Nutrient dynamics and macroalgal blooms: A comparison of five southern California estuaries

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ABSTRACT - Macroalgal blooms are a common ecological problem in estuaries worldwide and often occur in response to increased nutrient loading from developed watersheds. Although macroalgae are common in southern California estuaries, local estuaries are relatively understudied, particularly with regard to nutrients. The unique characteristics of the southern California region warrant a regional investigation of estuarine nutrient-macroalgal relationships. The objective of this study was to determine the degree of similarity in spatial and temporal patterns of water column nitrogen (N) concentrations and macroalgal abundance in five southern California estuaries: Carpinteria Salt Marsh Reserve (CSMR), Mugu Lagoon (Mugu West and Mugu Calleguas Creek (Mugu CC)), Upper Newport Bay (UNB), Los Penasquitos Lagoon (LPL), and Tijuana River Estuary (TJ). These estuaries span a latitudinal gradient from San Diego to Santa Barbara and represent a range of estuarine area, watershed size, and dominant land use practices. Estuaries also differed in physical structure from having straight, narrow channels with high tidal flushing to having broad, flat benches with restricted flow and muted tidal flushing. Several consistencies found were higher water column N concentrations at the heads of systems (up to 2000 μM), and increased N availability during wet-season sampling events, probably due to precipitation. However, the dominant form of N changed among systems from NO_3 to NH_4 to dissolved organic N (DON). Spatial and temporal patterns in water column nutrients and salinity suggest that watersheds were important nutrient sources. Additionally, the proximity of specific land use practices, such as agriculture, to estuaries may have had significant impacts on water quality. *Enteromorpha* was found in each system and *Ulva* was found in four study areas. Macroalgal abundance ranged from <300 to >2,000 g wet wt m^{-2}. The time of year when abundance was greatest varied from system to system and even within a system from one site to another. However, no clear, consistent relationships were found between water column N and macroalgal abundance; likely, the physical characteristics of each estuary mitigated the response of macroalgal abundance to nutrient availability. Macroalgae proliferated in nutrient-rich areas with suitable habitat, such as broad mudflats and high light availability, and were less abundant in areas with increased tidal flushing, which may have prevented the algae from accumulating.

INTRODUCTION

The increased occurrence of macroalgal blooms worldwide has been linked to increased N inputs resulting from anthropogenic activity in watersheds (Valiela *et al.* 1992, Nixon 1995, Paerl 1997). Although macroalgae are a natural component of these systems, their proliferation reduces habitat quality. Algal respiration and microbial decomposition may reduce dissolved oxygen content of estuarine waters (Sfriso *et al.* 1987, Peckol and Rivers 1995), negatively impacting fish and leading to mortality (Coon 1998). Extended periods of low oxygen may lead to changes in overall species composition, shifts in community structure, and loss of biodiversity (Raffaelli *et al.* 1991, Edgar *et al.* 2000, Bostrom *et al.* 2002). Consequently, understanding and controlling the factors that contribute to macroalgal blooms is important from both ecological and resource management perspectives.

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The links between watershed land use, estuarine water column nutrients, and resultant algal blooms in estuaries have been well studied along the Atlantic and Gulf coasts of the U.S. (Valiela *et al.* 1992, Peckol and Rivers 1995, Valiela *et al.* 1997). Studies have also been conducted in Europe (Raffaelli *et al.* 1989, Sfriso *et al.* 1992, Schramm 1999) and Australia (McComb and Lukatelich 1995). However, there is a general lack of data for Pacific coast estuaries (Bricker *et al.* 1999), particularly estuarine nutrient dynamics in southern California (Williams and Zedler 1992). Relative to the east coast of the U.S., southern California watersheds are small and extensively developed. The agricultural and urban land use may decrease nutrient retention capability compared to watersheds comprised of swamps and forests such as those on the Atlantic and Gulf coasts (Yarbro *et al.* 1984, Correll *et al.* 1992). Southern California is characterized by long, warm, and dry summers and short, cool, and wet winters with episodic rainfall. Historically, southern California estuaries functioned as marine embayments during the dry season (Onuf 1987), but current water use contributes to at least some freshwater flow year-round in many systems.

The green macroalgae *Enteromorpha* and *Ulva* appear to be abundant in many southern California estuaries (P. Fong, personal observation), yet have been quantified in only one system (Kamer *et al.* 2001). With only 10% of California's original wetlands remaining (Zedler 1996), it is critical to understand the processes structuring macroalgal communities, which can potentially negatively affect important fauna and biological and physical processes. The objectives of this study were (1) to relate patterns of nutrient availability to macroalgal abundance, in order to further an understanding of this relationship, and (2) to identify commonalities in estuaries in the unique southern California region. Thus, the study was conducted in five estuaries of various sizes with different land use practices in order to determine the degree of similarity of nutrients and macroalgae spatially and temporally between estuaries. Identification of any generalities in the nutrient-macroalgae relationship, as well as the influence of other environmental factors, will benefit the management of coastal watersheds.

METHODS

A 15-month survey was conducted to characterize nutrient dynamics and macroalgal blooms in five southern California estuaries (Figure 1). These estuaries constitute a latitudinal gradient across the southern California region and include a range of watershed sizes, land use practices (Table 1), freshwater influence, and tidal flushing rates. In order to make comparisons both within and among estuaries, three sites were chosen along a main channel of each estuary. General observations of tidal flushing were made at each study area. Precipitation data from October 2001 through January 2003 for each estuary were taken from U.S. National Oceanic and Atmospheric Administration (NOAA) weather stations closest to each estuary (Table 2).

Study Sites

Carpinteria Salt Marsh Reserve

Carpinteria Salt Marsh Reserve (CSMR), approximately 7 miles east of Santa Barbara, is the smallest of the five estuaries studied and is located in the smallest watershed, which is developed mainly by agriculture (Table 1). Two major streams enter the marsh, Santa Monica Creek and Franklin Creek (Page *et al.* 1995). Our sites were located on an artificially created channel west of Santa Monica Creek and its tributaries; portions of the tributaries drain into the channel. The upper channel drains the agricultural and urban development to the north. The mouth and middle sections of this channel are nar-

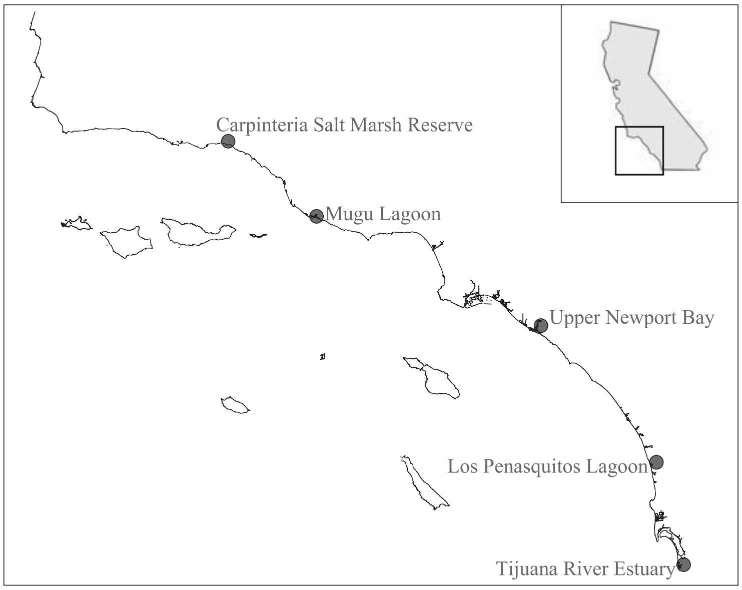

Figure 1. Location of the five study estuaries in southern California.

Table 1. General comparative information on estuary size, watershed size and land use. ND=no data.

Estuary	Size (ha)	Watershed Size (km^2)	Land Use (%)	Reference
Carpinteria Salt Marsh Reserve (34° 24' N, 119031'30"W)	93	283	72% Agriculture Remainder unknown	Page *et al.* 1995
Mugu Lagoon (34° 33'N, 117° 05'W)				
Mugu Lagoon-West	ND	ND	Agriculture and Duck Ponds	R. A. Cohen, unpub. data
Mugu Lagoon-Calleguas Creek	607	888	50% Open Space 26% Agriculture 24% Urban	California Regional Water Quality Control Board 2002
Upper Newport Bay	304	376	64% Urban 22% Open Space 12% Agriculture	Gerstenberg 1989
Los Penasquitos Lagoon (34° 24'N, 119°, 32'W)	154	246	50% Urban Remainder unknown	Ward *et al.* 2001
Tijuana River Estuary (34° 24.16N, 119° 32.00W)	720	4403	Unknown	ENTRIX *et al.* 1991

Table 2. Total cumulative precipitation recorded near each estuary. Santa Barbara-Carpinteria Salt Marsh Reserve; Ventura-Mugu Lagoon; Laguna Beach-Upper Newport Bay; Oceanside-Los Penasquitos Lagoon; San Diego-Tijuana River Estuary; ND=no data. Data generated from NOAA (2003).

	Total Cumulative Precipitation (inches)				
	Santa Barbara (CSMR)	Ventura (Mugu Lagoon)	Laguna Beach (UNB)	Oceanside (LPL)	San Diego (TJ)
2001					
Oct	0.62	0.01	0	0	0
Nov	4.24	5.81	1.61	1.09	0.95
Dec	2.23	3.8	1.35	1.14	0.7
Annual Total	**27.39**	**11.7**	**16.55**	**10.46**	**9.89**
2002					
Jan	1.03	7.29	0.3	0.41	0.52
Feb	0.46	5.44	0.3	0.38	0.17
Mar	0.4	ND	1.07	0.56	0.45
Apr	0.08	1.62	0.15	0.39	0.72
May	0.1	0.1	0.1	0	0.02
June	0.03	0	0.05	0	0
Jul	0	0.02	0	0	0
Aug	0	0.01	0.05	0	0
Sep	0.23	0	0	0.33	0.31
Oct	0.03	ND	0	0.09	0.19
Nov	6.82	1.54	1.54	1.17	0.58
Dec	6.15	2.84	2.84	2.01	2.31
Annual Total	**15.33**	**19.41**	**6.4**	**5.34**	**5.27**
2003					
Jan	0	0.02	0	0.2	0.04

row (3-6 m), shallow (1-2 m), and fairly straight, allowing tidal flushing to have strong impacts on the system.

Mugu Lagoon - (West and Calleguas Creek)

Mugu Lagoon is located within a Naval Base at Pt. Mugu, approximately 75 miles northwest of Los Angeles. For this study, the estuary was divided into two areas, Mugu Lagoon-West (Mugu West) and Mugu Lagoon-Calleguas Creek (Mugu CC), because each area has a different watershed and physical layout.

Mugu West, the western arm of Mugu Lagoon, drains the agricultural plains of Oxnard and adjacent duck ponds through a drainage canal (Table 1). The arm is approximately 1.5 miles long and consists of a broad (~150 m wide), shallow channel (<1 m). The upper area of the arm is highly impacted by roads and runways that interrupt the normal flow of tidal water (T. Keeney, personal communication). The lower portion is characterized by wide and gently sloping mudflats and a high salt marsh habitat border, resulting in muted tidal flushing.

Mugu CC is the second largest estuary in our study and comprises the central portion of Mugu Lagoon. Although large portions of this watershed are open space, agricultural development is immediately upstream of the estuary on the coastal plain (Table 1). Calleguas Creek, the main river flowing into the estuary, historically was dredged to 30 feet, Over time, it has filled to 15 to 20 feet by natural sedimentation from the river and the ocean inlet. In contrast to Mugu West, this system tends to be well flushed by tides (T. Keeney, personal communication).

Upper Newport Bay

Upper Newport Bay (UNB) is located 35 miles south of Los Angeles and is intermediate in size with a highly urbanized watershed (Table 1). San Diego Creek (SDC) and its major tributary drain 85% of the watershed and are the main freshwater inflow (Gerstenberg 1989). The main channel is wide with extensive broad mudflats and shallow banks; however, the center of the channel is dredged to 5 m below sea level for sediment retention purposes. UNB is separated from the Pacific Ocean by the Lower Bay, which has been dredged and developed into a marina with no natural area remaining. The Lower Bay acts as a buffer between the Pacific Ocean and the Upper Bay, muting tidal flushing.

Los Penasquitos Lagoon

Los Penasquitos Lagoon (LPL) is one of the smallest estuaries in this study (Table 1). The watershed is partially urbanized, but the rest of land use is unknown. Sampling sites were located along the inflow from Carmel Valley Creek; however, many creeks flow into the estuary. LPL is subject to periodic mouth closures due to sand accretion from longshore drift and storms. When the mouth is open, this system tends to be well flushed by tides.

Tijuana River Estuary

Tijuana River Estuary (TJ) is the largest estuary surveyed, with the largest watershed (Table 1). TJ is located at the U.S./Mexico international border. Most of the watershed is in Mexico and is highly urbanized just upstream. Freshwater from the Tijuana River flows year-round due to sewage discharge (BSI 1994).

Sampling was conducted along the main channel, which is wide (50-100 m), shallow (~1 m), and bordered by broad mudflats. Tidal flushing is vigorous, similar to portions of CSMR and in Mugu CC.

Sampling Protocols

In each estuary, three sampling sites were established along the main channel: at the head of the estuary where the major river enters, at the mouth of the estuary (or lower reach of the natural habitat), and mid-way between. Quarterly sampling began in December 2001 and continued through February 2003. LPL was not sampled in December 2001 due to mouth closure and the subsequent mechanical opening, which created transitory conditions.

At each site, water column salinity was measured with a handheld refractometer. Three water samples were collected for nutrient analysis and then placed in a dark cooler on ice. Upon return to the lab, samples were filtered (Whatman GF/C), frozen, and sent to the Department of Agriculture and Natural Resources Analytical Laboratory (DANR) at UC Davis where they were analyzed for NO_3 (NO_3 and NO_2), NH_4, and TKN (all forms of dissolved N except NO_3 and NO_2). NO_3 was reduced to NO_2 via cadmium reduction and measured spectrophotometrically after diazotation (Switala 1999, Wendt 1999). NH_4 was heated with solutions of salicylate and hypochlorite and determined spectrophotometrically (Switala 1999, Wendt 1999). TKN was determined by the wet oxidation of nitrogen using sulfuric acid and digestion catalyst. This procedure converts organic nitrogen to NH_4, which is subsequently determined (Carlson 1978). These automated methods have detection limits of 3.57 µM for all forms of N. DON was calculated by subtracting NH_4 from TKN.

At each site, intertidal macroalgal abundance was estimated by measuring algal biomass along a 30-m transect parallel to the waterline and 1 m downslope from the vascular vegetation. At five randomly chosen points along each transect, any algae present were collected from a 530.9 cm^2 area circumscribed by a plastic cylinder placed on the benthos. Each sample was placed in an individual bag in a cooler, transported to the laboratory, and refrigerated. Algal samples were transferred to low-nutrient seawater, where they were cleaned of macroscopic debris, mud, and animals. Samples then were sorted to species. For each sample, individual species were placed in a nylon mesh bag, spun in a salad spinner for 1 min, wet weighed, rinsed briefly in de-ionized water to remove salts, and dried at 60°C to a constant weight. Macroalgal biomass was normalized to area.

Statistical Analysis

Two-factor analysis of variance (ANOVA) was used to test for differences in water column NO_3, NH_4, and DON, and algal biomass within each estuary. ANOVA factors were site (head, middle, mouth) and season (December 2001; February, June, September, December 2002; and February 2003). Data were examined to determine if they complied with ANOVA assumptions of normality and equal variances. Unequal variances were corrected by transformations (Table 3). Mean values reported throughout the text were generated from untransformed data.

RESULTS

Carpinteria Salt Marsh Reserve

Salinity gradients occurred during all sampling periods (Table 4), with the lowest salinities at the head of the estuary, indicating some freshwater flow throughout the year. This gradient was strongest during the wet months (December 2001, February 2002, and February 2003) due to precipitation (Table 2).

Overall, NO_3 was the most abundant water column nutrient in CSMR (Figure 2). There were significant effects of site and season ($p<0.0001$ for both) as well as interaction ($p<0.0001$). Across all seasons, NO_3 concentrations were highest at the head and decreased down estuary, suggesting that the river was the primary NO_3 source. NO_3 concentrations were more than twice as high during the February 2002 sampling event compared to other rainy season samples. Precipitation in February 2002 was much less than in December 2001 or 2002 (Table 2), which may have caused nutrient inputs to be more concentrated.

NH_4 and DON concentrations were low relative to NO_3 across all sites and seasons (Figures 3 and 4). Maximum values for NH_4 and DON were each ~30µM compared to >1,000µM for NO_3, suggesting that NH_4 and DON may have been less important than NO_3 in overall nutrient availability. There were significant effects of site and season ($p<0.0001$ for both) on NH_4 as well as interaction ($p<0.0001$). There was a significant effect of site ($p=0.0485$) on DON and an interaction between site and season ($p=0.0022$).

Enteromorpha was the only green macroalga found at CSMR and was present at the head year-round. Biomass at the head was lowest in the dry months and highest in wet months (Figure 5). Maximum mean biomass (1760±452 g wet wt m^{-2}) occurred at the head in December 2001, though data were extremely variable. There were significant effects of site ($p<0.0001$) and season ($p=0.0065$) on algal biomass as well as interaction ($p=0.0008$).

Mugu Lagoon-Mugu West

Weak gradients in salinity occurred throughout the year, indicating the persistence of freshwater flow (Table 4). NO_3 was the most abundant water column nutrient in Mugu West (Figure 2) though levels overall were much less than those measured in CSMR. There were significant effects of site and season on NO_3 ($p<0.0001$ for both), as well as interaction ($p<0.0001$). Generally, NO_3 was highest at the head and decreased toward the mouth, suggesting that NO_3 originated from the watershed. At the middle and head, NO_3 concentrations appeared to decrease by more than half from December 2001 to the dry months of June and September 2002, and then increase again in December 2002 and February 2003.

Water column NH_4 and DON concentrations overall were relatively low and were usually less than NO_3 concentrations (Figures 3 and 4). There

Table 3. Transformations needed to correct for unequal variances.

ANALYSIS	SITE Carpinteria Salt Marsh Reserve	 Mugu Lagoon-West	 Mugu Lagoon-Calleguas Creek	 Upper Newport Bay	 Los Penasquitos Lagoon	 Tijuana River Estuary
Water						
NO_3	log (x+1)	log	-	square root	-	log
NH_4	log	-	log	-	log	log
TKN	log (x+1)	-	-	-	-	square root
Algae						
Biomass	log (x+1)	log $(x^{1/4})$	log (x+1)	log $(x^{1/4})$	log	log $(x^{1/4})$
% cover	log $(x^{1/4})$	log $(x^{1/4})$	log (x+1)	log (x+1)	-	log $(x^{1/4})$

Table 4. Water column salinity for each estuary. One measurement was taken at each site (Mouth, Middle, Head) during each sampling event. NS=not sampled.

	Sampling Event December 2001	 February 2002	 June 2002	 September 2002	 December 2002	 February 2003
Carpinteria Salt Marsh Reserve						
Mouth	27	22	36	NS	40	26
Middle	15	12	25	30	35	10
Head	2	2	10	21	NS	3
Mugu Lagoon-West						
Mouth	34	34	40	38	32	35
Middle	NS	34	NS	39	40	28
Head	28	35	32	36	35	24
Mugu Lagoon-Calleguas Creek						
Mouth	22	25	21	26	16	20
Middle	15	16	14	16	8	16
Head	2	10	5	9	5	10
Upper Newport Bay						
Mouth	28	26	40	37	37	32
Middle	23	13	31	34	35	27
Head	15	10	30	25	19	27
Los Penasquitos Lagoon						
Mouth	NS	13	35	35	26	0
Middle	NS	13	34	35	35	0
Head	NS	15	19	36	11	0
Tijuana River Estuary						
Mouth	34	35	39	40	41	30
Middle	10	28	35	40	40	0
Head	4	NS	37	40	36	0

were significant effects of site ($p<0.0001$) and season ($p=0.0005$) on water column NH_4 as well as interaction ($p<0.0001$). DON was significantly affected by site ($p<0.0001$) and there was interaction between site and season ($p=0.0017$). Peaks in NH_4 and DON availability occurred during rainy season sampling events.

The Mugu West macroalgal community was comprised of both *Enteromorpha* and *Ulva*. Biomass was highest at the head and mouth (maximum mean biomass: 2995±873 g wet wt m^{-2}) in June 2002. Patterns were different at the middle site, where biomass was greatest in December 2001, and September and December 2002 (Figure 5). There was a significant effect of season ($p<0.0001$) on total

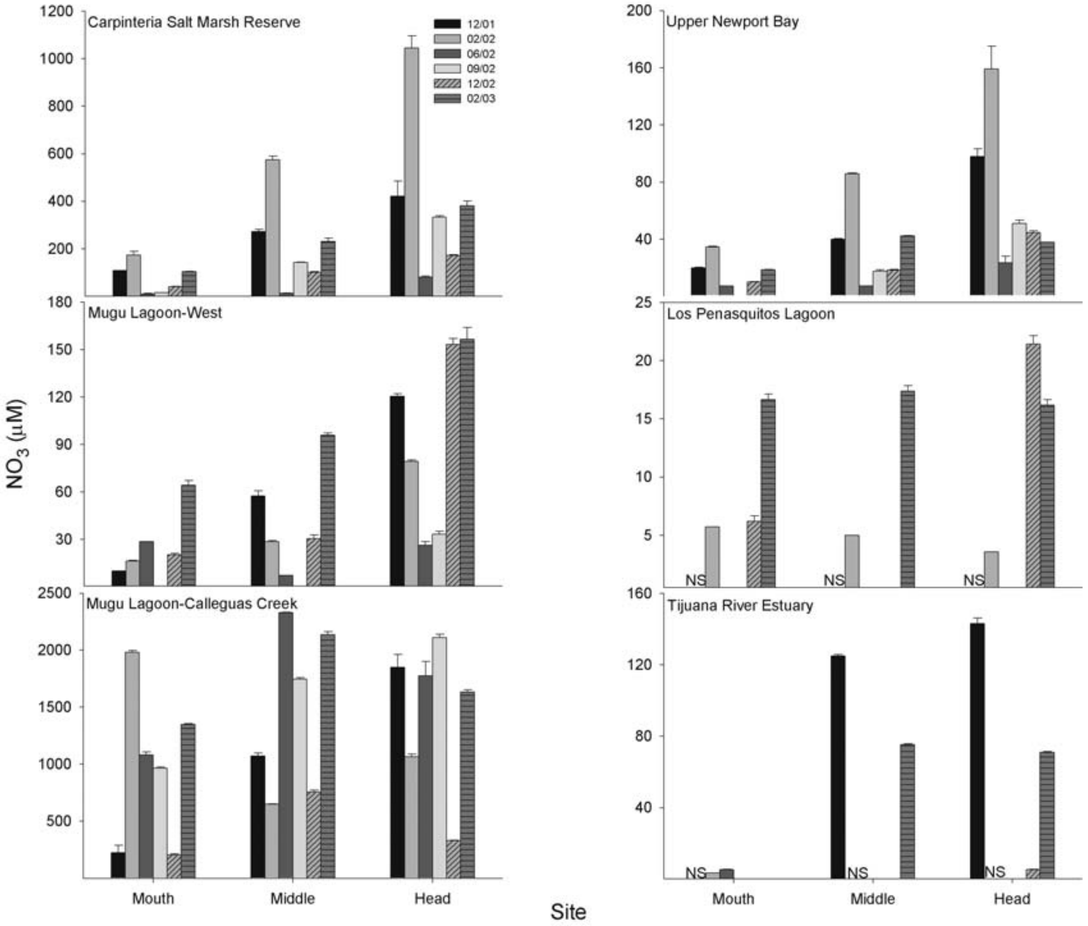

Figure 2. Water column NO3 in each estuary. NS=not sampled. Note different y axes. Error bars = 1 SE.

macroalgal biomass as well as interaction ($p<0.0001$).

Mugu Lagoon - Calleguas Creek

Gradients in salinity were evident during all sampling periods, indicating the persistence of freshwater flow throughout the year (Table 4). NO_3 concentrations were >500μM at all three sites in almost every season with only a few exceptions (Figure 2). The highest NO_3 concentrations measured in this study were in Mugu CC. There were significant effects of site and season ($p<0.0001$ for both), but patterns were inconsistent across space and time, resulting in interaction ($p<0.0001$). The only clear spatial concentration gradients occurred in December 2001 and September 2002, when NO_3 was highest at the head and decreased toward the mouth.

Water column NH_4 and DON were generally 10 times lower than NO_3 (Figures 3 and 4). Both NH_4 and DON were significantly affected by site (NH_4: $p<0.0001$; DON: $p=0.0020$), season ($p<0.0001$ for both), and interactions resulted ($p<0.0001$ for both).

Only relatively low and patchy accumulations of *Enteromorpha* were found in Mugu CC (Figure 5). The most biomass occurred at the mouth in June and September 2002 (maximum mean biomass: 292±114 g wet wt m^{-2}). In all other seasons, there was little or no biomass at all sites. There were effects of site ($p=0.0010$) and season ($p<0.0001$) on algal biomass as well as an interaction ($p<0.0001$).

Upper Newport Bay

Salinity gradients occurred during each sampling event. The lowest salinities were at the head of the estuary (Table 4), indicating freshwater flow throughout the year. These gradients were stronger during the wet months coinciding with precipitation (Table 2).

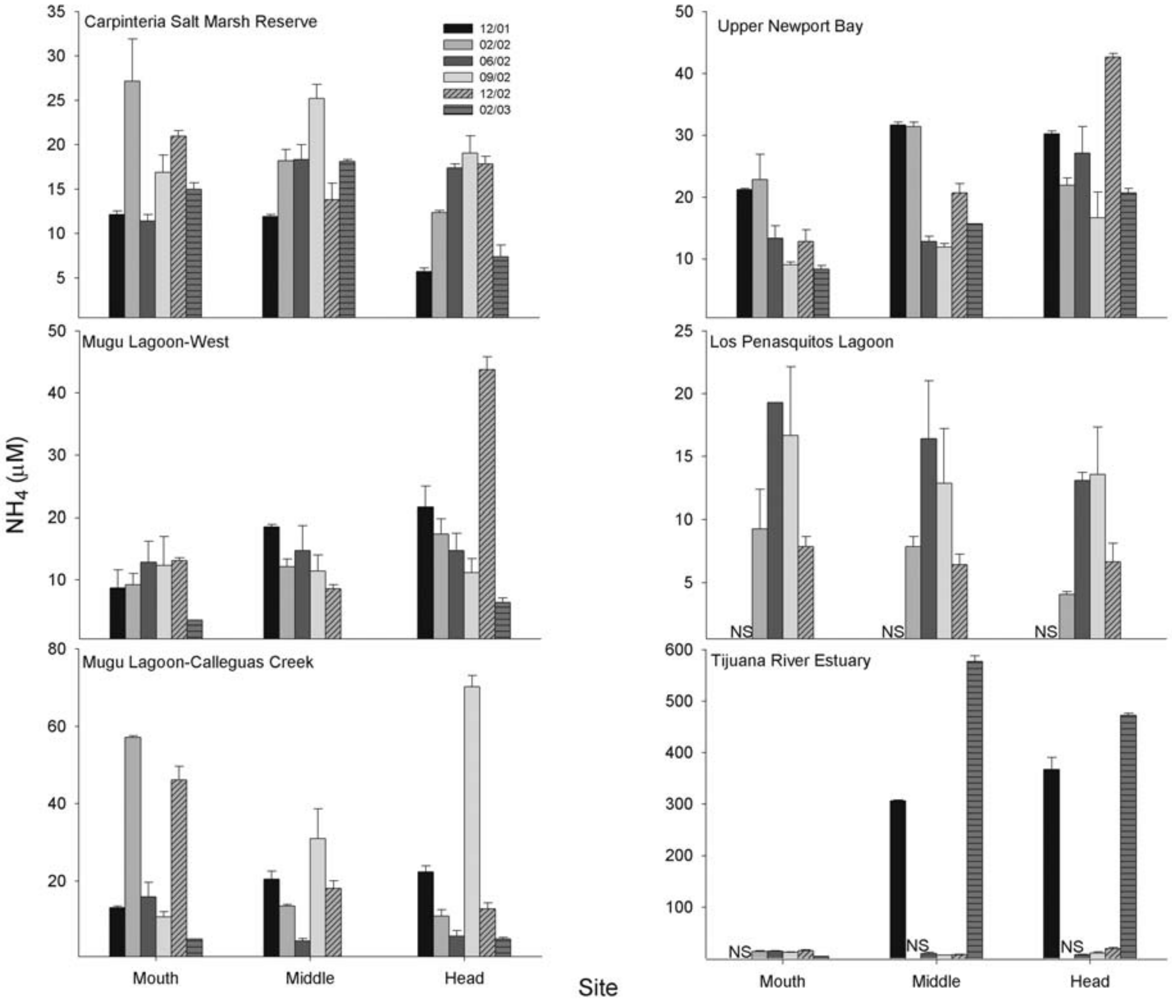

Figure 3. Water column NH4 in each estuary. NS=not sampled. Note different y axes. Error bars = 1 SE.

NO_3 concentrations were highest at the head and decreased toward the mouth, indicating the creek was the primary NO_3 source (Figure 2). Concentrations were similar to those measured in Mugu West. There were significant effects of site and season ($p<0.0001$ for both) on NO_3 concentrations as well as interaction ($p<0.0001$). NO_3 concentrations were highest in December 2001 and February 2002.

NH_4 and DON concentrations were generally low to moderate compared to NO_3 and the highest values tended to occur in the wet months (Figures 3 and 4). There were significant effects of site and season ($p<0.0001$ for both) on water column NH_4 as well as interaction ($p<0.0001$). There were significant effects of season ($p=0.0009$) and site ($p=0.0048$) on water column DON but no interaction. In June, September, and December 2002, NH_4 and DON concentrations were highest at the head and decreased toward the mouth.

The UNB macroalgal community was comprised of both *Enteromorpha* and *Ulva*. Maximum mean biomass (2012±438 g wet wt m^{-2}) occurred at the head in June 2002 (Figure 5). There were significant effects of site ($p=0.0024$) and season ($p<0.0001$) on algal biomass as well as interaction ($p<0.0001$). Biomass was measured year-round at the mouth but only in June and September 2002 at the other sites.

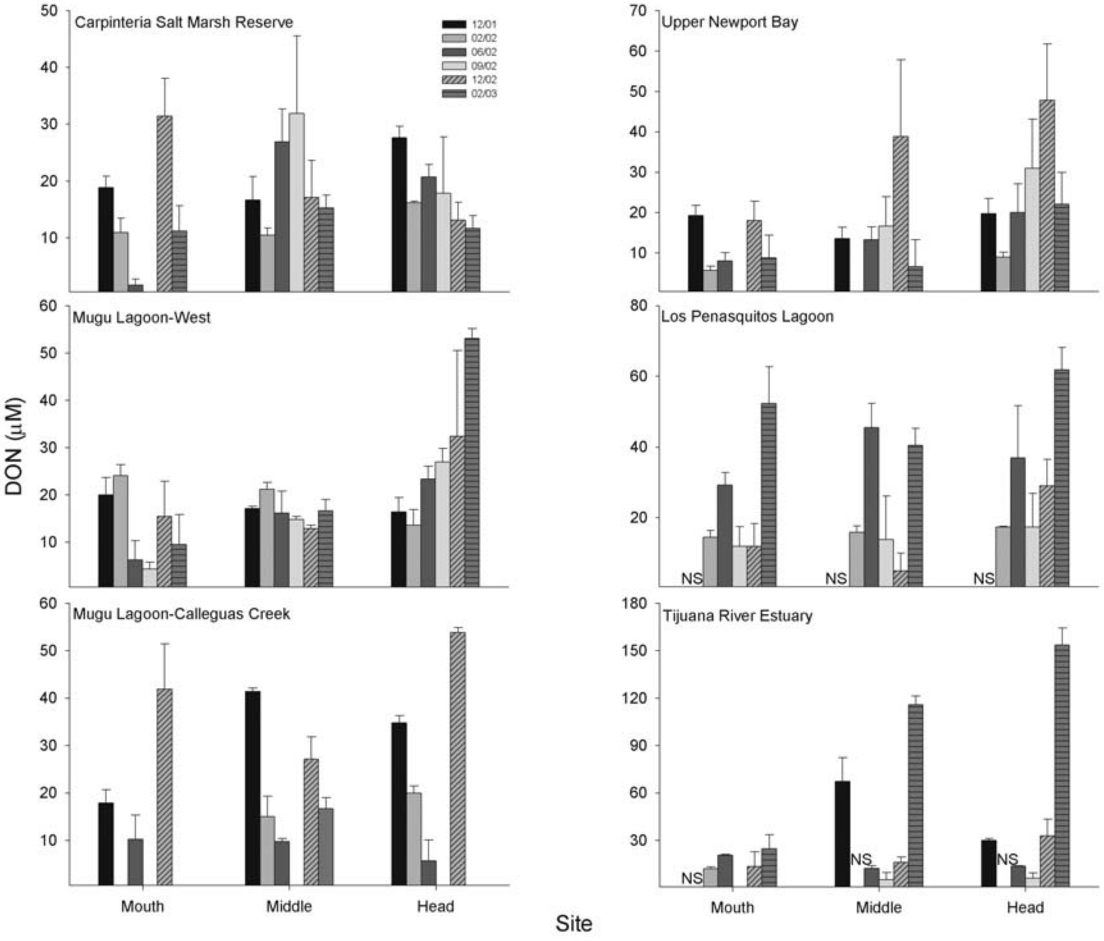

Figure 4. Water column dissolved organic nitrogen (DON) in each estuary. NS=not sampled. Note different y axes. Error bars = 1 SE.

Los Penasquitos Lagoon

Salinities varied among sampling events (Table 4). Moderate salinity was detected throughout the estuary in February 2002 when the system was well-mixed, probably following a rain event. Salinity was oceanic in September 2002, fresh in February 2003, and gradients indicated freshwater flow in June and December 2002.

Water column N was most abundant in the form of DON (Figure 4). In general, water column NO_3 concentrations were low relative to other estuaries in our study (Figure 2) and, due to a large number of samples below the detection limit of 3.57 µM, were not analyzed statistically. NH_4 was often available except in February 2003 (Figure 3), when NO_3 peaked. There was a significant effect of season on water column NH_4 ($p=0.0024$) with the highest concentrations in June and September 2002. Water column DON was also significantly affected by season ($p<0.0001$), being highest in June 2002 and February 2003.

LPL's macroalgal community was comprised of both *Enteromorpha* and *Ulva*. There were significant effects of site ($p=0.0178$) and season ($p<0.0001$) on algal biomass as well as interaction ($p<0.0001$). Maximum mean biomass (532±128 g wet wt m^{-2}) occurred at the mouth in September 2002 and biomass was measurable in June at all sites (Figure 5). In February 2002 and 2003, we observed macroalgae growing as small epiphytes on seagrass, but biomass could not be measured quantitatively.

Tijuana River Estuary

Strong salinity gradients occurred in December 2001 and February 2003; a weak gradient appeared to occur in December 2002 (Table 4). In June and September 2002, water was hypersaline and not variable across sites.

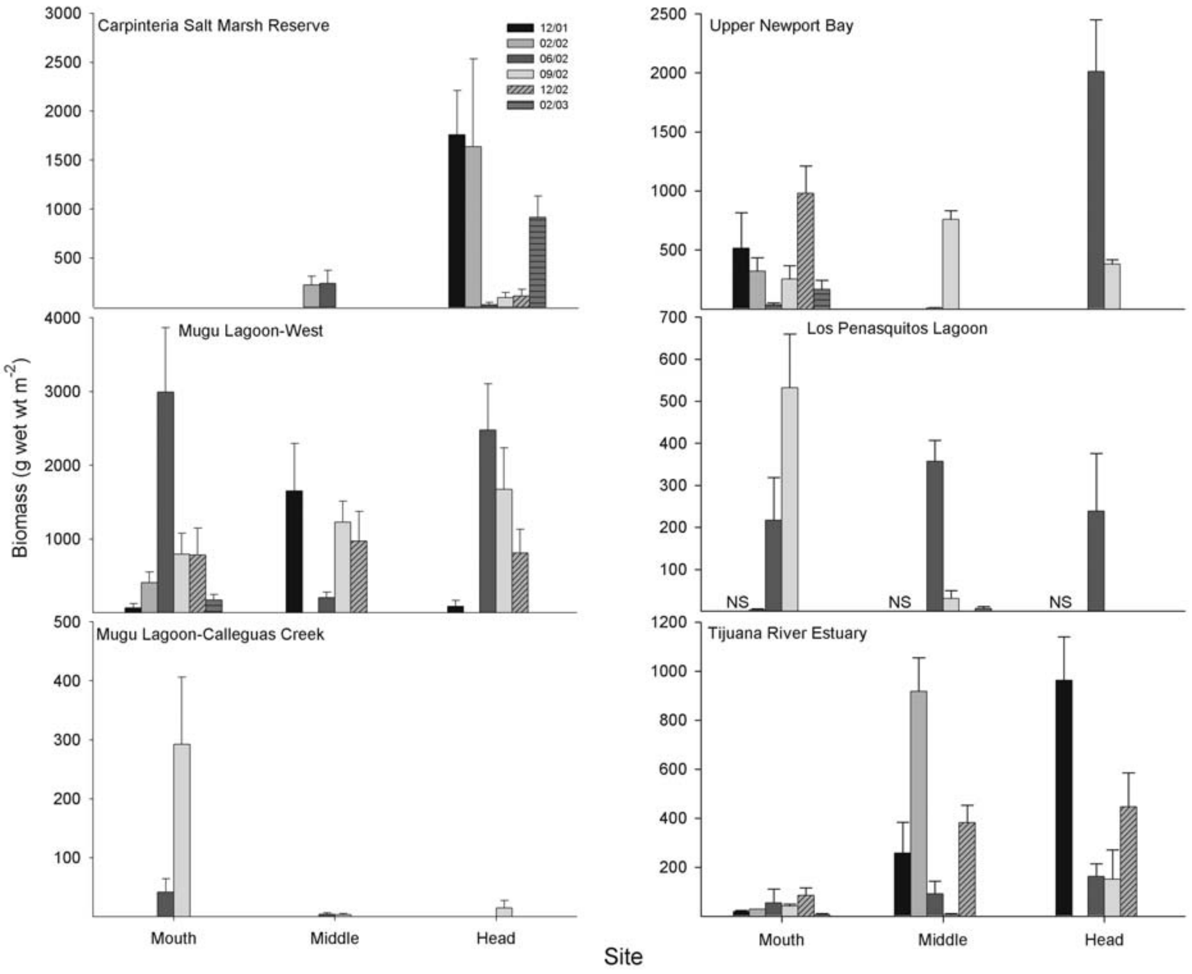

Figure 5. Macroalgal biomass in each estuary. NS=not sampled. Note different y axes. Error bars = 1 SE.

NH_4 was the abundant form of water column N during our study (Figure 3). NO_3, NH_4, and DON availability peaked in December 2001 and February 2003 (Figures 2-4). For both NH_4 and DON, there were significant effects of site and season ($p<0.0001$ for both) as well as interactions ($p<0.0001$ for both). High concentrations at the middle and head sites, combined with low concentrations at the mouth during wet months, imply that runoff from precipitation may have been the source.

TJ's macroalgal community was comprised of both *Enteromorpha* and *Ulva*. Maximum mean biomass (963±178 g wet wt m^{-2}) occurred at the head in December 2001 (Figure 5). There were significant effects of site and season ($p<0.0001$ for both) on algal biomass as well as interaction ($p<0.0001$). Biomass was lowest at the mouth; the highest biomass at the middle and head sites occurred during the wet months.

DISCUSSION

Even within the relatively small geographic region of southern California, patterns in N sources and macroalgal abundance varied considerably among estuaries. The lack of similar patterns between water column N and algal biomass demonstrates that algal blooms cannot be predicted by water column nutrient concentrations alone. However, we did find consistent patterns during this study that further our understanding of estuarine nutrient-macroalgal dynamics.

In four of the six study areas (CSMR, Mugu West, UNB, and TJ), spatial and temporal patterns in water column nutrients suggested that the watershed was an important nutrient source, particularly for

NO_3, which was the most abundant form of N in most systems. One indication that the watershed was a source of NO_3 to the water column was the persistence of concentration gradients. These gradients suggested that inflowing rivers carried a large amount of N from the watershed that was diluted by mixing with tidal water and/or uptake by primary producers and sediments as it traveled down estuary, such as in both CSMR, which Page *et al.* (1995) also found, and UNB. This differs from other California estuaries, such as Elkhorn Slough, where the ocean is a dominant dry-weather nutrient source during upwelling events (ACT 2003). However, patterns in nutrient distribution similar to ours have been seen by Rizzo and Christian (1996) in North Carolina, Hernandez *et al.* (1997) in Spain, and Nedwell *et al.* (2002) in the U.K. Valiela *et al.* (1992) and Paerl (1997) also reviewed the role of watersheds as primary nutrient sources to estuaries.

Our results indicated a seasonal variance in the magnitude of watershed sources of N. Although much of our sampling was conducted in a very dry year, water NO_3 concentrations were generally higher in the wet season and lower in the dry season, indicating that runoff associated with rainfall had higher levels of NO_3. Estuaries located in other Mediterranean climates, such as the Peel-Harvey system in Western Australia and Venice Lagoon in Italy, have been shown to have similar patterns with higher nutrient inputs when river flow is higher (McComb and Lukatelich 1995, Marcomini *et al.* 1995). In a previous UNB study conducted 1996-1997, water column N concentrations were slightly lower in winter than spring, yet winter flow rates into the estuary were seven times higher (Boyle 2002), resulting in maximum loading in winter. Thus, the differential interaction of flow and concentration in wet and dry years may still result in greater nutrient inputs in winter.

Our data suggested that, in addition to watershed land use, the proximity of certain land use practices to the estuary might be an important determinant of nutrient availability and macroalgal abundance. For example, agriculture accounts for only 26% of the land use in the Mugu CC watershed, but it is the prominent land use practice directly upstream of estuary. With very few exceptions, Mugu CC had the highest NO_3 concentrations of all the estuaries for all sampling times and across sites. Nutrients were particularly high in June, perhaps due to increased seasonal fertilizer application and irrigation directly upstream. Similarly, there is a high degree of urbanization in the TJ watershed directly upstream of the estuary, and TJ had very high NH_4 concentrations in wetter months. The spatial gradient of NH_4 suggested the watershed as the source, which is unusual since NH_4 is usually transformed to NO_3 under aerobic conditions typical of rivers. However, TJ has been subjected to periodic sewage spills from the border city of Tijuana, which may have resulted in relatively high NH_4 concentrations compared to other estuaries in our study.

Variance in tidal flushing rates among estuaries and season may have confounded our results regarding N availability. Tidal amplitude affects flushing rates and can result in dilution of nutrients. In an effort to maintain consistency at each estuary, all water samples were taken within a 3-h to 4-h window of low tide; however, tidal amplitude varied among estuaries within the same sampling season because each estuary was sampled on different days. In addition, because estuary size and individual bathymetry were different, flushing rates and water retention times may vary considerably among estuaries. For example, in UNB, water column nutrients were 10 times higher at low vs. high tide at the head of the estuary (K. Kamer unpublished data). In Famosa Slough, another southern California estuary, nutrient concentrations almost doubled during a 3-h time period spanning inflowing, slack, and outflowing tides (Fong and Zedler 2000). Therefore, although our data showed patterns in the magnitude of nutrient availability from the watershed, caution is needed when making broad comparisons regarding these patterns.

Spatial patterns in algal abundance were determined by nutrient availability and physical forces. In CSMR, maximum algal abundance occurred at the head of the estuary, reflecting water column N availability. However, few algae were found at the mouth of CSMR, which has a steep bank and was probably impacted heavily by scouring and high tidal action. Similarly, Sfriso *et al.* (1992) cited strong tidal currents as an explanation of low *Ulva* biomass near port entrances in the Lagoon of Venice, a nutrient rich system. In both Sfriso *et al.* (1992) and our study, nutrients stimulated algal growth within the system, but physical forces may have prevented accumulation of biomass at some sites, suggesting that physical characteristics also determine algal abundance spatial patterns. In contrast, water column nutrients were lower in TJ and Mugu West than in CSMR, yet algae were consistently present across sites and over time. TJ and Mugu West provide very suitable habitat for algal proliferation with wide banks, broad mudflats, and high light penetration; in these systems, sufficient nutrients combined with large areas of suitable habitat facilitated prolific blooms. Similarly, macroalgal mats in the nutrient-rich River Deben estuary (Suffolk, U.K.) were not associated with high immediate nutrient concentrations (Nedwell *et al.* 2002). Rather, the algae may have proliferated where suitable substrate for attachment was available.

Mugu CC and LPL had relatively low macroalgal abundance, probably due to the unique physical environment of each system. Mugu CC had the highest water column N but also high scouring, high turbidity, and limited mudflat area, making this an unsuitable habitat for blooms. LPL had lowest water column N as well as extremely variable salinity, and these factors may have limited algal growth. Overall, extremes in salinity, light availability, and tidal scouring may inhibit algal growth, regardless of nutrient availability.

Timing of peak macroalgal abundance was variable among estuaries. The 2001-2002 water year was dry, so even the "wet" season was relatively dry. The most biomass occurred in Mugu West, UNB, and LPL during the warm dry season whereas in TJ and CSMR, peak biomass occurred during the cool wet season. Each system has unique geomorphology, water flow characteristics, and watershed development, all of which may impact timing of macroalgal proliferation. For example, Mugu Lagoon and CSMR have watersheds heavily dominated by agriculture, which could have increased nutrient loading in the driest part of the year because of intense fertilization and irrigation in the summer. In UNB and Mugu West, algae were able to proliferate year-round regardless of the degree of precipitation. Longer-term studies, combined with a more in-depth understanding of the hydrology of these systems as well as specific nutrient loading data, would help address the complexity of the timing of blooms.

Both nutrient and macroalgal data indicate that the estuaries in this study were subject to high nutrient inputs. Although variable, most of the estuaries in this study had dissolved inorganic N concentrations orders of magnitude higher than estuaries on the East Coast of the U.S. or in Europe that are considered eutrophic (Valiela *et al.* 1992, Taylor *et al.* 1995, Flindt *et al.* 1997). Additionally, even in our systems that had relatively low macroalgal abundance, the values are comparable to the 600 g m^{-2} biomass found in Waquoit Bay, an East Coast estuary subject to nuisance algal blooms (Valiela *et al.* 1997). Similarly, higher algal biomass (2-3 kg wet weight m^{-2}) found at CSRM, Mugu West, and UNB is comparable to amounts found in other eutrophic estuaries throughout the world (Hernandez *et al.* 1997, Flindt *et al.* 1997).

Although watersheds of these six study areas were identified as major sources of nutrients, the variability encountered in our results suggests other important nutrient sources. Benthic flux, groundwater, and aerial deposition are important nutrient sources in East Coast estuaries (Valiela *et al.* 1992, 1997; Paerl 1997), and their relative importance in southern California estuaries needs to be determined. However, until the mechanisms and processes of these systems are understood and a general paradigm of nutrient pathways is developed, management of these systems may need to be done on a case-by-case basis.

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