PATTERNS AND CAUSES OF VARIABILITY IN THE COVER, BIOMASS, AND TOTAL ABUNDANCE OF *ULVA* SPP. IN ELKHORN SLOUGH, CALIFORNIA

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By
Timothy J. Schaadt
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APPROVED FOR THE INSTITUTE OF EARTH SYSTEMS AND SCIENCE POLICY

____
Dr. Michael H. Graham, Moss Landing Marine Laboratories

____
Dr. Michael S. Foster , Moss Landing Marine Laboratories

____
Dr. Nicholas A. Welschmeyer, Moss Landing Marine Laboratories

APPROVED FOR THE UNIVERSITY

____

ABSTRACT

PATTERNS AND CAUSES OF VARIABILITY IN THE COVER, BIOMASS, AND TOTAL ABUNDANCE OF *ULVA* SPP. IN ELKHORN SLOUGH, CALIFORNIA

By

Timothy J. Schaadt

Ulva spp. occur as conspicuous mats on mudflats of Elkhorn Slough throughout the year, however, no efforts have been made to quantify the intra-annual variability of these algae. It is important to understand variation of *Ulva* spp. because of potential ecological impacts due to the presence/absence of these algae. This work focuses on temporal (season) and spatial (section) variability in *Ulva* spp. in Elkhorn Slough, CA. I measured changes in *Ulva* cover and biomass seasonally and ultimately combined them to determine changes in total abundance from July 2003 to July 2004. Over this time period, there was a significant seasonal difference in *Ulva* cover and biomass with peak cover in October 2003 and peak biomass in January 2004. There was also a significant interaction in the variation of *Ulva* biomass between season and section, suggesting section-specific variation in biomass. Total abundance followed the same pattern of change as cover, suggesting that *Ulva* mat cover was a better indicator of total abundance in Elkhorn Slough. Variation in mat dynamics (e.g. growth, cover, accumulation) can occur at different spatial and temporal scales. To determine if seasonal changes were occurring at sub-seasonal time scales, the experiment was repeated at a smaller spatial and temporal scale from June 2004 to August 2004, with bi-weekly samples of cover and biomass. It was found that seasonal variation in cover was significantly greater than sub-seasonal variation; however, seasonal and sub-seasonal biomass measurements were not significantly different. These results indicated that changes in cover were more gradual over time and biomass was highly variable at both time scales. Tides were also investigated at two locations as a possible factor regulating *Ulva* mats in Elkhorn Slough, because tides are a constant source of movement in the estuary. In one region, I observed significant variability in *Ulva* mat biomass that was related to increased tidal range; in another region the same relationship was not significant. Although the affect of tides was not consistent among regions, my data indicate that tidal range can play an important role in the regulation of *Ulva* mats. Seasonal variability in algal mat dynamics occurred in Elkhorn Slough and some of these factors were also observed varying sub-seasonally potentially due to the effect of tides on *Ulva* mats.

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CHAPTER I

Introduction to the Thesis

Species interactions within a community are important factors in maintaining biological diversity. Removal of certain species (foundation species) from a community can result in a significant decrease in species diversity through loss of habitat or primary production. For example, the presence of macroalgal foundation species can explain much of the diversity of subtidal kelp forests (Graham 2004), rocky intertidal kelp communities (Dayton 1975), and rhodolith beds (Steller et al. 2003). In these cases, the removal of kelp or rhodoliths reduced or eliminated a majority of macro- and micro-organisms that were associated with the macroalgae through either trophic or habitat linkages.

In estuarine systems, species diversity is thought to be controlled by environmental factors such as water temperature, salinity, and nutrients (Pregnall and Rudy 1985, Fong et al. 1996, Martins et al. 2001, Lin and Hung 2004), as well as primary production and interactions with phytoplankton, salt marsh plants, and macroalgae (Hull 1987, Allen 1992, Valiela et al. 1997, Lavery et al. 1999, Bolam and Fernandes 2002, Nelson et al. 2003a, Cardoso et al. 2004, Cummins et al. 2004). In addition, macroalgae can be important habitat modifiers by reducing water flow during tidal exchange and ameliorating desiccation stress for small invertebrates within algal mats (Hull 1987, Allen 1992, Bolam and Fernandes 2002). Estuaries are some of the most productive environments in the world (Pomeroy and Stockner 1976, Martins et al. 1997, Valiela et al. 1997, Lavery et al. 1999, Kamer et al. 2001) and typically the absence of macroalgae on estuarine intertidal mudflats results in reduced species abundance and diversity of mudflat invertebrates (Hull 1987, Allen 1992, Lavery et al. 1999, Cardoso et al. 2004). However, large accumulations of algal mats can also cause underlying sediments to become anoxic, resulting in decreased abundance of some invertebrate species through changes in sediment chemistry (Sfriso et al. 1987, Trimmer et al. 2000). The varying abiotic and biotic conditions within an estuary can lead to a variety of habitat niches for a multitude of species throughout an estuary.

Estuarine macroalgal diversity is low compared to open coast intertidal communities, yet some species such as *Ulva intestinalis*, (formerly Enteromorpha intestinalis see Hayden et al. 2003) can be extremely abundant. This green macroalga is fast growing and monostromatic with a distinct tubular morphology. It is commonly found as dense aggregations or accumulations referred to as "algal mats". Estuarine ulvoids typically have opportunistic and ephemeral life histories that are well suited for the changing dynamics (tides, nutrient pulses, fresh water input, etc.) of an estuary (Abbott and Hollenberg 1976, Pomeroy and Stockner 1976, Thom 1984, Pregnall and Rudy 1985, Lavery et al. 1991, Pihl et al. 1996). Given the low macroalgal diversity in some estuaries, these few but abundant species are commonly important contributors to estuarine primary production and habitat provision. *Ulva* can account for up to 30% of total primary production within an estuary and can grow faster than most other estuarine macroalgae (Pomeroy and Stockner 1976, Owens and Stewart 1983, Thom 1984, Pregnall and Rudy 1985, Pihl et al. 1999). Amphipods, decapods, other invertebrates, and even humans, take advantage of highly productive *Ulva* assemblages (Pomeroy and Stockner 1976, Warwick et al. 1982, Lowthion et al. 1985, Pregnall and Rudy 1985, Allen 1992, Zimmerman and Caffrey 2002). Invertebrates use habitat created by *Ulva* for protection from desiccation and as attachment during periods of high currents (Warwick et al. 1982, Allen 1992). The dense aggregations of individual *Ulva* thalli also block sunlight and reduce thermal stress to invertebrates within the mats. However, persistent aggregations can lead to anoxia, inhibit larval development (Nelson et al. 2003b), and alter existing biogeochemical pathways (Sfriso et al. 1987, Valiela et al. 1997, Nelson et al. 2003a).

Various abiotic and biotic factors have been shown to regulate the cover and abundance of *Ulva* mats. Fong et al. (1996) showed that *Ulva* could survive in salinities of 15 to $35^{o}/_{oo}$ with adequate quantities of nutrients and light. Fong et al. (1996) also found that greater levels of nitrogen significantly increased total *Ulva* biomass. Temperature also was suggested as a limiting factor, but the observed range was between 10° and 17° C, similar to water temperature for many temperate estuaries (FitzGerald 1978, Warwick et al. 1982, Thom 1984, Pregnall and Rudy 1985, Lavery et al. 1991, Pihl et al. 1996, Kamer et al. 2001). These factors can vary in complex ways within an estuary and lead to variability in other biological processes.

Variation in mat dynamics (e.g. growth, cover, accumulation) can occur at different spatial and temporal scales. Spatial variation in mat dynamics can occur on scales of meters among mats (Allen 1992, Lavery et al. 1999) or kilometers among sampling locations (Sfriso et al. 1987, Curiel et al. 2004, Lin and Hung 2004). Mat dynamics can also be highly variable at temporal scales from daily to seasonal. Daily changes in light availability and nutrient pulses can affect algal growth (Zimmerman and Kremer 1984, Fong and Zedler 1993, Fong et al. 1996, Kamer et al. 2001, Martins et al.

2001). Weekly and monthly changes in tidal height and emersion times affect recruitment, growth, and desiccation (Townsend and Lawson 1972, Lowthion et al. 1985). Seasonal changes in temperature, freshwater input, and nutrient availability can affect growth, reproduction, and accumulation (Pregnall and Rudy 1985, Fong and Zedler 1993, Martins et al. 1997, McClelland and Valiela 1998b, Martins et al. 2001, Rubenstein and Wikelski 2003). In addition to these spatiotemporal differences in mat dynamics are other spatial differences such as proximity to the main and tidal channels (pers. obs.), distance from nutrient sources such as streams and rivers (Sfriso et al. 1987, Hernandez et al. 1997, Sfriso et al. 2003), and water flow modified by macrophyte presence and absence (Allen 1992, Widdows and Brinsley 2002).

Seasonality in growth, distribution, abundance, and biomass of a dominant macroalga within an ecosystem can account for major changes in primary production, food web structure, habitat availability, and species diversity (Lowthion et al. 1985, Sfriso et al. 1987, Allen 1992, Back et al. 2000, Choi et al. 2001, Kharlamenko et al. 2001, Bolam and Fernandes 2002, Brun et al. 2003, Kelaher and Levinton 2003, Okey 2003, Ramirez et al. 2003, Nelson et al. 2003a, Nelson et al. 2003b, Cardoso et al. 2004, Graham 2004). In estuaries, *Ulva* blooms are quite common and seasonal changes in mats have caused changes in invertebrate faunal abundance and sediment chemistry (Allen 1992, Astill and Lavery 2001, Kelaher and Levinton 2003, Cardoso et al. 2004). Eutrophication in estuarine environments can also result in seasonal variability in macroalgal abundance and this affects the primary production of the system, food webs, and community structure (Lowthion et al. 1985, Sfriso et al. 1987, Lavery et al. 1991, Cloern 2001, Kamer et al. 2001, Martins et al. 2001, Nedwell et al. 2002, Nelson et al.

2003b, Cummins et al. 2004, Lin and Hung 2004). However, understanding temporal and spatial scales of variation in estuarine algae (e.g. growth, cover, biomass, etc.) is necessary to explain the extent of impacts when blooms occur (Benedetti-Cecchi et al. 2001, Kelaher and Levinton 2003).

Elkhorn Slough is located on the central coast of California and connects to the ocean via Monterey Bay (Figure 1). The estuary developed through plate tectonics, glacial movements, and changes in sea level over the last 500,000 years (Caffrey et al. 2002). In 1946, during construction of Moss Landing Harbor, the United States Army Corps of Engineers created a new opening to the estuary directly into Monterey Bay. This increased tidal range and changed the estuary from a brackish calm environment to a high tidal energy environment with salinity matching Monterey Bay (Caffrey et al. 2002). The opening of the harbor also increased the number and diversity of species living in the estuary, reflecting a more marine environment (Caffrey et al. 2002). The estuary has numerous tidal channels and waterways that lead away from the main channel. The region of interest for this study was from the mouth of the estuary at the Highway 1 Bridge to Elkhorn Road (at Hudson’s Landing), with the eastern border the high tide mark to the railroad bridge and the western border the high tide mark along old dikes, typically ending where the *Salicornia* marsh gave way to chaparral.

Tubular *Ulva* spp. are commonly found on the intertidal mudflats in and around Elkhorn Slough, CA (Zimmerman and Caffrey 2002) and were the focus of this study. This form of *Ulva* occurs year-round as dense algal mats between patches of *Salicornia virginica* (pickle weed) or as drift floating in the main channel. *Ulva* has also been observed on the beaches near Elkhorn Slough and within Monterey Bay Canyon, where it is an important source of fixed carbon and nitrogen to deep water consumers (Okey 2003). In Chapter I of this thesis, I investigated seasonal variation in cover and abundance of *Ulva* in Elkhorn Slough. I defined intra-annual patterns that establish a baseline estimate of algal mat variation that can be compared and contrasted to future work on long term algal mat variation Elkhorn Slough and other estuaries. Chapter I also presented a Slough-scale method for investigating changes in *Ulva* mat cover and abundance. The method was used to describe patterns of algal mat dynamics which, in turn, were used to determine whether or not local scale (< 1 km^2) phenomena should be further investigated (e.g. are nutrient pulses from local agricultural runoff affecting algal mat dynamics). In Chapter II, I investigated sub-seasonal variability in algal mat dynamics and specifically tested whether there was a significant difference in variability of algal mat cover, biomass, and abundance between seasonal and sub-seasonal temporal scales. Understanding variation at this time scale allowed more efficient sampling methods to be determined and a more precise estimation of algal mat variation. Tides were discussed as a possible mechanism regulating *Ulva* mat cover and abundance over short time scales, of a few days to a few weeks. Tides are rarely considered as regulating algal mat dynamics, but may be a key a short time scales. Overall, I established a baseline estimate of cover and abundance of *Ulva* mats in Elkhorn Slough over varying spatial and temporal scales, provided information to guide for future sampling, and investigated the cause of this variation.

CHAPTER II

SEASONAL VARIATION IN *ULVA* COVER, BIOMASS, AND TOTAL ABUNDANCE IN ELKHORN SLOUGH, CA.

Introduction

Eutrophication in shallow coastal waters is a constant concern given its potential to alter primary production of coastal waters and cause anoxia (Pregnall and Rudy 1985, Sfriso et al. 1987, Morand and Briand 1996, McClelland and Valiela 1998a, Cloern 2001, Kamer et al. 2001, Martins et al. 2001, Zimmerman and Caffrey 2002, Brun et al. 2003, Lin and Hung 2004). Estuaries are particularly vulnerable to eutrophication caused by development of surrounding watersheds for agricultural usage, and environmental conditions such as winds and currents that result in long water residence times (Morand and Briand 1996, Cloern 2001). The runoff from fields or dairy lands has been shown to cause nutrient (e.g. nitrate, phosphate, ammonia) pulses that can lead to increases in macroalgal primary production (Pregnall and Rudy 1985, Sfriso et al. 1987, Valiela et al. 1997, McClelland and Valiela 1998b, Martins et al. 2001, Widdows and Brinsley 2002). Such "blooms" have been observed for *Ulva* spp., which have high nutrient uptake rates and opportunistic life histories (Lowthion et al. 1985, Sfriso et al. 1987, Fong and Zedler 1993, Fong et al. 1996, Valiela et al. 1997, Kamer et al. 2001, Zimmerman and Caffrey 2002). Lowthion et al. (1985) observed that industrial discharge and nutrient rich water were associated with excessive ulvoid growth and that the increased macroalgal growth decreased the area of *Spartina* marsh by reducing habitat and sunlight. Sfriso et al. (2003) also noted that macroalgae could replace seagrass beds in locations with high nutrient concentrations, reducing this potential nursery habitat for fishes and decreasing overall species diversity (Thayer et al. 1975, Penhale 1977, McClelland and Valiela 1998, Moore and Wetzel 2000, Kharlamenko et al. 2001, Hovel and Lipcius 2002).

Processes that affect eutrophication may vary seasonally (e.g. freshwater runoff from seasonal rains), however, other processes not related to eutrophication can cause seasonal patterns in algal mats. Although *Ulva* mats can occur year-round, mat growth and abundance typically vary seasonally (Thom 1984, Lowthion et al. 1985, Pregnall and Rudy 1985, Sfriso et al. 1987, Fong and Zedler 1993, Solidora et al. 1997, Sfriso et al. 2003, Nelson et al. 2003b, Lin and Hung 2004), often leading to significant intra-annual changes in primary production in estuaries (Pregnall and Rudy 1985, Sfriso et al. 1987). Ulvoid growth and abundance has been previously classified in many ways, including: presence/absence, number of recruits, biomass or mat thickness as weight (dry or wet) per unit area, distribution or cover, and total abundance or weight (Townsend and Lawson 1972, Lowthion et al. 1985, Pregnall and Rudy 1985, Sfriso et al. 1987, Lavery et al. 1991, Allen 1992, Valiela et al. 1997, Pihl et al. 1999, Benedetti-Cecchi et al. 2001, Bolam and Fernandes 2002, Lin and Hung 2004). In seasonal systems, *Ulva* biomass per area typically peaks in early spring or early fall. Spring blooms are often caused by increased water column nutrients from winter rain and runoff, increasing water temperatures, and increasing light, whereas fall blooms are often caused by changes in day length and water temperatures that favor ulvoid growth (Pregnall and Rudy 1985, Fong and Zedler 1993, Fong et al. 1996, Pihl et al. 1996, Valiela et al. 1997, Choi et al. 2001). Although seasonality has been observed world-wide, qualitative observations by Zimmerman and Caffrey (2002) suggested the absence of an obvious seasonal trend in

Elkhorn Slough. While *Ulva* spp. are present in Elkhorn Slough year-round, intra-annual fluctuations in cover, biomass, and abundance may potentially occur seasonally throughout the estuary and be important to algal mat dynamics (see **CHAPTER I**).

Various techniques have been used to measure changes in *Ulva* mats in shallow coastal environments such as field sampling, aerial photography, and computer modeling (Lowthion et al. 1985, Hull 1987, Pihl et al. 1996, Hernandez et al. 1997, Martins et al. 1997, Pihl et al. 1999, Back et al. 2000, Astill and Lavery 2001, Choi et al. 2001, Martins et al. 2001). Some studies investigating general trends in spatial and temporal variation of algal mat dynamics in coastal wetlands have focused on specific regions or permanent sampling stations (Hernandez et al. 1997, Lavery et al. 1999, Choi et al. 2001, Kamer et al. 2001). Environmental conditions (e.g. water temperature, salinity, nutrient concentration, etc.) within estuaries, however, can change over short spatial scales (Kamer et al. 2001, Ramirez et al. 2003, Widdows et al. 2004). Given such multi-scale variability in environmental conditions, restricting sampling to specific regions can bias estuary-wide trends based on these regions (Underwood 1997). In a homogeneous environment this would not be a concern because patterns of variation should be similar throughout the environment. Most estuaries, however, are heterogeneous and subject to many different environmental factors that vary within the estuary (e.g. tidal currents, nutrient pulses, water temperature, freshwater and saltwater flow) (Pregnall and Rudy 1985, Sfriso et al. 1987, Lavery et al. 1991, Fong et al. 1996, Hernandez et al. 1997, Valiela et al. 1997, McClelland and Valiela 1998a, McClelland and Valiela 1998b, Lavery et al. 1999, Martins et al. 1999, Benedetti-Cecchi et al. 2001, Cloern 2001, Kamer et al. 2001, Martins et al. 2001, Lotze and Worm 2002, Sfriso et al. 2003). A sampling design that allows samples to be taken throughout an estuary provides less biased estimates that may facilitate a better understanding of system-wide changes in algal mat dynamics.

Aerial photography has been used previously to identify spatial and temporal patterns of *Ulva* in coastal embayments (Pihl et al. 1996, Curiel et al. 2004). This technique is useful because 1) it covers large areas with less effort than field sampling, 2) can be done regularly without disturbing the environment, and 3) provides information on spatial and temporal variation for the entire system. Photographs, however, cannot be used to estimate within-mat biomass (Sfriso et al. 1987, Lavery et al. 1991, Pihl et al. 1996, Curiel et al. 2004). Hyper-spectral imaging was tried as a method to determine within-mat biomass, but it could not detect layering.

The overall goal of this study was to develop methods for monitoring changes in abundance of *Ulva* by sampling seasonal changes in cover and biomass to better understand algal mat dynamics and its causes in Elkhorn Slough. I first determined the magnitude of seasonal variability in *Ulva* cover, biomass, and abundance. Then I determined whether variability in cover, biomass, or both was the most important variable describing *Ulva* abundance in the estuary. Is the variability of *Ulva* mat abundance driven by the amount of mudflat available as habitat (cover) or by the thickness of mats (within-mat biomass)? If the former is true, the aerial photography may be necessary to determine seasonal patterns of total *Ulva* abundance in the estuary; if the latter is true, the field measurements of within-mat biomass may be sufficient to characterize *Ulva* abundance. An alternative is that cover and biomass are both important factors in determining *Ulva* abundance and therefore both parameters must be measured to accurately assess abundance. I determined cover, biomass and their interaction, as well as their spatial variation within Elkhorn Slough. The latter was used to determine if local scale phenomena were important regulating factors in algal mat dynamics.

Methods

To determine spatial and temporal variation in *Ulva* mat abundance, cover and biomass were measured and combined such that cover multiplied by biomass equaled abundance. For the purposes of this study, cover was defined as the amount of mudflat area (m^2) covered by *Ulva*. This included mudflats exposed within the tidal range of -0.5 m to +1.0 m Mean Lower Low Water (MLLW). Biomass (gDW m^{-2}) was defined as the dry weight of samples from within *Ulva* mats. Samples were collected from within mats because mats in Elkhorn Slough primarily occur as dense accumulations or not at all, and because resolution of aerial photographs used to estimate cover did not detect *Ulva* mats with less than 100% cover. Abundance (kg DW) of *Ulva* in Elkhorn Slough was the product of cover and biomass. Temporal (SEASON) variation was determined by sampling every three months to be an indication of seasons. Spatial (SECTION) variation was determined by dividing the estuary into five sections. The divisions were originally designed to ensure that biomass samples would have been collected throughout the estuary, and in addition, the divisions allowed a discussion of spatial variation.

Cover

Aerial photography was used to estimate the area of *Ulva* mats (m^2) exposed in Elkhorn Slough at low tide (see Table 1 for sample dates and sizes). On each sampling date, approximately 30 digital aerial photographs were taken from an altitude of 1500 m with a Pentax 645 digital camera and a 75 mm lens (EcoScan Resource Data Watsonville, CA). Pixel size (determined from size of known objects within the photographs) was 0.25 m^2. In order to limit edge effects, enhance detection of algal mats, and be consistent with field sampling, however, *Ulva* mats were defined as assemblages or accumulations ≥1 m^2 in area with 100% *Ulva* mat cover. Mats of this size commonly occurred on Elkhorn Slough mudflats. The photographic images were processed and analyzed using MatLab (source code given in APPENDIX I) by identifying which pixels contained *Ulva*, using a range of user defined RGB values, and then counting all such pixels within a given area. The total number of pixels was then multiplied by four to determine cover as 1 m^2 mats throughout the estuary. A two-way Analysis of Variance (ANOVA) was used to test for spatial (SECTION) and temporal (SEASON) differences in biomass among sections and among seasons. Variance components and magnitude of effects (ω^2) were calculated as described in Graham and Edwards (2001). The interaction between SECTION and SEASON was not calculated due to the lack of replication. Graphical trends were used to interpret patterns that would suggest an interaction between the two factors.

Biomass

A pilot study was done to determine the optimal quadrat size and number of replicates for sampling *Ulva* biomass within mats on the mudflats of Elkhorn Slough. In May 2003, 20 *Ulva* mat samples each were collected by hand at random with 0.0625 and 0.25 m^2 quadrats from an approximately 100 m x 15 m area with an *Ulva* mat that covered most of the area; quadrats larger than 0.25 m^2 could not be efficiently dried and thus were not appropriate sample unit sizes. Wet mass did not provide an accurate estimate of biomass because the sponge-like nature of the mats produced high variation in water content (10% - 70%). All samples were dried to a constant mass at 55^{o}C for 24-48 hours. From these initial data, power analyses ($\alpha = 0.05$, $\beta = 0.80$) were used to determine the relationship between sample size (n) and effect size (detectable difference in biomass) using each of the two different quadrat sizes (analyses conducted with Systat v10). The analyses estimated that using the 0.25 m^2 quadrat, a 20% difference in mean biomass throughout the estuary could be detected with 30 samples; the smaller quadrat required 70 samples to detect the same difference. A 20% differential was used because it was thought to be higher than natural variation in the system. Therefore, I used at least 30 0.25 m^2 quadrats to estimate *Ulva* biomass per sampling period (Table 1). Biomass was not sampled in Section 1 in April 2004 due to natural loss of biomass in this section on this date. To account for the missing data I took the average values of April from all other sections.

Variation in *Ulva* mat biomass was determined temporally (SEASON) and spatially (SECTION). In each section, sample quadrats were collected haphazardly by throwing quadrats onto an *Ulva* mat of 100% cover >1 m^2. This was done to be consistent with the aerial photographic methods, and because it was thought that the variability in larger mats (mats >1 m^2) would be more indicative of patterns of variation of *Ulva* abundance than in smaller, more ephemeral mats. The haphazard approach for collecting the samples within a mat was used to eliminate a bias towards picking portions of mats that seemed to be thicker/thinner. Number of quadrat samples varied among dates due to changes in the cover and abundance of *Ulva* and difficulty in cleaning samples. Samples were processed in the same manner as in the pilot study. A two-way ANOVA was used to test for spatial (SECTION), temporal (SEASON), and SECTION X SEASON interaction in biomass among sections and among seasons. Variance components and magnitude of effects were calculation as described in Graham and Edwards (2001). Due to the negligible effect of SECTION, I used the “pool the minimum violator” technique (Graham and Edwards 2001). Post hoc Bonferroni analysis was used to test for differences among sections and seasons.

Abundance

To estimate seasonal changes in *Ulva* abundance (kgDW) for the whole Slough, estimates of within-mat biomass (gDW m^{-2}) per season were multiplied by the estimate of *Ulva* cover (m^2) per season. While within-mat biomass estimates combined with aerial image analysis probably under estimated total biomass, the inaccuracy is likely to be small relative to the entire area of Elkhorn Slough. Further, sampling methods were consistent throughout the study so any error should be consistent among seasons. No analysis was performed on abundance data due to lack of independence of cover, biomass, and abundance measurements known as unit-sum constraint (Sokal and Rohlf 1995).

Results

Cover

Seasonal patterns of cover were similar for Sections 1, 2, 3 and Sections 4 & 5 (Figure 3). There was a significant difference among seasons but not among sections, with season accounting for a much greater amount of the variation in cover data (ω^2, Table 2). The anomalously high pattern observed in Figure 3 suggests an interaction, but may be biased by the values for Sections 4 & 5 in October 2003. The highest total area covered occurred in October 2003 in Section 5 (260064 m^2) and the lowest in April 2004 in Section 5 (364 m^2). The greatest percent change of cover among dates within any section was also in Section 5 from April to July 2004 (135032 m^2), over a 300 fold increase in three months. When combined, the large seasonal changes among sections resulted in an overtly seasonal *Ulva* mat cover (Figure 4) of the entire estuary with maximum cover in October 2003 (636947 m^2) and minimum in April 2004 (62473 m^2). The greatest seasonal change was a 6 fold increase from April to July 2004 (431153 m^2). Between July 2003 and July 2004, the only replicate of season, there was a four fold increase in cover, but, the two measurements do not allowed for statistical comparison.

Biomass

Biomass varied seasonally in individual sections (Figure 5), but not all sections had the same pattern. The ANOVA found significant variability in SEASON and SEASON-SECTION interaction with no significant difference among SECTION (Table 3). The three-fold difference in ω^2 suggests that the variability in *Ulva* biomass was more strongly associated with season at the local scale of within sections, but 85% of the variability was unexplained. Post hoc Bonferroni analysis of the ANOVA revealed a significant ($p=0.005$) change in biomass in Section 1 from January 2004 to July 2004, and although it was over a six month period, this was the only significant difference for any section compared to other sections during the same season or sections compared across seasons. Although the effect of season explained little variability in biomass it is interesting to note that within-mat biomass peaked in January 2004 (Figure 6), one season after the October 2003 peak in cover.

The greatest biomass estimate for any section during any season was April 2004 in Section 3 (203.0 ± 47.2 gDW m^{-2}) and the lowest was July 2004 in Section 1 (67.6 ± 6.4 gDW m^{-2}). Seasonal patterns in *Ulva* biomass were also observed for the whole estuary from July 2003 to July 2004 (Figure 6). Peak biomass occurred in January 2004 (149.8 ± 11.8 gDW m^{-2}) and the minimum was in July 2004 (89.8 ± 6.6 gDW m^{-2}). The greatest change between two seasons was a 1/3 decrease in biomass from April 2004 (139.1 ± 16.5 gDW m^{-2}) to July 2004.

Abundance

Patterns of algal mat abundance for sections followed the seasonal trend of cover, rather than within-mat biomass (Figure 7). The greatest abundance for any section during any season was in Section 5 in October 2003 (42178 kg DW) and the lowest abundance was in Section 5 in April 2004 (29 kg DW). The greatest change in abundance occurred primarily in Sections 4 & 5. In these sections, abundance changed orders of magnitude between seasons, from April to July 2004 Section 4 increased 20 fold and Section 5 increased 600 fold, due to 2750% and 36996% change in cover respectively. These large increases were due mostly to low *Ulva* cover in April 2004, because from April to July 2004 biomass in Section 4 & 5 changed 25% and 38% respectively.

For the estuary as a whole, *Ulva* mat abundance followed the same seasonal patterns that were observed in cover (Figure 8). Maximum seasonal *Ulva* abundance was in October 2003 (88195 kg DW) and minimum in April of 2004 (9312 kg DW). The greatest seasonal change in abundance was an 8 fold increase from July (11229 kg DW) to October 2003. This change was due mostly to a 685% change in cover because the change in biomass was only 12%. Between July 2003 and July 2004, the only replicate of season, there was a four fold increase in abundance, but, the two measurements do not allowed for statistical comparison.

Discussion

Ulva had a fall peak in cover and abundance and a winter peak in biomass, which rejected the null hypothesis of no seasonal variability in biomass, cover, and/or abundance. Seasonal variability in biomass (range 90 – 150 gDW m^{-2}, lowest value 60% of max) during the study was much less than the variability in cover (range 62,000 – 636,000 m^2, lowest value 10% of max, Tables 2 & 3, Figures 3 & 5). The variability in abundance followed the pattern of variability in cover. The contribution of changes in biomass (12 – 54% seasonal change) was much smaller than cover (57 – 590%). Thus, the influence of biomass (i.e. mat thickness) was a less important factor in determining the seasonality of *Ulva* in Elkhorn Slough. Pihl et al. (1996) observed a larger upper limit to seasonal biomass range (94 – 442 gDW m^{-2}) over a one month period; however, their study was also conducted over a much larger area along the Swedish coast. Curiel et al. (2004) reviewed changes in algal cover in the Lagoon of Venice and found that from 1981 to 1998 algal cover decreased from 53.1 km^2 to 4.3 km^2. The magnitude of change found over a 17 year period in the Lagoon of Venice was similar to the change found in during the 15 months of this study. A potential explanation of this difference is that the lagoon was subject to a smaller tidal range (~1 m maximum during spring tides) whereas Elkhorn Slough is subject to over 2 m tidal range during spring tides (Caffrey et al. 2002, Curiel et al. 2004), and this difference may be an important factor in regulating the biomass and cover of algae within an estuary (Hull 1987, Lin and Hung 2004).

In temperate regions, *Ulva* blooms have been found in summer and fall when water temperatures and light are at potentially optimal levels (Lowthion et al. 1985, Pregnall and Rudy 1985, Fong and Zedler 1993, Hernandez et al. 1997, Kamer et al.

2001), the same apparent optimal conditions are seen in tropical climates in winter and spring (Lin and Hung 2004). Fong and Zedler (1993) showed that, in aquaria, maximum growth was found with relatively low light levels (values typically found in fall) and increased water temperatures (~ 18 – 20°C). This condition exists in Elkhorn Slough during late August and September as water temperatures are at their peak and light levels are relatively low due to coastal fog during that time of year (Caffrey et al. 2002). Monterey Bay Aquarium Research Institute (MBARI) recently deployed moorings in Elkhorn Slough as part of the Land/Ocean Biogeochemical Observation (LOBO) project. LOBO 1 was deployed in October 2003 in Section 1 and data are available from November 2003 to present (available at www.mbari.org/lobo/loboviz.htm). There were large pulses of nitrate into the estuary in January 2004 while water temperature was relatively constant (Figure 9). These pulses of nutrients may be related to increased biomass found during January 2004 (Figure 6). Conversely, decreased nitrate concentrations along with increasing salinity and water temperature might explain decreased *Ulva* mat biomass in July 2004 (Figure 6). Although nitrate concentration observed during this study were at saturating levels, Fong et al. (2004) found algal growth increased with increased nitrate pulses up to 600 μM, a concentration not observed in this study. These factors potentially lead to optimal conditions for growth and potential accumulation of *Ulva* during early fall through winter, although more work is needed to test this hypothesis.

Cover patterns can only be discussed as trends because of the lack of replication of cover measurements. Lowthion et al. (1985) observed no trend in cover of mats in Langstone Harbour, England annually from 1973 – 1982, but noted that the lack of trend was because of large variation in the measurement (infra-red aerial photography and manual counting of grids on the picture) of mat cover. In using the MatLab program to determine the cover of *Ulva* in Elkhorn Slough, there was only one measurement recorded per sampling event and therefore no estimate of measurement error (i.e. pixels that contained *Ulva* being missed or empty pixels being counted in the estimate). However, the process used to determine cover was consistent for all sampling events and because of this, and the large differences observed in field observations of cover of *Ulva* mats, the patterns in Figures 2 & 3 are likely true indicators of seasonal patterns in cover. The most likely error in the differences would have been an over/under estimation of cover. The concern with over-estimating cover is that a management decision to remove the alga could result in loss of habitat, loss of a food source, and reductions in the abundance of associated species (Allen 1992, Lavery et al. 1999, Widdows et al. 2004). Under-estimation of macroalgal cover may result in a lack of action that could result in anoxia and damaging changes to water and sediment chemistry from excessive macroalgal growth (Valiela et al. 1997, Curiel et al. 2004).

Another concern is the lack of replication of cover in interpreting patterns in cover and abundance. Although graphically it appears that there was a potential interaction between seasons and sections, it is unclear how much of the variability would be explained by the interaction. The lack of replication is also a concern with respect to the significance of the SEASON effect, and how much of that effect was due to the large peak in Section 4 & 5 in October 2003. To determine if those sections were driving the significant seasonal variability, data for the two sections were removed for October 2003 and reanalyzed. Without Sections 4 & 5 in October 2003, SEASON was still a significant source of variation in cover ($p < 0.001$) and abundance ($p < 0.010$). The lack of replication of cover also inhibits statistical comparisons of July 2003 and July 2004 for cover and abundance. Post hoc Bonferroni analysis found no difference ($p = 0.193$) between the two July measurements of biomass.

There is also the issue of spatial variability within Elkhorn Slough, variability that dominated the patterns of cover and abundance, and whether or not local (km) factors regulate *Ulva* mats. Sections 4 & 5, the two sections farthest from mouth of the estuary, had peaks in cover and abundance in October 2004 (Figures 3 & 6) that were three times the peaks in any other section. These two sections seemed to represent a divide into an upper and lower slough. Potential factors that are seasonally different that affect the cover and abundance of *Ulva* in the upper versus lower slough are water temperature, salinity, nutrient input, and tidal influence (Pace 1978). Current work by Younan (in progress) and earlier work by Pace (1978) found differences in water temperatures and salinity in the main channel of Elkhorn Slough that followed a pattern similar to the differences in algal mat cover and abundance found in this study. These previous works also suggested that the area I have defined as Section 3 was a transitional area between upper and lower slough, however the results of this study indicated that Section 3 behave likes the lower slough. Along with LOBO 1, MBARI deployed LOBO 2 in October 2004 in Section 4 and data are available from November 2004 to present. Although concurrent data are not available for this study, water temperature (Figure 10), nitrate (Figure 11), and salinity (Figure 12) for both moorings are plotted to show relative differences between upper and lower Slough. Water temperature and salinity had a greater range at LOBO 2 while nitrate had a greater range at LOBO 1 (Figures 10, 11, and 12, note differences in scale of measurements). Fong et al. (2004) showed that Enteromorpha intestinalis responded rapidly (~ 4 weeks) to nutrient pulses (nitrate and phosphate), but at higher concentrations no growth occurred. They hypothesized that the alga had evolved mechanisms to uptake nutrients when available and use remaining resources for growth, but when nutrients were readily available at high concentration resources were diverted to only uptake with nothing left for growth. The differences in *Ulva* mat cover found in this study may be related to rapid response of *Ulva* to lower concentration pulses of nutrients in the upper Slough during early fall.

In general, *Ulva* mats in Elkhorn Slough appear to be as variable as they are in other temperate estuaries around the world. While it seems that the estuary is similar to other estuaries, more work is needed to determine regulating factors for Elkhorn Slough. I have suggested that, because the patterns of change are similar, the controlling mechanisms are as well. Following this logic, future work on determining seasonality of *Ulva* mat should determine seasonal changes in water temperature, salinity, and nutrients and if a quantitative relationship exists among these factors and algal mat dynamics. However, a major difference not discussed in this chapter is the variation and magnitude of tidal range. Since the opening of the estuary in 1946, tidal energy has increased as well as erosion and flushing (Caffrey et al. 2002). The opening of the estuary to more direct marine influence changed the environment from a calm coast inlet with semi-brackish waters to high energy with oceanic salinities (Caffrey et al. 2002). These changes may be vital to growth and accumulation of *Ulva* and investigating the relationship between mats and tides may provide crucial information in developing a model of variation of *Ulva* in Elkhorn Slough.

CHAPTER III

SUB-SEASONAL VARIATION IN *ULVA* MAT BIOMASS AND COVER IN ELKHORN SLOUGH, CA.

Introduction

Variation in ecological parameters, such as growth or abundance, can occur over a multitude of temporal scales, and the variability in time scale over which these parameters are measured can blur our understanding of the processes that regulate them (Zimmerman and Kremer 1984, Lowthion et al. 1985, Fong and Zedler 1993, Pihl et al. 1996, McClelland and Valiela 1998a, Lavery et al. 1999, Kamer et al. 2001, Martins et al. 2001, Nedwell et al. 2002, Kelaher and Levinton 2003, Lin and Hung 2004). For example, the effects of coastal upwelling on near shore systems is traditionally studied over seasonal timescales (Service et al. 1998, Bruland et al. 2001) that can drive phytoplankton blooms or changes in kelp production. Higher frequency processes (e.g. internal tides), however, have been found to significantly affect nutrient pulses in kelp forests (Zimmerman and Kremer 1984). The effects of such high frequency processes can be amplified in situations where the affected organism is opportunistic, fast growing, and ephemeral, as is the green alga *Ulva intestinalis*. High frequency processes affecting *Ulva* mats may change primary production, sediment chemistry, and species diversity (Pregnall and Rudy 1985, Allen 1992, McClelland and Valiela 1998a, McClelland and Valiela 1998b, Cardoso et al. 2004). Although seasonal variability in *Ulva* may be significant in Elkhorn Slough (**CHAPTER II**) there may be higher frequency processes, such as nutrient pulses or tidal influence, that are driving variability of *Ulva* in this system. The idea that long-term processes overlap shorter-term variability is known in the oceanographic literature as aliasing (see Schlax and Chelton 1994).

Previous work has found measurable changes in *Ulva* mat cover over relatively short time scales (Pihl et al. 1996, Martins et al. 2001). Pihl et al. (1996), working on the Swedish coastline, observed an increase in biomass from ~50 – 600 gDW m^{-2} that occurred in approximately five weeks at one study location. Two weeks after this peak in biomass a sharp change in weather conditions occurred (high winds and increased day-time temperature) and the algal mats disappeared. These algal mats returned to near peak values over a similarly short time scale. Martins et al. (2001) observed large (> 5 fold) month-to-month variation in green macroalgal biomass in Mondego Estuary on the west coast of Portugal. They concluded the variation was due to river management of sluice gates that varied the amount of freshwater input into the estuary. These studies demonstrated that algal mats are highly susceptible to environmental changes such as weather change or freshwater input, and that mats were highly opportunistic with relatively rapid growth and accumulation. While seasonal patterns were established in both studies, Pihl et al. (1996) also observed changes at sub-seasonal (weekly) time scales suggesting high frequency processes affecting mats.

In Elkhorn Slough, changes in cover and biomass of *Ulva* were observed seasonally over a fifteen month period, with a peak occurring in fall 2003 and general decrease until spring 2004 (**CHAPTER II**). However, I did not determine variation at sub-seasonal time scales (i.e. week to week or month to month). Seasonal patterns of variability in cover and biomass could correlate with physical changes that occur seasonally (e.g. day length). However, those seasonal patterns did not reveal higher frequency changes in cover and biomass that could be the same order of magnitude as seasonal changes. Aliasing patterns of variability in cover and biomass may lead to incorrect determination of what factors control the variability of *Ulva* mats.

In addition to "weather" and salinity, other processes that may vary week-to-week or month-to-month are light, nutrient pulses, and variations in tidal range. Although the affect of tides has been postulated as a regulating factor for algal populations, there is a lack of direct evidence that tidal processes affect algal mat cover or biomass as defined in **CHAPTER II** (FitzGerald 1978, Lowthion et al. 1985, Hernandez et al. 1997, Lavery et al. 1999, Back et al. 2000, Astill and Lavery 2001, Choi et al. 2001, Widdows and Brinsley 2002, Okey 2003). It may seem intuitive that water movement due to tidal action influences the recruitment, growth, and detachment of *Ulva* mats, yet a direct link has never been established. Lavery et al. (1999) compared algal mat biomass changes at harvested and non-harvested beaches in Australia. They found no significant difference after two months, and concluded that the effects of tidal action at the well flushed beaches were similar to harvesting. Lowthion et al. (1985) discussed the probability of algal mat movement from the rise and fall as well as the resultant of water movement caused by tides throughout the estuary. They proposed that the difficulty they faced in characterizing algal mat cover and abundance could be related to movement of algal mats as a result of tidal action that created a continually changing environment (Lowthion et al. 1985).

The movement caused by tides can be broken down into four basic mechanisms; tidal currents, rise of tides, changes in emersion times, and tidal range. Although the mechanisms are not independent, each has the potential to be a source of variation of

Ulva mat cover, biomass, and abundance. Tidal currents increase the probability of detachment of *Ulva* mats, especially during the ebbing tides from the higher high water to the lower low water (Pihl et al. 1996, Widdows and Brinsley 2002). Air may be trapped inside the tubular morphology and within and under the entire mat, and as a flood tide enters the estuary the mats are pulled from the benthos (per. obs.). During spring tides when tidal height is increased and tidal currents are strongest there is an increased chance of detachment and eventual export out of the system. Emersion times of longer than four hours have been found to inhibit *Ulva* recruitment to the substrate (Townsend and Lawson 1972), however, the mudflats in Elkhorn Slough retain moisture and may mitigate this effect. Tidal range affects *Ulva* mats through the other three mechanisms discussed. Increased tidal range amplifies tidal currents, water level, and increases immersion and emersion times.

Although tidal action may be responsible for changes in growth and accumulation, the lack of tidal action can also hinder algal mats. In estuaries with lower tidal ranges (approximately 1 m or less), the lack of water motion initially causes rapid growth and accumulation. With no loss through daily or weekly changes in tidal action, however, algal mats eventually deplete available resources (i.e. nutrients and sunlight to algae not at the surface) and essentially suffocate themselves (Back et al. 2000, Sfriso et al. 2003, Lin and Hung 2004). Tides have also been suggested to be responsible for the export of floating mats and as drift accumulation along the bottom (Hernandez et al. 1997, Astill and Lavery 2001, Okey 2003).

Temporal variability in tidal action that affects *Ulva* mat cover and biomass would produce a higher frequency of variation than seasonal processes. Tidal action affecting *Ulva* would show patterns that reflected spring and neap tides, intermediate peaks in these measurements before seasonal peaks. If variability was completely seasonal there would be a gradual increase/decrease (with some noise around the measurements) in *Ulva* until the max/min is reached. While seasonal signals in cover and biomass may be significant (**CHAPTER II**) tides could be producing equally significant changes within a season (more significant than just noise). If tidal action alters *Ulva* mats, variation in mats would occur more often within a season due to higher frequency variation of tides versus other seasonal processes.

The first goal of this study was to compare variability in algal mat dynamics (i.e. *Ulva* biomass and cover) between two different time scales, seasonal (every three months) and sub-seasonal (approximately every two weeks). If seasonal variation in algal mat dynamics is greater than sub-seasonal variation, then seasonal sampling of algal mat dynamics is sufficient to describe changes in *Ulva* mats in Elkhorn Slough. Significant differences between the time scales would suggest, however, that sampling at one particular time scale may not be appropriate for determining the variability of the system. Furthermore, if the sampling time scale used was inappropriate for the variability within the ecosystem, the resultant data and conclusions about possesses controlling algal mat dynamics could be misleading. By understanding the time scale of variation of *Ulva* in Elkhorn Slough it is possible to understand not only the processes controlling algal mats, but also the bottom-up effect on other organisms that use the algal mats (e.g. birds foraging, invertebrate habitat, etc.). The second goal was to examine if sub-seasonal variability in algal mat biomass could be related to changes in tidal action. Describing the variation in algal mat biomass that is attributable to tides will allow some discussion of a potentially significant controlling process. *Ulva* mat cover was not used because small changes to mats that decreased biomass would not necessarily change their cover. If variation in *Ulva* mats is related to tidal action, then increased tidal action should increase variation in *Ulva* mats assuming the variation is measurable at the time scale it is measured. In understanding the role of tides as a regulating factor in algal mat biomass, cover, and abundance, future work can develop more inclusive models of changes in algal mats in Elkhorn Slough that include tides and tidal action.

Methods

Sub-seasonal sampling was done within Kirby Park (Section 4, Figure 13). The study location (Elkhorn Slough) was described in the **METHODS** section of **CHAPTER II.** This study site was chosen because its seasonal cover and biomass was highly variable (**CHAPTER II**), and the hillside east of the study site allowed photographs to be taken to determine changes in cover. Samples were taken approximately every two weeks from the end of June 2004 to August 2004 [June 22 (Day 1), July 2 (D 11), July 16 (D 25), August 3 (D 43), and August 16 (D 56)]. This sampling period was chosen because seasonal sampling identified this period as being between the max/min for *Ulva* mats and long days provided more photographic opportunities. Samples were taken during low tide (~0.0 m mean lower low water) to be consistent with seasonal sampling (**See CHAPTER II**). Biomass samples were collected from Section 1 because it was assumed that any measurable effect of tides would more easily detected closer to the mouth of the estuary where tides first enter Elkhorn Slough. Variability in cover was not measured due to lack of resources.

Seasonal versus Sub-seasonal

Cover: Seasonal cover data were described and analyzed in **CHAPTER II**. For consistency in seasonal and sub-seasonal data, *Ulva* cover was used only from the site in Section 4. Data for sub-seasonal cover were obtained from photographs of the site (~950 m x 12 m) taken with a digital camera from a hillside adjacent to the mudflat within two days of biomass sampling (see below). Area of *Ulva* mats (m^2) was calculated by tracing polygons around *Ulva* mats using ImageJ (free software available at http://rsb.info.nih.gov/ij/). This software program calculated area from a reference length defined within the photograph. The angle at which the photographs were taken distorted the image, potentially altering cover measurements. To mitigate for this effect, a correction factor of 0.28 was applied to the measurements of cover that was determined by comparing a known length within the aerial photographs (**CHAPTER II**) and hillside photographs, and calculating the difference between the two images. An F-test (as described in Zar 1999) was used to compare the variability (mean square error) between the five seasonal sampling dates and five sub-seasonal sampling dates. The test was used to determine if there was a significant difference in the variability of *Ulva* mat cover between seasonal and sub-seasonal sampling.

Biomass: To estimate sub-seasonal changes in biomass, 10 samples of biomass were collected, rinsed, dried, and weighed for an estimate of dry weight per m^2 from within the site on each sampling date as described in **METHODS** in **CHAPTER II**. Seasonal biomass was the mean biomass for each season in Section 4, giving five seasonal estimates to compare with five sub-seasonal estimates (**CHAPTER II**).

An Analysis of Variance (ANOVA) was used to test for temporal differences in biomass among sub-seasonal data. Differences among the five sample dates were determined by a one-factor (DATE) ANOVA. For all analyses, data were tested for homogeneity of variance using Cochran’s C test. Data did not meet the assumption of equal variance and were subject to square-root transformation of the raw data, analysis was then performed on the transformed data (Underwood 1997). Post-hoc analysis (Bonferroni) was used to determine differences between sample dates. To compare seasonal (5 measurements) and sub-seasonal (5 measurements) variability an F-test (Zar 1999) was used to test for significant differences in cover and biomass.

Within Tides

To investigate if changes in *Ulva* mat biomass were related to changes in tides, mats were sampled intensely over a range of different tides. Two locations were used in Section 1; Location 1 (“North”) was on the North side of the main channel influenced by tides including a long tidal creek, and Location 2 on the South (“South”) side influenced by tides including a short tidal creek. The samples were collected by first marking all potential sampling sites (areas containing *Ulva* mat that could be sampled) with a piece of PVC pipe approximately 1 m in length, and then randomly selecting sample sites for each sampling date. All sampling sites were marked at the beginning in order to track gain (deposition) and loss (export) as tides could be affecting mat movements both ways. Initial sample sites were chosen within areas of 100% cover over at least a 1 m^2, this was to be consistent with seasonal samples (**CHAPTER II**). Biomass samples were collected at each marker using a 0.25 m^2 quadrat, a size consistent with seasonal and sub-seasonal sampling. Samples were brought back to the lab, cleaned, dried, and weighed to estimate dry weight per m^2. North was sampled in September, October, and December 2004. South was sampled in January and February 2005 (number of samples collected and dates are given in Table 4). Unequal sample sizes were due to loss of sampling markers, except in January when sampling was spread over four dates instead of three. To determine the relationship between tidal range and *Ulva* mat biomass, the percent change of *Ulva* mat biomass was calculated. Percent change was defined as any change (removal or deposition) in average biomass between sampling dates. To determine if there was a relationship between changes in *Ulva* mat biomass and changes in tidal range a linear regression was done with a positive relationship supporting the hypothesis that increased tidal range increases the variability of mats in Elkhorn Slough.

Results

Seasonal versus Sub-seasonal

Cover: Sub-seasonal *Ulva* mat cover (Figure 14A) ranged from a maximum on August 3 (4024 m^2) to a minimum on June 23 (2143 m^2) for the site in Section 4. There was a general increase in cover from a minimum in June 23 a maximum on August 3, with a sharp decline until the final sampling date on August 16. The greatest change per day was 130 m^2 d^{-1} (a reduction of ~ 50 % in 14 days) between the final two samples in August. Seasonal *Ulva* mat cover (Figure 15A) ranged from a maximum in April 2004 (9230 m^2) to a minimum in January 2004 (51 m^2). Cover was variable throughout the year, but the greatest change was a 180-fold increase over three months. This rapid increase over a short period of time could have been caused by a gradual change due to growth and accumulation or a massive deposition from some other part of the estuary. *Ulva* mats were commonly observed floating with the incoming and outgoing tides.

The F-test revealed a significant difference in variation of *Ulva* mat cover between seasonal and sub-seasonal samples ($F_{0.05, 4, 4} = 17.34$, $p > 0.05$), with seasonal sampling being greater than sub-seasonal. This result was expected given the difference in the range of *Ulva* mat cover observed during the two different time scales.

Biomass: Sub-seasonal *Ulva* mat biomass (Figure 14B) peaked on June 22 (183 gDW m^{-2}) and was least on July 16 (76 gDW m^{-2}). The greatest change between any two dates was a 46% decrease in biomass between June 22 and July 2 (101 gDW m^{-2}). ANOVA results showed a significant difference among sampling dates (Table 5). Post hoc Bonferroni analysis showed a significant difference between the maximum biomass estimate (June 22) and minimum measurements (July 16 and August 3, both $p < 0.05$).

Seasonal *Ulva* biomass (Figure 15B) peaked in July 2003 (160 gDW m^{-2}) and was least during July 2004 (88 gDW m^{-2}). The greatest change was a 26% decrease from July 2003 to October 2003. Differences in *Ulva* mat biomass among seasons was not significant (ANOVA; $F_{0.05, 4, 67} = 2.41$, $p = 0.058$).

The F-test used to test for difference between seasonal and sub-seasonal *Ulva* mat biomass measurement found no significant difference between the two time scales ($F_{0.05, 4, 4} = 2.48$, $p > 0.050$).

Within Tides

Within-tide *Ulva* mat biomass (Figure 16) varied from a minimum (27.5 ± 5.8 gDW m^{-2}) during December sampling to a maximum (115.2 ± 12.4 gDW m^{-2}) during January sampling. Tidal range varied from 1.1 m in September to 2.5 m in December and January (dotted line Figure 16). The minimum percent change was between September 12 and 15 (2%) and the maximum percent change was between December 8 and 12 (56%). There was a significant positive relationship between percent change in *Ulva* mat biomass and tidal range at North ($F_{0.05, 1, 4} = 9.834$, $p < 0.050$, Figure 17A) but not South ($F_{0.05, 1, 3} = 0.154$, $p = 0.721$, Figure 17B).

Discussion

There was a significant difference in variability of *Ulva* mat cover between seasonal (greater) and sub-seasonal sampling. The most likely explanation for the difference was that processes regulating cover of mats within the estuary act at both time scales and over a longer (seasonal) time scale allows for more growth and accumulation to occur. Back et al. (2000) related the mass occurrence of algal mats on the Baltic Sea coast to seasonal changes in water temperature as the ice melted in late winter and peak biomass was found in early spring. Martins et al. (2001) observed a relationship between freshwater input and macroalgal growth and abundance, which varied seasonal and depended on total precipitation and river management. The increased seasonal growth leads to increased total abundance and therefore more macroalgal biomass that could be distributed.

There was no significant difference in the variability of *Ulva* mat biomass between the two sampling time scales. Although the power of the test was low ($\beta < 0.80$), the result suggested that the variability of biomass could be explained by processes occurring at shorter (sub-seasonal) time scales. It is unlikely that changes in abiotic factors (e.g. water/air temperature, PAR) would account for measurable changes in biomass on a bi-weekly basis. Pihl et al. (1996) observed however, that following period of sustained (several days) high winds (15-20 m s^{-1}) biomass was measurably reduced. It is more likely that the physical movement of biomass by tides or winds regulates *Ulva* mat biomass in Elkhorn Slough. Seasonal variability in *Ulva* mat cover may not occur if there was no mechanism for increasing distribution, such as the constant movement of biomass via tidal action. Without constant movement of mats and recruits, *Ulva* may accumulate in smaller areas and be self-limiting as mats grew and reduced sunlight and available nutrients as observed by Lin and Hung (2004) in Taiwan.

While tidal action may be responsible for a majority of the variability of *Ulva* mat biomass, it was important to consider alternative explanations. The range in average *Ulva* mat biomass was ~78 - 180 gDW m^{-2} for sub-seasonal sampling in Section 4 compared to ~90 - 150 gDW m^{-2} (**CHAPTER II**) for seasonal sampling throughout the entire Section; the range of average weights was greater over the shorter time scale. It could be argued that the smaller sample size during sub-seasonal sampling biased the average values; however, the average sample size for seasonal sampling was fourteen versus ten for sub-seasonal samples and power analysis ($\alpha = 0.05$, $\beta = 0.80$) was equal for both sampling sizes. Another potential bias may be that sub-seasonal biomass samples were collected from within a smaller area inside the boundaries of Section 4. When samples are distributed over smaller sampling area the expectation would be for less variation, but, biomass variability was greater in the smaller area.

The influence of tidal action on *Ulva* mat biomass was observed more directly when sampling within tides (Figure 16). As tidal range increased, mat biomass decreased on all occasions except in October when an apparent deposition event occurred. At North, the relationship between tidal range and percent change in biomass was significant (Figure 17A) suggesting that tides play a major role in regulating *Ulva* biomass and, though not measured, potentially cover. At South, the relationship was not significant (Figure 17B), suggesting that while tidal range plays a major role in *Ulva* mat movement, it may be a localized phenomenon. It is clear that more locations need to be investigated to better determine the relationship between tides and *Ulva* mat biomass.

Hillside photographs were taken in July 2004 before and after aerial photographs of the same mudflat. The estimate of cover from the aerial photos was about 1000 m^2 less than either of the other two measurements (Figure 18). Possible explanations are that the hillside over-estimates cover, the correction factor was incorrect, the aerial photographs underestimated biomass, or large *Ulva* mats were moved during the early part of July. The tidal range during the first sub-seasonal sampling date in July was ~ 2.5 m, the second sub-seasonal date was ~ 1.9 m, while the seasonal aerial flight was ~ 1.4 m. The large variation in cover could be explained by the difference in these ranges. It appears that the week after spring tides *Ulva* cover was decreased, suggesting export of mats during this period. This would also explain the decrease in cover between the final two sampling dates in August when tidal range peaked (~2.1 m) two days before samples were collected. *Ulva* mats covering the mudflat during the first part of each month could have been removed during the larger tidal range, resulting in a low measurement of cover in subsequent measurements.

Physical movement of algal mats seems likely to explain short term (sub-seasonal) variation in *Ulva* mat biomass, and seasonal growth and accumulation coupled with the physical movement may regulate longer term (seasonal) *Ulva* mat cover in Elkhorn Slough. The combination of processes acting at differing time scales leads to a dynamic algal population. Another potential source of sub-seasonal variation related to tides is variability in nitrate entering the estuary. Pulses of nitrate were observed during the first two weeks of sampling and subsequently concentrations decreased (Figure 19). Laboratory analysis by Fong et al. (2004) found that increased nutrient concentrations (including nitrate) on average increased growth by 30% over a four week period.

Maximum pulses of nitrate into the estuary were within the concentrations investigated by Fong et al. (2004), suggesting that the effect of tidal nutrient pulses could be a source of sub-seasonal variation of *Ulva* mat biomass in Elkhorn Slough. It is unlikely that there was any relationship between nutrient pulses and within tide variation of mat biomass, even though *Ulva* has relatively high nutrient (nitrogen and phosphorus) uptake rates (Bjornsater and Wheeler 1990). Bjornsater and Wheeler (1990) did find that increased nutrient concentrations led to increased growth rate in ulvoids that peaked after ~5 days of enrichment. However, this increase in growth rate occurred with continuous nutrient enrichment. Nutrient pulses in Elkhorn Slough are variable throughout the day, mostly related to the movement of nutrient rich tidal waters. During the rainy season, agricultural runoff may create a condition that simulates continuous nutrient enrichment and could explain fall peak in cover and abundance (**CHAPTER II**).

Although sub-seasonal and within tide variation are important for modeling variability in *Ulva* mat cover and biomass, the dominant patterns of variability in *Ulva* abundance were seasonal (**CHAPTER II**). Future work in Elkhorn Slough and estuaries world-wide should investigate the relationship of tides and algal mats so that links can be established and proper management decisions can be made. This work has shown that tides influence *Ulva* mat biomass and potentially mat cover and abundance.

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Table 1. Sampling dates for biomass, number of biomass samples collected, and flight date for the aerial photography for each season and section.

	Jul-03	**n**	**Oct-03**	**n**	**Jan-04**	**n**	**Apr-04**	**n**	**Jul-04**	**n**
Section 1	7/7/2003	19	10/7/2003	20	1/17/2004	20	Not Sampled	NA	7/7/2004	20
Section 2	7/9/2003	9	10/8/2003	9	1/18/2004	10	4/13/2004	10	7/3/2004	9
Section 3	7/9/2003	10	10/22/2003	10	1/18/2004	7	4/13/2004	10	7/2/2004	10
Section 4	7/11/2003	10	10/22/2003	17	1/23/2004	20	4/22/2004	5	7/5/2004	20
Section 5	7/15/2003	8	10/22/2003	8	1/29/2004	10	4/14/2004	10	7/2/2004	10
Flight	7/3/2003		10/22/2003		1/18/2004		4/21/2004		7/7/2004	
Total Samples		56		64		67		35		69

Table 2. ANOVA results for *Ulva* cover data including variance components (VC) and magnitude of effects (ω^2, expressed as %). VC is the relative amount of variability contributed by each factor and ω^2 is the percent of total variability of each factor.

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P	VC	ω^2
SECTION	8.37×10^9	4	2.09×10^9	1.136	0.375	4.00×10^7	1.19
SEASON	4.46×10^{10}	4	1.12×10^{10}	6.058	0.004	1.49×10^9	44.20
Error	2.95×10^{10}	16	1.84×10^9			1.84×10^9	54.61

Table 3. ANOVA results for *Ulva* biomass data including variance components (VC) and magnitude of effects (ω^2, expressed as %). VC is the relative amount of variability contributed by each factor and ω^2 is the percent of total variability of each factor.

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P	VC	ω^2
SEASON	98387.12	4	24596.78	4.149	0.003	266.24	3.7
SECTION	1457.83	4	364.46	0.061	0.993	0	0
SEASON*SECTION	250969.43	16	15685.59	2.646	0.001	683.12	9.4
Error	1695441.76	286	5928.12			5928.12	86.9

Table 4. Sampling location, month, date, and number of biomass samples collected in Section 1 to determine within tide variation.

North

Month	Dates	n
September	8, 12, 15	8, 6, 6
October	12, 17, 22	15, 15, 15
December	8, 12, 16	15, 15, 15

South

Month	Dates	n
January	6, 9, 12, 15	10, 10, 10, 10
February	3, 7, 10	15, 14, 14

Table 5. ANOVA results testing for differences in sub-seasonal biomass among sampling dates.

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
DATE	123.262	4	30.815	3.777	0.010
Error	367.138	45	8.159		

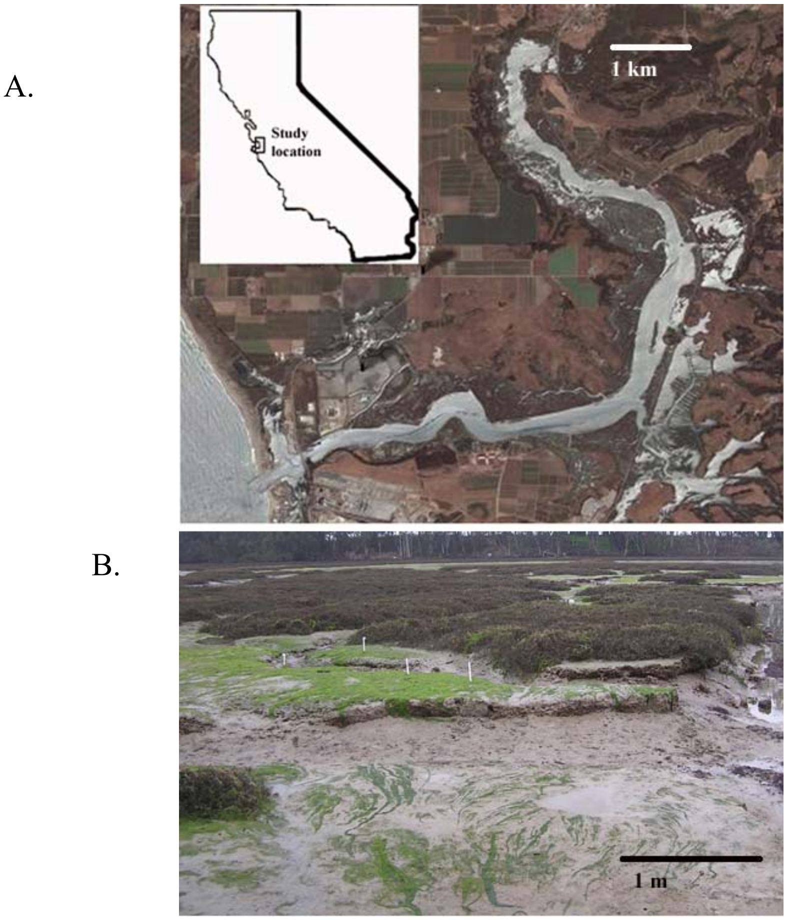


Figure 1. (A) Satellite photograph of Elkhorn Slough and surrounding land. (B) Example of cover of *Ulva* mats on the mudflats.

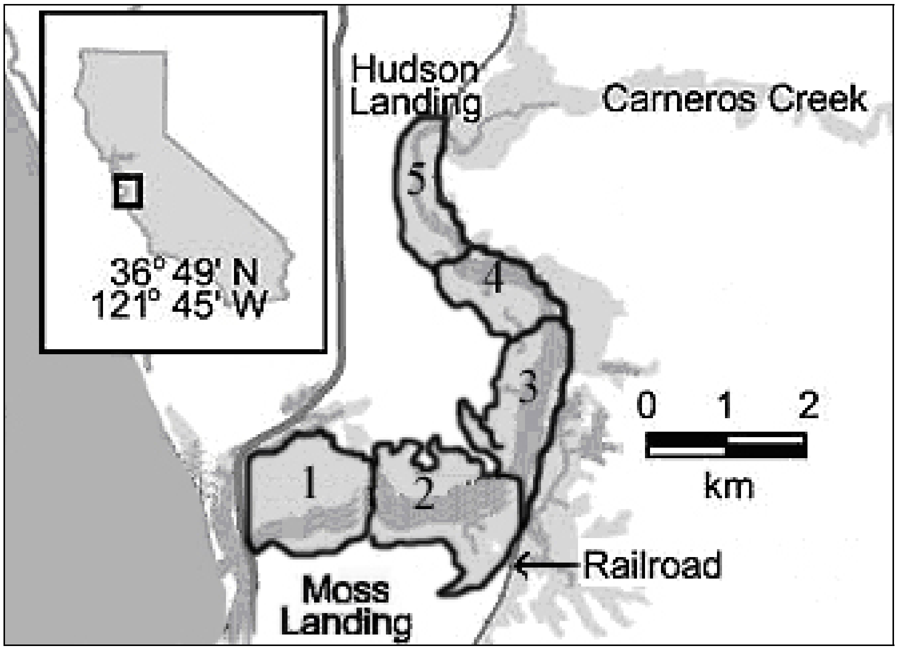


Figure 2. Elkhorn Slough divided into the five sections used in this study.

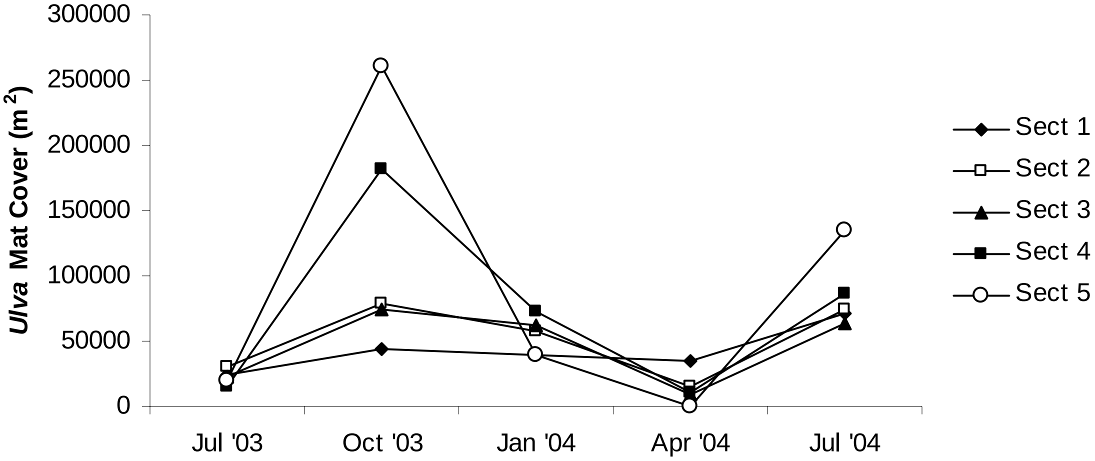


Figure 3. Seasonal variation of cover of *Ulva* mats within sections of Elkhorn Slough from July 2003 to July 2004.

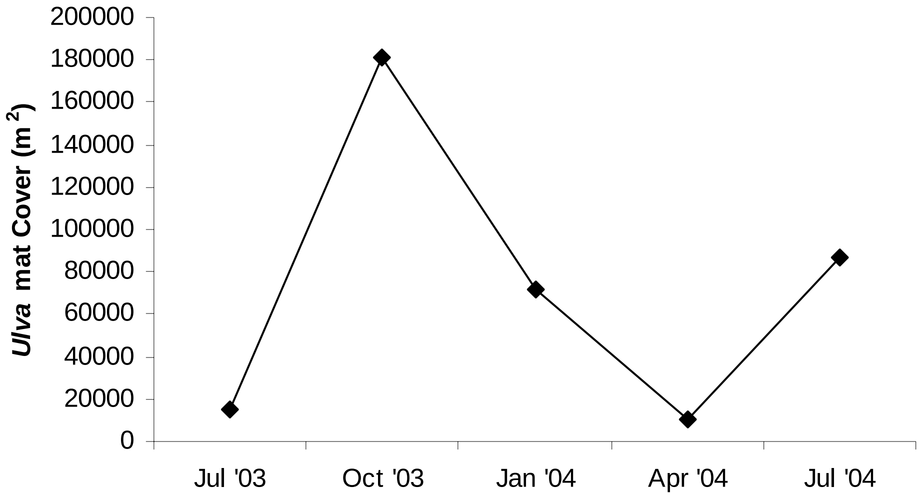


Figure 4. Seasonal changes of cover for all sections from July 2003 to July 2004.

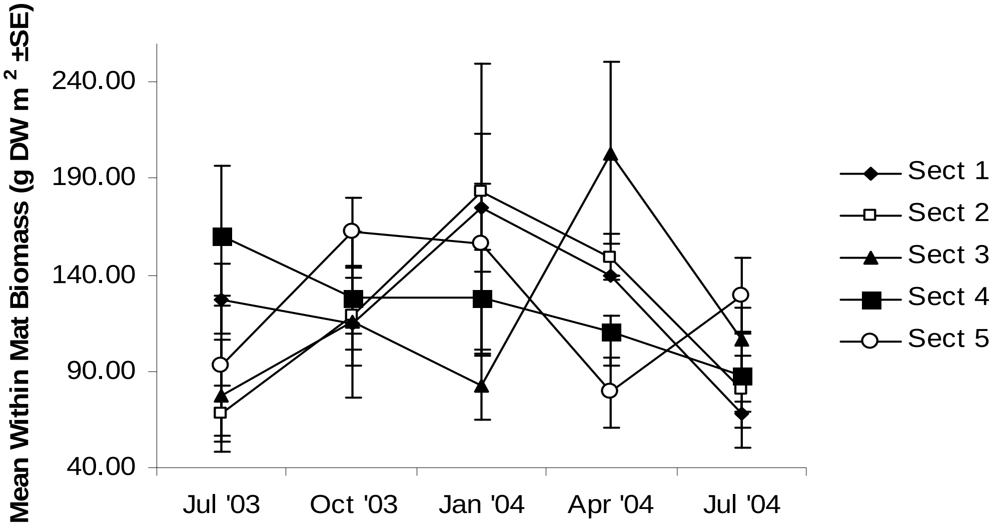


Figure 5. Seasonal changes of within-mat biomass (mean gDW m^{-2} ±SE) by section.

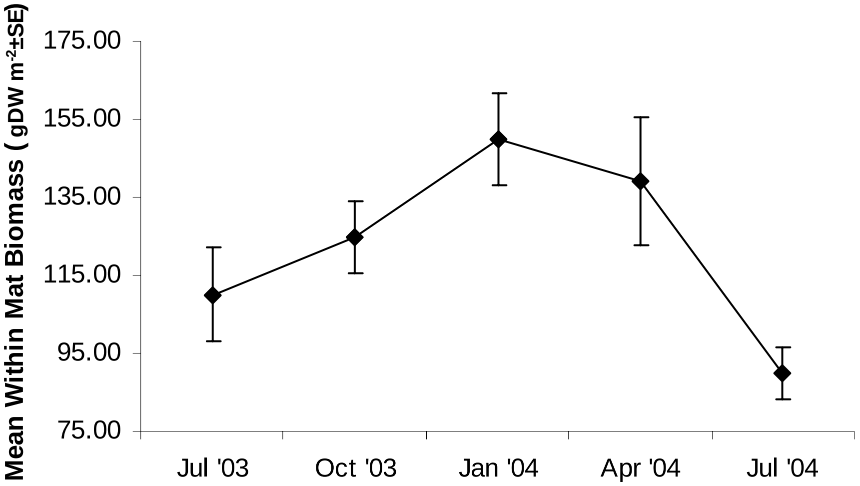


Figure 6. Seasonal changes of biomass (mean gDW m^{-2} ± SE) from July 2003 to July 2004.

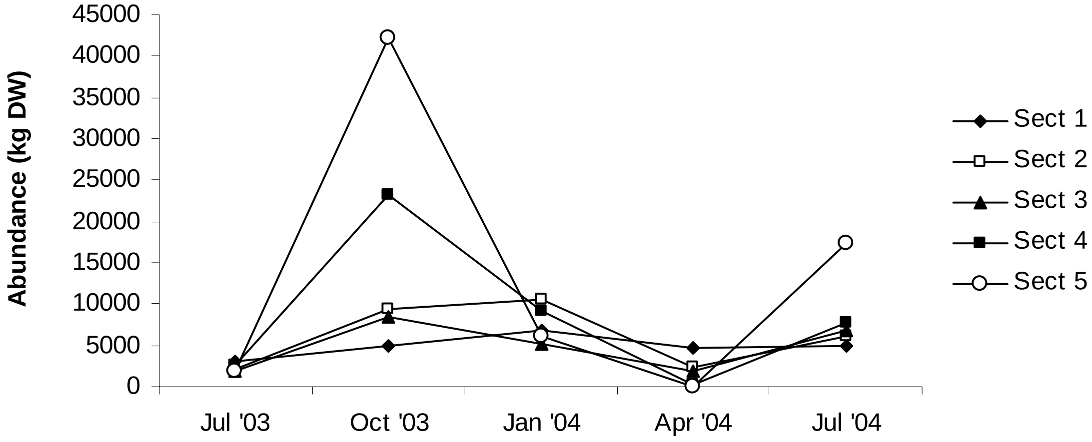


Figure 7. Seasonal variation in abundance, total biomass (kg DW), among sections in Elkhorn Slough from July 2003 to July 2004.

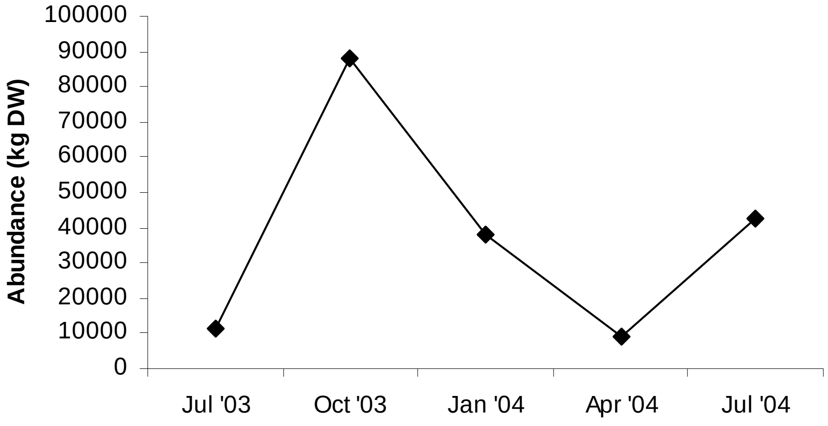


Figure 8. Seasonal changes of total biomass (kg DW) for all sections from July 2003 to July 2004.

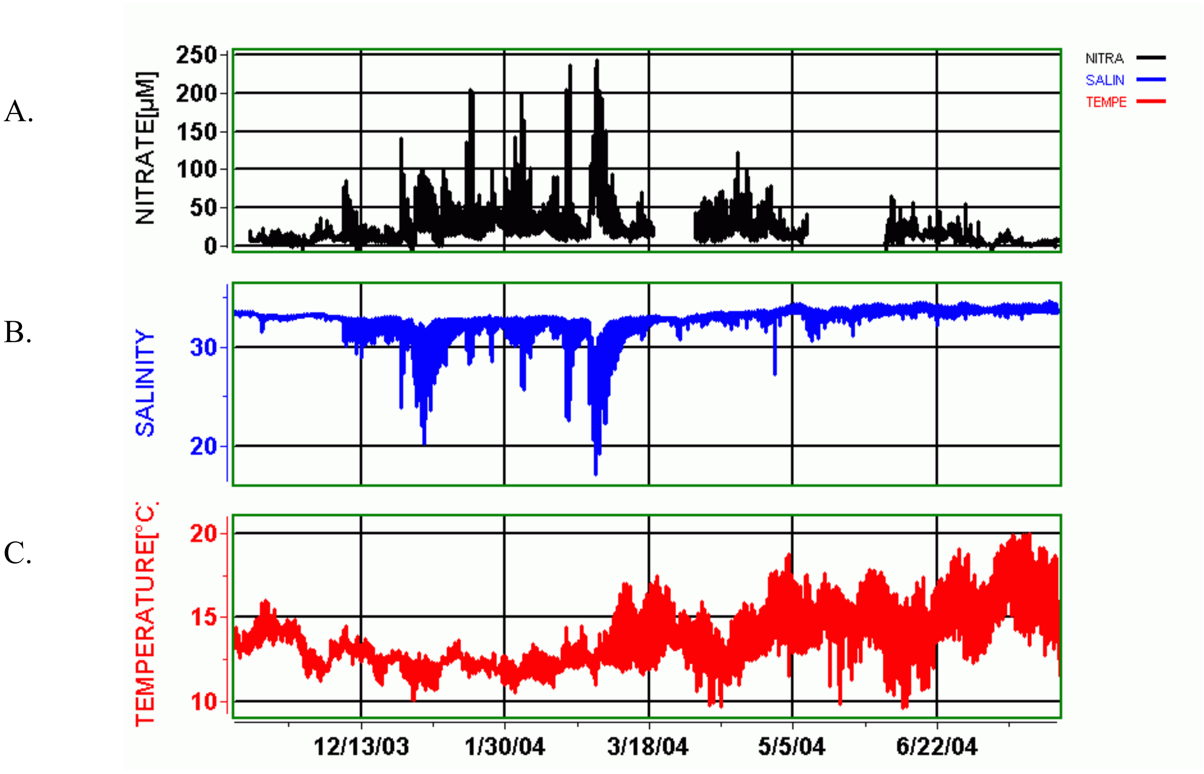


Figure 9. Nitrate (A, µM), Salinity (B, psu), and Water Temperature (C, ^{o}C) measured hourly at LOBO 1 in Section 1 of Elkhorn Slough from October 2003 to July 2004.

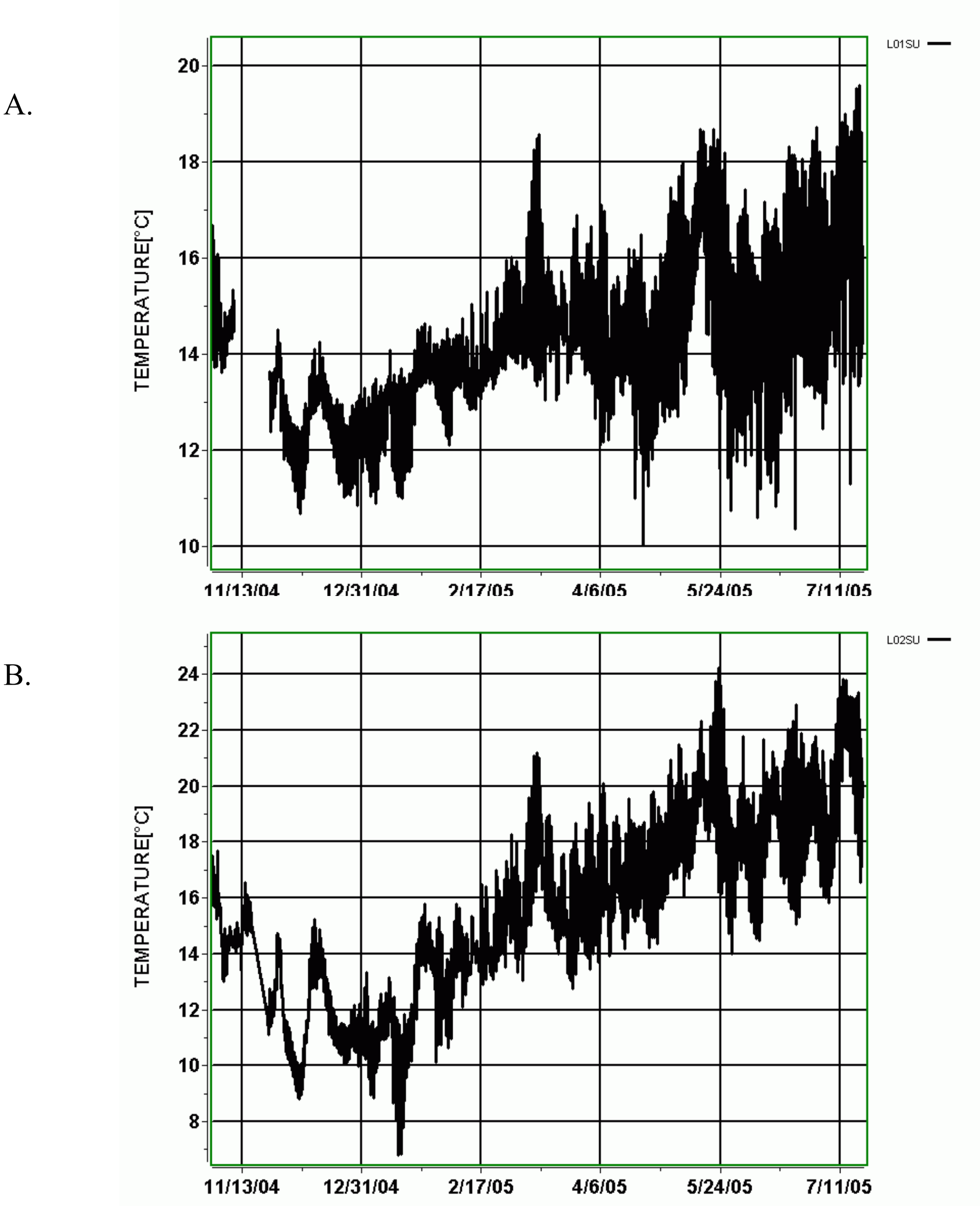


Figure 10. Water Temperature (°C) measured hourly at LOBO 1 in Section 1 (A) and LOBO 2 in Section 4 (B) in Elkhorn Slough from November 2004 to July 2005.

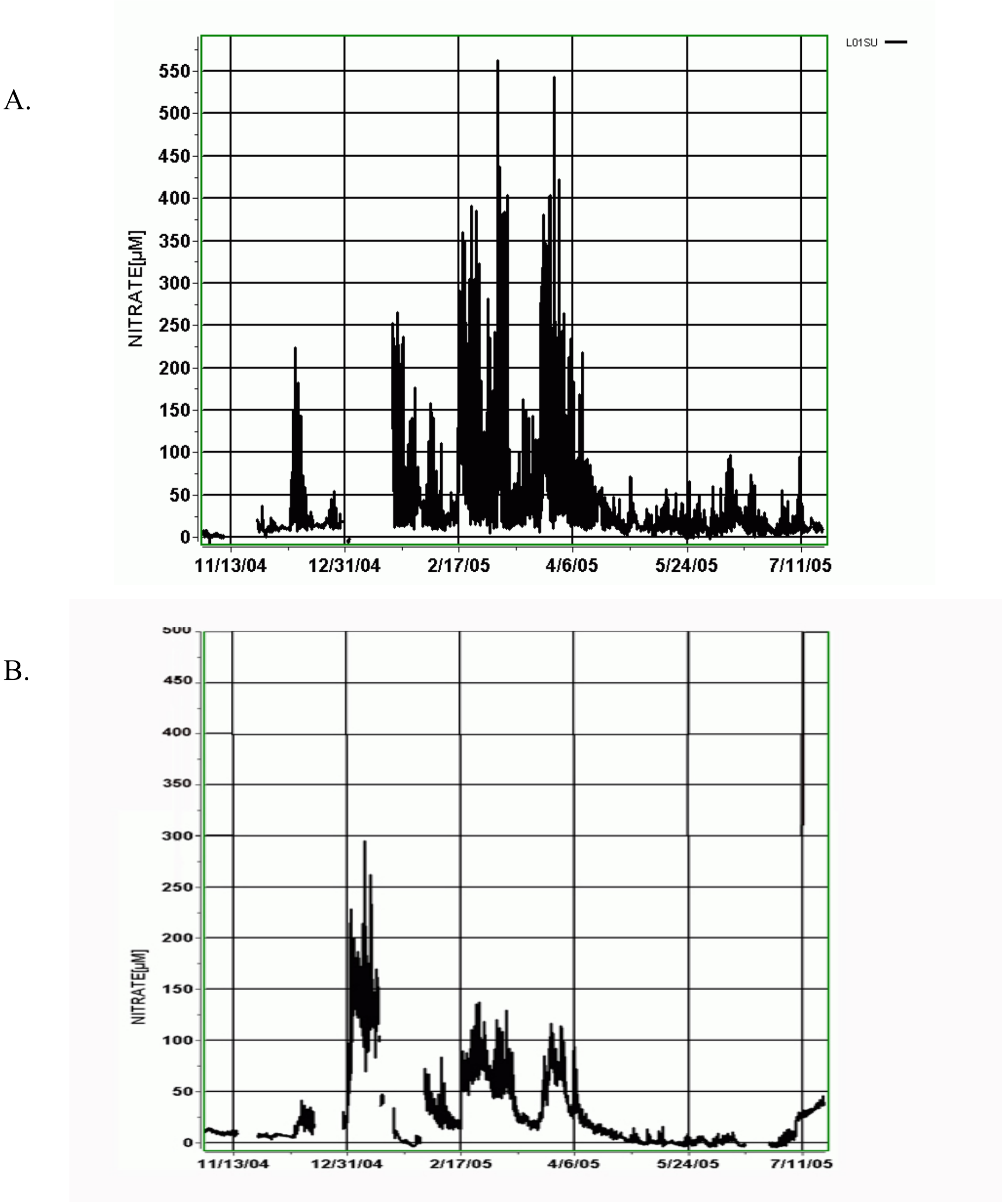
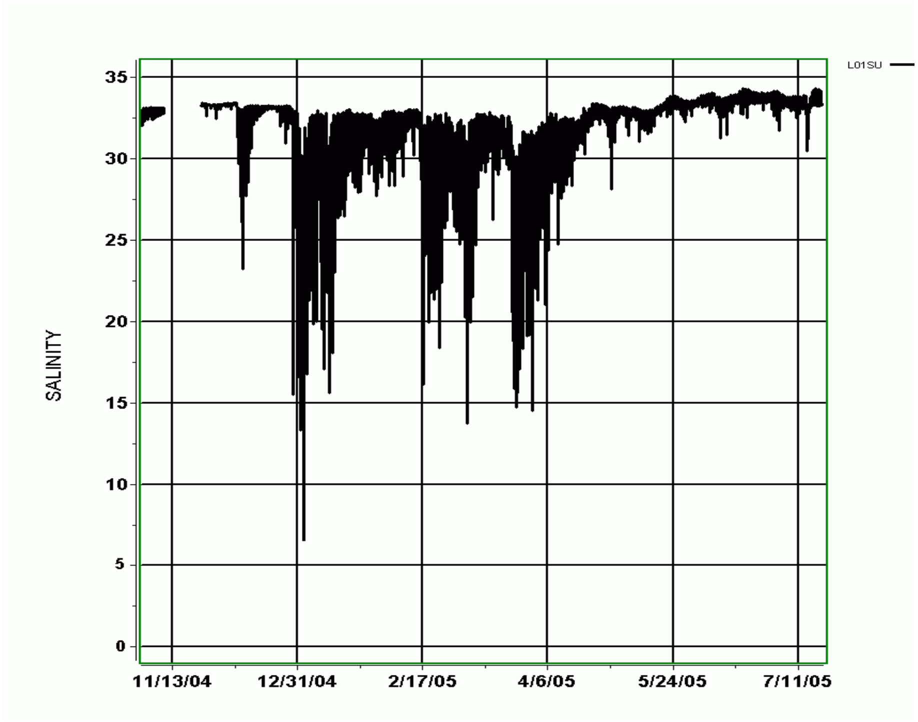


Figure 11. Nitrate (µM) measured hourly at LOBO 1 in Section 1 (A) and LOBO 2 in Section 4 (B) in Elkhorn Slough from November 2004 to July 2005.

A.



B.

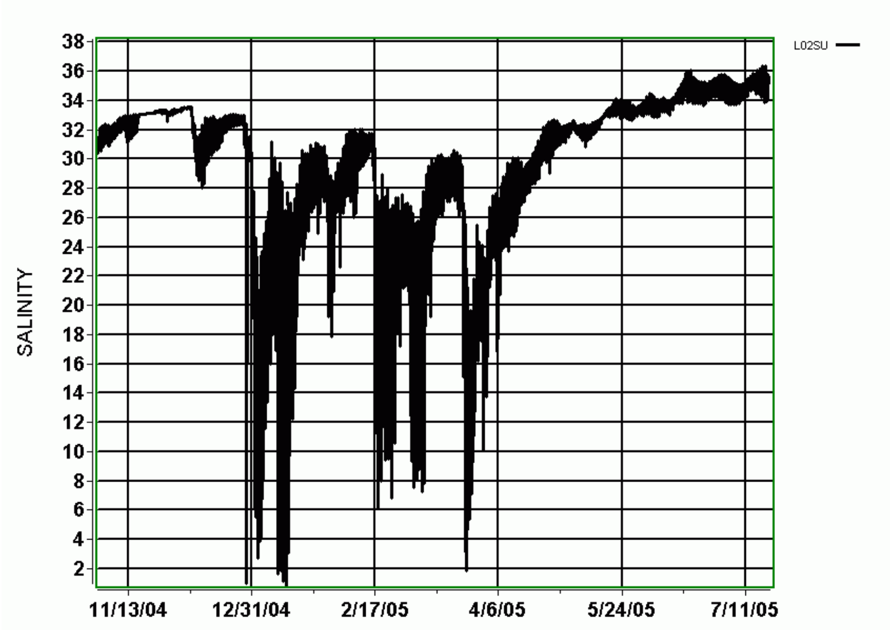


Figure 12. Salinity (psu) measured hourly at LOBO 1 in Section 1 (A) and LOBO 2 in Section 4 (B) in Elkhorn Slough from November 2004 to July 2005.

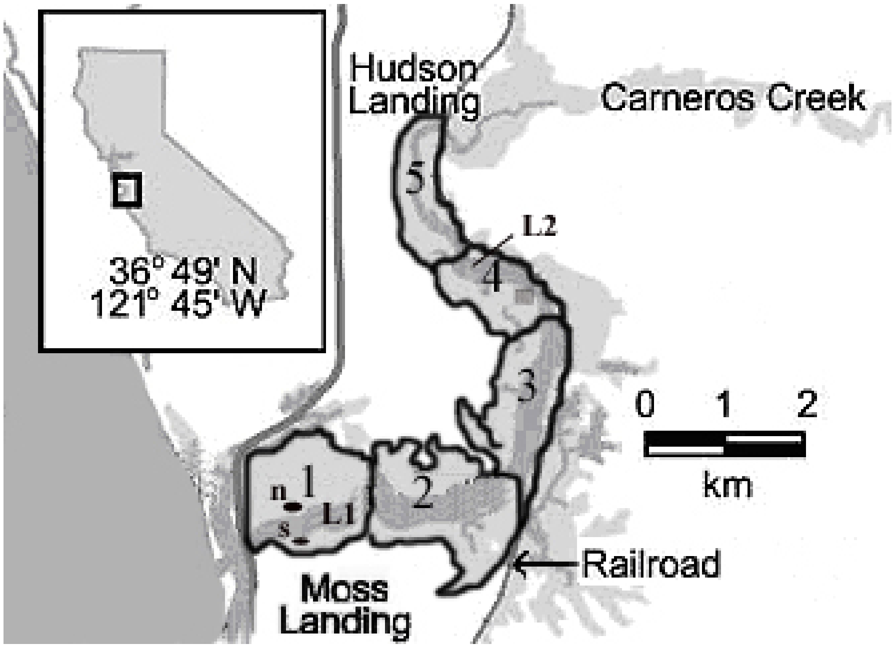


Figure 13. Elkhorn Slough divided into five sections. Data for sub-seasonal variability was collected in the shaded area in Section 4. Data for within tides was collected in Section 1. LOBO 1 (L1) in Section 1 and L2 in Section 4.

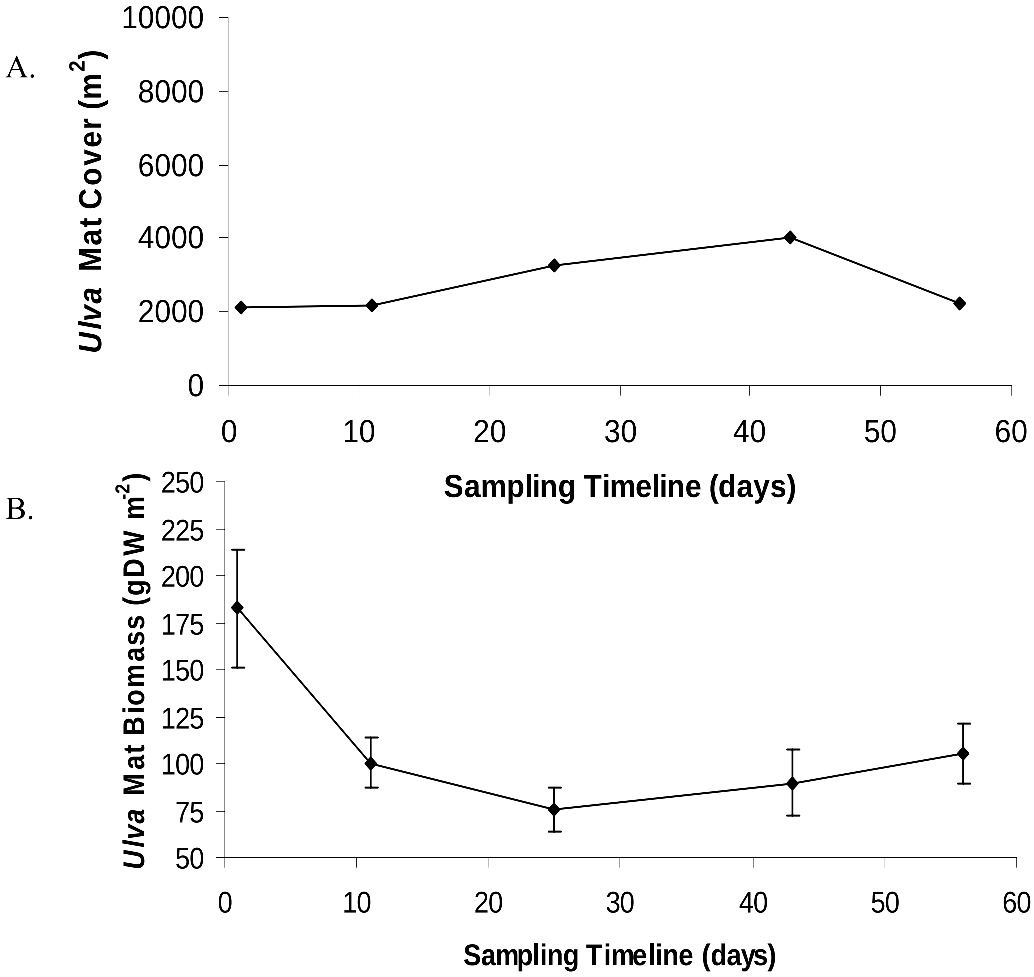


Figure 14. Sub-seasonal variation of *Ulva* mat cover (m^2, A) and *Ulva* mat biomass ($gDW\ m^{-2}$ ± SE, B) in the site in Section 4, June – August 2004.

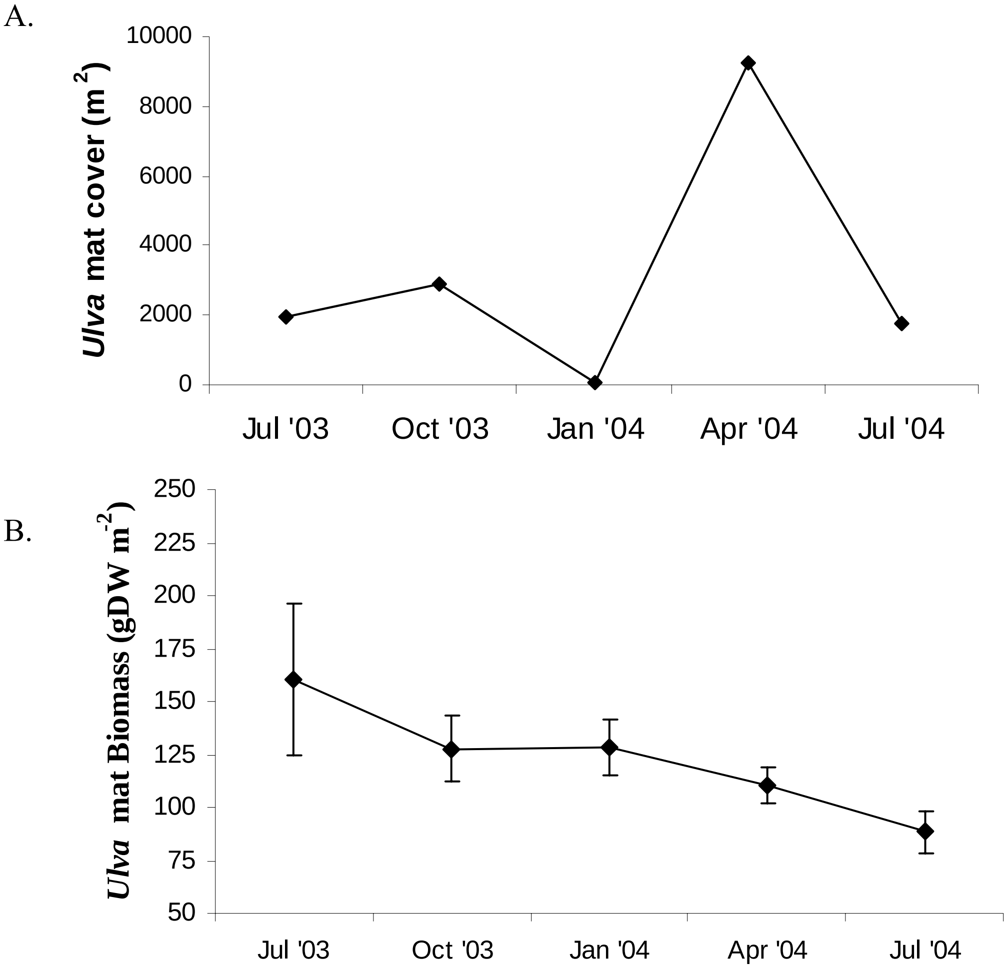


Figure 15. Seasonal variation of *Ulva* mat cover (m^2, A) and *Ulva* mat biomass (gDW m^{-2} ± SE, B) in the site in Section 4, June – August 2004.

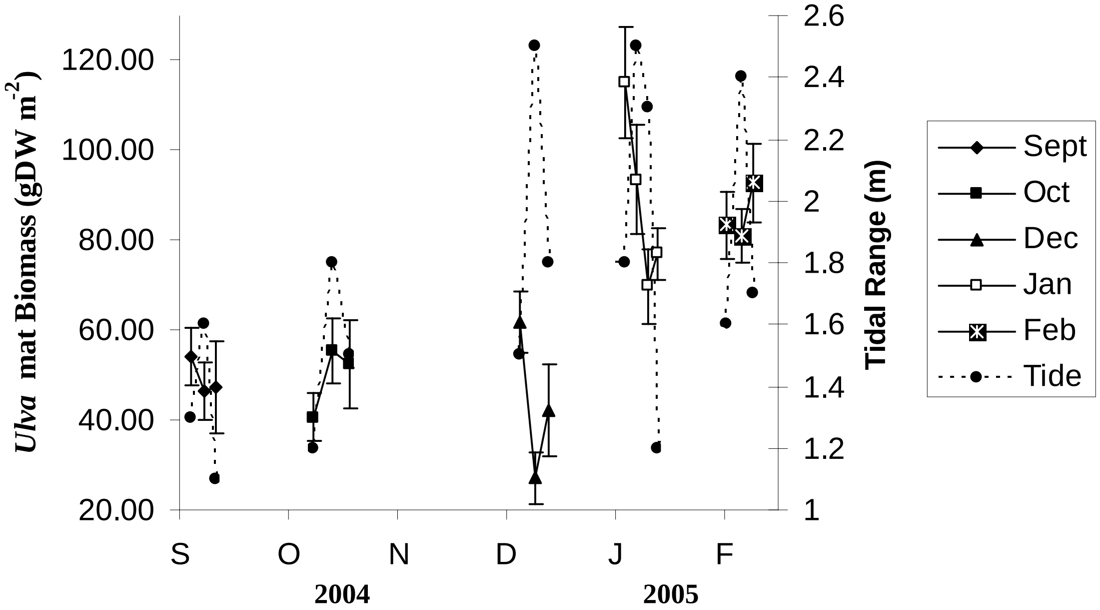


Figure 16. Variation in mean *Ulva* mat biomass (gDW m^{-2} ± SE) during each within tide sampling period. The dotted line represents tidal range (m) on the sampling day. North was sampled in September, October, and December. South was sampled in January and February.

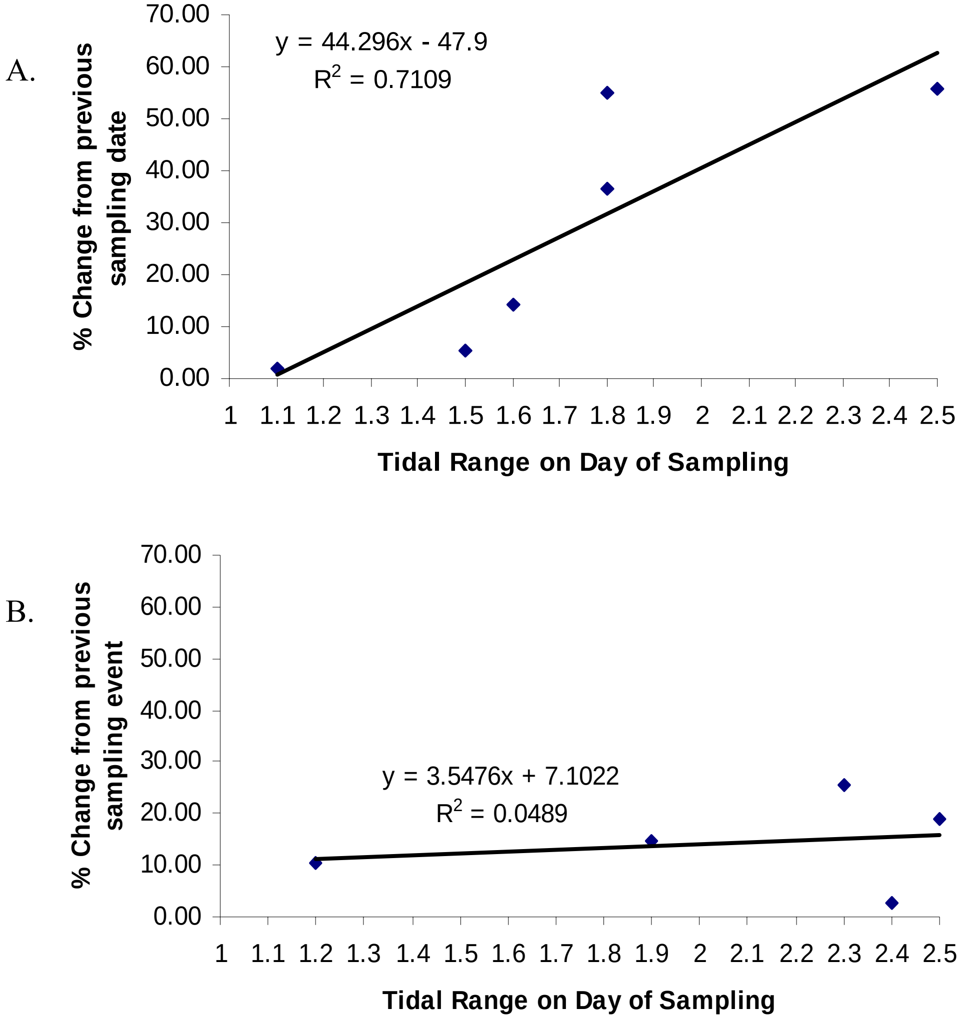


Figure 17. Changes in average *Ulva* mat biomass versus tidal range during within tide sampling for North (A) and South (B) locations. Linear regression equation is given and plotted.

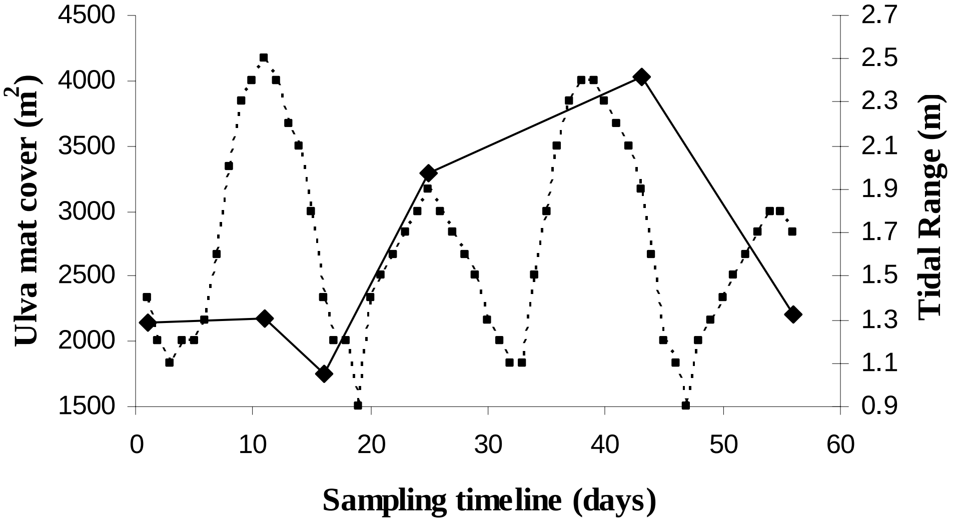


Figure 18. Sub-seasonal variation in *Ulva* mat cover (m^2) for the site in Section 4. Day 16 was seasonal cover data was determined from aerial photographs. Tidal range for each day during the sampling timeline is given as a dotted line.

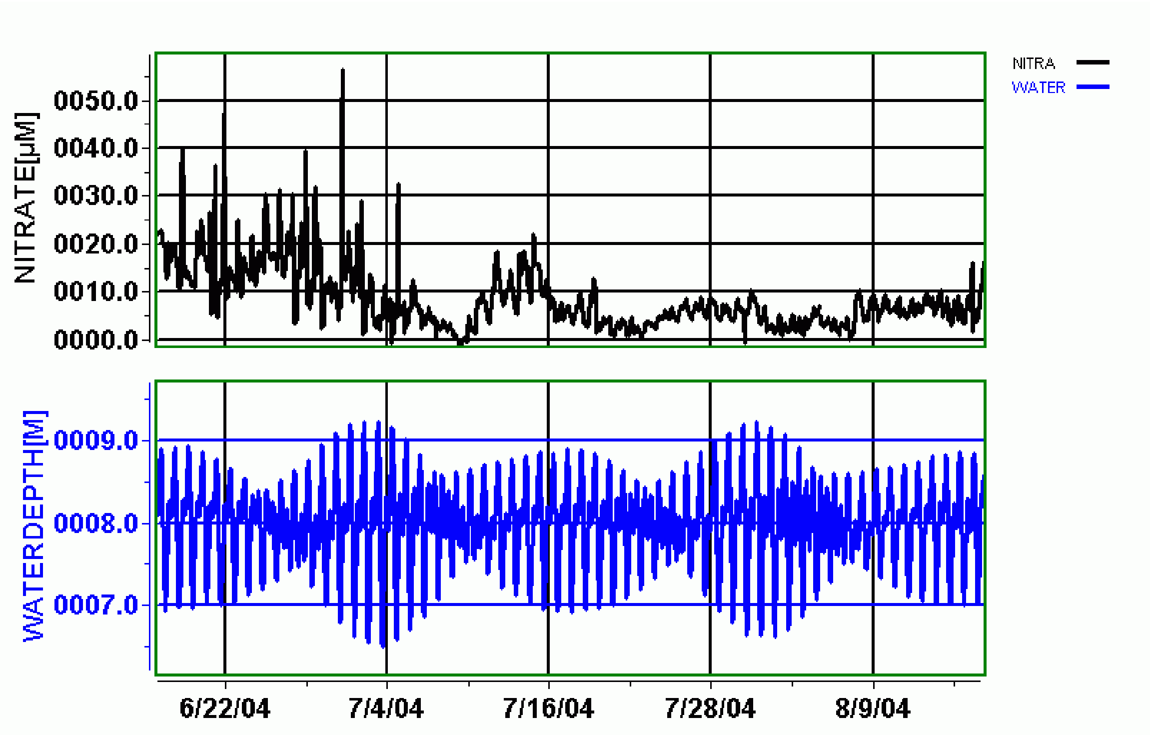


Figure 19. Sub-seasonal variation in Nitrate (µM) concentration and water depth (m, used as a proxy for tides). Data were collected at LOBO 1 mooring in the main channel of Elkhorn Slough in Section 1.

APPENDIX I

MatLab source code for photographic processing and analysis

```
function [r_min, r_max, g_min, g_max, b_min, b_max] = ulva
% User Friendly analysis program to analyze aerial photgraphs
% of Elkhorn Slough.
% 19 August 2004; TJ Schaadt
% 02 September 2004; TJ Schaadt  changed script to a function to work
%                               in conjuction with "count"

global r_min r_max g_min g_max b_min b_max
global sample F

[F P] = uigetfile('*.jpg', 'Choose image to analyze:');
sample = imread([P F]);            % open file.

fprintf('\n')
fprintf('*****Read Me******** \n')
fprintf('Select an area (2x2cm on screen) containing the color \n')
fprintf('of green that represents Ulva \n\n')
fprintf('Press the enter button to see the image \n\n\n\n')

% pause
imshow(sample)
sample_2 = imcrop;

close(1)

fprintf('\n')
fprintf('*****Read Me******** \n')
fprintf('Now use the crosshair to select twenty (20) individual pixels \n\n')
fprintf('Maximize the window to ease the selection process')
fprintf('Press the enter button to see the image \n\n\n\n')

% pause
imshow(sample_2)


[x,y] = ginput(20);
Q = impixel(sample_2,x,y);


r_min = min(Q(:,1));
r_max = max(Q(:,1));
```

```
g_min = min(Q(:,2));
g_max = max(Q(:,2));
b_min = min(Q(:,3));
b_max = max(Q(:,3));


close all

[total_pixels,shaded_pixels] = count


function [total_pixels,shaded_pixels] = count
% Function to follow Ulva function

global r_min r_max g_min g_max b_min b_max
global sample F
fprintf('\n')
fprintf('*****Read Me******** \n')
fprintf('Now the choose an image \n')
fprintf('Use the mouse to zoom in on a section of the image you want to analyze \n\n')
fprintf('****Note****** \n')
fprintf('The area that you select to analyze can be \n larger than the area previously
         selected \n\n')
fprintf('Press the ENTER button to choose image \n')

% pause

% [F P] = uigetfile('*.jpg', 'Choose image to analyze:');
% sample = imread([P F]);            % open file.

imshow(sample);
sample_2 = imcrop;
close(1)
imshow(sample_2);


r_index = find(sample_2(:,:,1) >= r_min & sample_2(:,:,1) <= r_max);
                                                        %These 3 lines find and index
g_index = find(sample_2(:,:,2) >= g_min & sample_2(:,:,2) <= g_max);
                                                        %the value found inbetween the
b_index = find(sample_2(:,:,3) >= b_min & sample_2(:,:,3) <= b_max);
                                                        %set values for Ulva


rg_intersect = intersect(r_index,g_index);          % Finds all the values that are
rb_intersect = intersect(r_index,b_index);          % common to both of the matrices
```

```
rgb_index = intersect(rb_intersect,rg_intersect);


x = sample_2(:,:,1);    %These 3 lines assign the RGB values to the variable x,y,z
y = sample_2(:,:,2);
z = sample_2(:,:,3);

x(rgb_index) = 250;     %These 3 lines change the image so that the pixels with Ulva turn
        red
y(rgb_index) = 0;
z(rgb_index) = 0;


shad = cat(3,x,y,z);  %Here a new image is created with the red Ulva pixels

imshow(sample_2);     % Shows the cropped image

figure, imshow(shad)  % Shows the shaded, cropped image

[m,n] = size(x);
total_pixels = m*n;         % gives total number of pixels in the photo


[q,w] = size(rgb_index);
shaded_pixels = q;          % gives number of shaded pixels in the photo


fprintf('%s',F)
```