,150,200),lab=expression("0","50","100","150","200"),cex.axis=.8)
        #make axis label horizontally oriented

box()

par(mar=c(4.5,4.1,0,.5))

hist(TP,nclass=40,xlab=expression(paste("Total phosphorus (",mu,"g"," l"^{-
        1},")")),xlim=c(0,3000),main=c(""),col="grey",ylim=c(0,80),axes=FALSE,cex.lab=.9)

axis(1,at=c(0,500,1000,1500,2000,2500,3000),lab=c("0","500","1000","1500","2000","2500","3
        000"),cex.axis=.8)

axis(2,las=1,at=c(0,25,50,75),lab=expression("0","25","50","75"),cex.axis=.8) #make axis label
        horizontally oriented

box()
```