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DYNAMICS AND ECOLOGICAL IMPLICATIONS OF THE
ULVA-ZOSTERA ECOTONE IN ELKHORN SLOUGH, CALIFORNIA

A Thesis

Presented to

The Faculty of Moss Landing Marine Laboratories

San José State University

In Partial Fulfillment

of the Requirements for the Degree of

Master of Science

by

María Vila Duplá

August 2019

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The Designated Thesis Committee Approves the Thesis Titled

DYNAMICS AND ECOLOGICAL IMPLICATIONS OF THE
ULVA-ZOSTERA ECOTONE IN ELKHORN SLOUGH, CALIFORNIA

by

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ABSTRACT

DYNAMICS AND ECOLOGICAL IMPLICATIONS OF THE *ULVA-ZOSTERA* ECOTONE IN ELKHORN SLOUGH, CALIFORNIA

by María Vila Duplá

Ecotones are transitional areas between adjacent ecological communities that have unique ecological qualities defined by space and time scales, and by the interactions between adjacent systems. Ecotones play an essential role in supporting biologically diverse communities, and are sensitive indicators of global change. An *Ulva-Zostera* ecotone extends along the northern shore of Seal Bend in Elkhorn Slough, an estuary located in central California. Although previous studies have mentioned the presence of the *Ulva-Zostera* ecotone, this was the first study to focus on understanding its driving factors, spatiotemporal dynamics, and overall ecological implications. A combination of habitat monitoring, water quality assessments, sediment analyses, and recruitment and transplants experiments across the ecotone was used to describe the ecological characteristics of the system. Ecotone dynamics were driven by seasonality of *Ulva* spp. Distribution of *Ulva* spp. across the ecotone was limited by processes affecting its early developmental stages. The presence of *Zostera marina* initiated these mechanisms via modification of the environment and recruitment of grazers. Grazing was found to regulate macroalgal abundance, and specific grazer groups played an essential role in this. These results can be widely applied to guide future research efforts focusing on understanding and predicting habitat shifts and consequent ecosystem transformations.

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INTRODUCTION

Ecological research focuses on patterns and processes in variable systems and at numerous spatial and temporal scales (Allen and Starr 1982). Examining patterns in nature and developing theories based on the patterns observed is key to developing predictive theory for ecology (Levin 1992). Patterns imply repetition, and thus allow for prediction and modeling (MacArthur 1972). Observations of patterns or lack of patterns in the environment are the essential starting points for any ecological study, as they are the basis from which explanatory models about processes are developed (Underwood 2000). Ecological experiments attempt to link spatiotemporal patterns with ecological processes by characterizing patterns, developing hypotheses about the underlying processes, and evaluating them with experiments or models (Jeltsch et al. 1999, Fortin and Dale 2005). Areas of research that constantly make predictions from observable patterns include biogeography (e.g. Hillebrand 2004), conservation ecology (e.g. Paine 1980), and allometry (e.g. Kleiber 1947). Ecologists have become increasingly interested in describing and quantifying the underlying processes behind spatial patterns (McIntire 2009). Fletcher and Fortin (2018) concluded that the first step in understanding any ecological process is to identify its spatial patterns. Spatial patterns are displayed by both physical and biological variables in nature (Levin 1992). While physical structure is sufficient to explain some spatial patterns, complex ecological interactions are often associated with patterns of species abundance and distribution (Underwood and

Chapman 1996). The imprecision of biological processes and the possibility that multiple processes might be causing a single spatial pattern complicate pattern analysis (McIntire 2009). Despite limitations, ecological patterns are used to inform theory, which in turn informs applied ecology (Chave 2013).

Ecotones, also known as habitat boundaries, are transitional structural elements within high diversity biological systems, both at the community and species level (Naiman et al. 1990). The “ecotone effect” refers to the pattern of increased species richness and abundance, and occurrence of unique species, at these system boundary regions (Odum 1953). There is also evidence that ecotones hold high biological diversity at the species level, which can translate into morphological and genetic diversity (Kark and van Rensburg 2006). This can occur because, according to the Gradient Model, sharp environmental gradients may lead to adaptive divergence and speciation, even if there is some gene flow across ecotones (Moritz 2001). Therefore, the presence of ecotones can be indicative of a system’s greater ecological value compared to other systems (Risser 1993).

As transition regions between two or more ecological communities, the presence of ecotones is often explained by ecoclines, which are transition regions of physical properties (Attrill and Rundle 2002). The systems on either side of the ecotone tend to be characterized by different environmental factors that change across the ecotone boundary (Janauer and Kum 1996). Boundaries are often associated with increased beta-diversity (Kark 2013), although this may

not be true for those that experience dramatic spatial and temporal fluctuations (van der Maarel 1976).

Transitional zones between habitats have traditionally been considered distinct from the habitats themselves (e.g. Livingston 1903, Clements 1905). They may act as semipermeable barriers that allow exchange of energy, nutrients, and propagules (Holland 2012). Changes in population or community structure and distribution at these boundaries between habitats are known as the "edge effect" (Forman and Godron 1986). For individual species, this implies a positive, negative or neutral change in abundance. Increased species abundances at the ecotone boundary are the most commonly reported pattern in the literature, and may be explained by spillover at the boundary, the ways in which edges enhance habitat quality, or by influencing resource availability and distribution (Hansen et al. 1992).

Ecotones are often sorted into different levels depending on spatial scale. These levels are biome, landscape, patch, and population (Gosz 1993). This classification based on scale can be extremely helpful for identifying the range of constraints, patterns and processes associated with ecotones. While biome or landscape ecotones are probably constrained by climatic and topographic factors, transitional zones at finer scales are usually shaped by a larger number of factors, due to the fact that fine-scale variation is integrated at broad scales (Gosz 1993). Therefore, soil characteristics, interspecific interactions, physiological controls and population genetics have to be added to

microclimatology and microtopography as possible constraints on community ecotones (Hansen et al. 1992). While some ecotones are generated by disturbance, others originate from edaphic boundaries due to climate, hydrology, or sediments (Hansen et al 1988). Natural ecotones tend to be irregularly shaped. If we place a transect across an ecotone, we expect to see increased spatial variation or increased patchiness right at the transition (Gosz 1993). Similarly, as one approaches ecotones, homogeneous patches decrease in size and the variety of patches increases (Delcourt and Delcourt 1992).

Ecotones are commonly formed in coastal areas and estuaries, where the distributions of many macrophyte foundation species overlap (Hauxwell et al. 2001). Foundation species are habitat-forming species that facilitate the presence of other organisms and communities by provisioning habitat and energy, and by modifying their abiotic environment in several ways (Graham et al. 2016). They provide various ecosystem services, including sediment stabilization and increased accretion, and reduction of hydrodynamic energy from currents and waves (Bos et al. 2007). Foundation species are also the main primary producers in coastal and estuarine ecosystems, and are responsible for maintaining diverse communities (Bouma et al. 2005). Marine communities are often structured by foundation species (Aquilino and Stachowicz 2012), and the resilience of communities highly depends on the nature and health of associated macrophytes (Olafsson 2017).

As marine macrophytes, macroalgae and seagrasses are associated with key ecosystem services, such as carrying out photosynthesis and supplying organic matter, providing habitat and reducing physical stress to associated organisms. Macrophytes play a foundational role in marine ecosystems, and primary consumers depend on most macroalgal and seagrass taxa for fixed carbon and nutrients (Paine 2002). Many marine macrophytes act as ecosystem engineers that reduce hydrodynamic energy (Bouma et al. 2005). Aquatic vegetation with emergent structures that reach the water surface are often more effective in reducing wave height (Augustin et al. 2009). Much like coral reefs, sea lettuce mats and eelgrass meadows act as barriers that protect organisms living in them from strong waves and currents (Maxwell et al. 2015). The modification of hydrodynamic forces often results in increased sediment deposition, which has important implications for organisms associated with foundation species (Bos et al. 2007). Marine macrophytes also create shade and can prevent dessication of associated organisms in intertidal habitats (Maxwell et al. 2015). The ecosystem services provided by seagrass beds are among the highest for all aquatic ecosystems (Costanza et al. 1997), and include nutrient fixation, erosion prevention, and nursery function (Reusch and Hughes 2006). Eelgrass makes a perfect nursery habitat for commercially and ecologically important fish and invertebrate species, and serves as shelter from predators (Mackenzie Jr. 2005). Habitat and energy provisioning services, as well as the functional importance of macrophytes, vary depending on their size and distribution relative to the scale of

the physical structure of their system (Dayton 1972). Thus, large and abundant macrophytes have a foundational role in regulating structure, diversity and production of coastal and wetland ecosystems (Graham 2004).

Estuarine ecosystems are unique in that they are diversity hotspots because of gradients in water properties caused by the input of both ocean water and fresh water into the system (McLusky and Elliot 2004). These gradients, combined with differing nutrient runoff in different sections of the estuary, increase diversity of seaweeds and aquatic plant species (Rykaczewski and Dunne 2010). Such patterns of habitat diversity can be observed in Elkhorn Slough, an upwelling-influenced estuary located in Monterey Bay, California (36.8259°N 121.7569°W) (Elkhorn Slough Foundation 2002). The main sources of freshwater flowing into Elkhorn Slough are Carneros Creek and McClusky Slough to the north and Moro Cojo Slough to the south (Bassett 2010). Its main channel is approximately 11 km long and 3 m deep on average, with a tidal excursion of 5 km, and tidal currents of 0.5-1 m/s (Smith 1973). During the rainy season, nitrate concentrations are usually high in the estuary and can reach values of up to 450 μM , mainly due to agricultural runoff from nearby farms (Chapin et al. 2004). Conversely, land-based nitrate input is reduced during the dry season and nitrate concentrations are 0-20 μM (Chapin et al. 2004); however, upwelled ocean water remains an important source of nitrate entering the estuary, since it accounts for 80-90% of the nitrogen load during the dry

season (Chapin et al. 2004). These seasonal and spatial characteristics have an influence on the biological components of the estuary.

The dominant macrophytes in the Elkhorn Slough system are *Zostera marina* and two species within the *Ulva* genus: *U. intestinalis* and *U. lactuca* (Hughes 2016). These macrophytes overlap in several locations throughout the main channel, forming ecotones that vary in scale. The largest *Ulva-Zostera* ecotone extends for 400m along the northern shore of Seal Bend, 1-2 km from the mouth of Elkhorn Slough (Fig. 1A). The eelgrass and macroalgal populations vary in width, and the boundary of the *Ulva-Zostera* ecotone is irregularly shaped and is visible in aerial images and during low tide (Fig. 1B). The ecotone boundary is home to a wide variety of epigrazers, some of which are very important in the Elkhorn Slough system (Grant 2009). In many systems, macroalgal biomass is directly associated with decreased eelgrass biomass, showing the potential for negative interactions between macrophytes (Hessing-Lewis 2011, Hughes et al. 2016). There are various macrophyte species in the estuary, which leads to a variety of habitats found in a relatively small area.

Ulva is a fast-growing green alga that forms mats used by invertebrates as attachment surfaces (Thiel and Fraser 2016). These mats block sunlight and reduce thermal stress on mesograzers and the habitat they provide boosts recruitment of invertebrates, like amphipod crustaceans and polychaete worms (Lyons et al. 2014). High temperatures and storms have been reported as the major threats affecting sea lettuce populations (Filbee-Dexter & Scheibling 2012).

Ulva shows little response to low pH levels and CO₂ increases, unless they are coupled with temperature, salinity, and high nutrients (Connell and Russell 2010). Other factors limiting the distributional range of *Ulva* are possibly grazing and competition with other aquatic plants (Green and Fong 2016). Blooms of *Ulva* and other macroalgal species caused by eutrophication can have severe effects on estuarine environments (Mackenzie 2005). Sea lettuce overgrows and causes the death of aquatic plants and mollusk species, occupying significant portions of shallow estuarine water and restricting feeding zones of birds, fish and invertebrates (Raffaeli et al. 1989). In addition to being an opportunistic species, the spread of *Ulva* mats alters water chemistry by adding and removing nutrients from the system throughout its life cycle (Teichberg 2010). One of the most important ecosystem services *Ulva* spp. provides is the removal of phosphates and nitrates as they grow in the spring and consequently release nutrients when they disintegrate in the fall (Deegan et al. 2002). *Ulva* blooms can also have indirect effects on higher trophic levels and often disrupt ecosystem dynamics (Lyons 2014). The two commonly used conservation approaches to buffer these changes triggered by *Ulva* spp. are preventing nutrient runoff at their watershed sources and removing macroalgal biomass by either harvesting or increased flushing (Valiela et al. 1997).

Zostera marina is a perennial seagrass found in North America and Eurasia that provides critical services such as nutrient recycling, sediment stabilization, and carbon sequestration (Bostrom and Bonsdorff 2000). It also provides an

important nursery habitat commonly used as an indicator of ecological quality (Short et al. 2006). The seagrass is often carbon-limited, and fairly sensitive to light, nutrients, and sediment variability (Leoni et al. 2008). The effects of decreased light are a reduction in both shoot morphology and shoot density, and growth rate (Moore and Wetzel 2000). High temperatures can slow or disrupt ontogenetic transitions, affecting flowering and seed germination (Waycott 2007). Degraded water quality due to anthropogenic climate change is the main cause of disappearance of at least 29% of the known global coverage of seagrass habitats (Waycott et al. 2009). Species that seek refuge in eelgrass beds include crabs, scallops and juvenile salmon (Boström et al. 2014).

Macrophytes can also determine topographic complexity and trophic interactions within an ecosystem (Angelini 2011). However, the abiotic conditions driving ecoclines that favor a particular habitat provider at certain levels are poorly understood. Therefore, determining what factors might be responsible for the spatial variability in macrophyte relative abundance at the ecotone level is an important research priority (Bostrom et al. 2017). Among the spatially variable abiotic factors that might influence ecotone dynamics are physical properties of the water such as temperature, salinity, pH, dissolved oxygen, desiccation, Photosynthetic Active Radiation (PAR) and nutrient concentrations (Janauer 2001). Photosynthetic Active Radiation refers to the amount of light (400-700nm) that photosynthetic organisms can utilize for photosynthesis (Carruthers et al. 2001). In recent studies, Photosynthetic Active Radiation (PAR) has been

suggested to be the main factor responsible for the distribution of *Zostera marina* in coastal habitats (Gao et al. 2011). Stevenson et al. (1996) concluded that salinity and porewater nutrients appear to have a greater effect on the spatial distribution of macrophytes than temperature or pH. Other field observations and laboratory experiments have demonstrated that light, temperature and nutrient supply are key environmental factors that stimulate germination of *Ulva* spp. and facilitate algal blooms that disfavor *Zostera* (Worm et al. 1999). On the other hand, temperature and light levels are most likely responsible for most of the seasonal variability (Campbell et al. 2014). However, there is evidence suggesting that eelgrass is resilient to high fluctuations in macroalgal biomass and production through time, and is more affected by local climate and nutrient loading in estuaries (Hessing-Lewis 2011).

Piriou and Duval (1990) reported termination of *Ulva* growth at the beginning of the summer, with increased light intensity and longer photoperiods, hinting a strong sensitivity of *Ulva* spp. to light. It seems clear that when sufficient light is available, nutrient availability and optimal temperature ranges lead to macroalgal proliferation (Olafsson 2017). Interception of light by epiphytic and filamentous algal species like *Ulva* spp. on leaf surfaces causes a decline in submerged aquatic vegetation (Twilley 1985). Drift algae can originate from hard substrata surrounding eelgrass beds and its spatial distribution within the ecotone might be associated with eelgrass species composition and zonal distribution (Bell and Hall 1997). Interspecific resource competition has to be added to environmental

variables as a biotic factor to take into consideration at the scale of the ecotone boundary (Green and Fong 2015).

Proliferation of bloom-forming algae like *Ulva* spp. associated with seagrass population decline is common in eutrophic estuaries in the North Temperate Zone and has become an increasing problem worldwide (Valiela et al. 1997). High frequencies of algal bloom occurrence are mostly attributed to eutrophication, and increased availability of nutrients leads to shifts of macrophytes (Raffaelli et al. 1998). Availability of nitrogen and phosphorus originating from land, via either anthropogenic sewage or fertilization runoff, is possibly a major factor influencing composition and dynamism of the *Ulva*-*Zostera* ecotone (Wang et al. 2012). While nitrogen supply affects maximum seasonal rates of macroalgal growth in coastal and estuarine ecosystems (Lapointe et al. 1992), Valiela et al. (1997) found that phosphorus can be the limiting factor for macrophyte production in carbonate-rich waters for certain taxa.

Sediment composition has also been reported to affect gametophyte development (Devinny and Volse 1978), spore attachment (Lilly et al. 1953), and distribution (Ebling et al. 1960) of macroalgal species. Among the sediment characteristics associated with macrophyte ecology are grain size and particle heterogeneity (Schiel et al. 2019), and concentration of organic matter in the sediment (Silveira 2015). Schiel et. al (2019) observed important changes in community structure, such as shifts in dominant macrophyte species, as a response to changes in sediment type. Sandy sediments are thought to support

poor macrophyte growth, possibly due to their low organic matter content (Barko and Smat 1986). Effects of sedimentation on macroalgae appear to be species-specific, and dependent on reproductive strategies (Eriksson and Johansson 2005).

While previous studies have mentioned the presence of the *Ulva-Zostera* ecotone at Seal Bend (e.g. Grant 2009, Hughes 2016), it was not the main focus of these studies. Aerial images can be used to estimate ecotone dynamics at large spatiotemporal scales, but small-scale changes and processes underlying the patterns observed have not been examined. Little attention has been given to determining what are the factors limiting the distribution of *Ulva* spp., and their relative importance in this particular system. This was the first study to focus on understanding its driving factors, spatiotemporal dynamics, and overall ecological implications of the ecotone.

The purpose of this project is to shed some light on the biological and physical processes and patterns associated with the *Ulva-Zostera* ecotone in Elkhorn Slough, as well as describe changes in population ecology of *Ulva* spp. across the macrophyte-driven ecotone. I focused on identifying the main factors correlated with ecotone dynamics, and quantifying the relative importance of each one of the factors limiting the distribution of *Ulva* spp. My approach was to monitor water quality, macrophyte density, and sediment characteristics, and conduct recruitment and transplant experiments. The ultimate goal was to further

understand the nature and dynamics of ecotonal zones in estuarine environments, from an ecological perspective.

MATERIALS AND METHODS

Study System

The study location was the *Ulva-Zostera* ecotone found in the main channel of Elkhorn Slough, throughout Seal Bend (Figure 1). Seal Bend is 500 m long S-E and 500 m wide W-E, and located approximately 1-2 km away from the mouth of the estuary. Elkhorn Slough is home to many ecologically and commercially important species such as flat fishes, harbor seals, leopard sharks, and Southern sea otters (Wasson et al. 2002). Common taxa that associate with the *Ulva-Zostera* ecotone include juvenile fishes and invertebrates like sea slugs, isopods, crabs, and snails (Grant 2009).

Figure 1. Study location. (A) Map of Elkhorn Slough and Seal Bend. (B) Close-up photograph of the *Ulva*-*Zostera* ecotone boundary at Seal Bend.

At Seal Bend, I specifically addressed the following objectives:

1. Monitor spatial and seasonal changes in macrophyte density across the *Ulva-Zostera* ecotone.
2. Quantify seasonal dynamics and shifting of the ecotone boundary.
3. Determine whether abiotic factors including water quality, porewater nutrients, and sediment type influence the distribution of *Ulva* spp. across the ecotone.
4. Examine whether competition for light and space limits the distribution of *Ulva* spp. across the ecotone.
5. Evaluate whether grazing is a key factor limiting the distribution of *Ulva* spp. across the ecotone.

Sampling and Experimental Design

The study site included a total of 5 permanent transects to account for the spatial variability of the ecotone (Figure 2). All transects were 30 m in length, and randomly placed across the transitional zone perpendicular to the shore, with tidal height ranging between -0.1 m and 0.5 m at the beginning of each sampling period (Table 1). All measurements and samples were collected right at the boundary (mark zero on transect) and at various distances from it (marks 5 m, 10 m, and 15 m on the transect) in both directions, into the *Ulva* spp. zone and the *Zostera* bed (Figure 2). This sampling design is common in ecotone research, as it allows for the description of patterns based on spatial variation of biological and physical parameters (Janauer and Kum 1996). Experiments and observations

were repeated across one additional transect placed outside of the eelgrass bed, but with the same depth distribution, to be used as a control. The boundary at the control was initially set as a function of tidal height, using the average tidal height at the boundary mark on the other five transects as a reference. Sampling was repeated every two months for thirteen months, for a total of seven sampling periods, to assess seasonal variability.

Figure 2. Sampling design. Location of transects across the *Ulva*-*Zostera* ecotone for measurements, collections, and experiments. The darker green area is the eelgrass bed, while the lighter green area leading to the marsh is the macroalgal-covered mud. The dashed line is the ecotone boundary, while the continuous lines indicate how transects were placed across the *Ulva*-*Zostera* ecotone.

Table 1. Sampling dates, times, and tidal height of the ecotone boundary at time of sampling.

Date	Time	Low/High tide	Tidal height (m)
5/12/18	3-5:30 PM	Low	0.2
5/13/18	3:30-5 PM	Low	0.3
5/26/18	3:00-3:45 PM	Low	0.3
6/24/19	2:15-4:30 PM	Low	0.5
7/5/18	10:15-11:30 AM	Low	0.2
9/8/18	3:45-6:00 PM	Low	0.4
9/22/18	3:30-4:30 PM	Low	0.5
11/3/18	2:15-3:45 PM	Low	0.4
11/4/18	2:00-4:15 PM	Low	0.2
11/17/19	1:30-2:30 PM	Low	0.4
1/27/19	10:30AM-12:45 PM	Low	0.4
1/28/19	11:30AM-2:15 PM	Low	0.2
2/11/19	9:15-10:45 AM	Low	0.5
3/11/19	8:45-11:45 AM	Low	0.3
3/12/19	9:45AM-12:30 PM	Low	0.2
3/25/19	9:00-10:30 AM	Low	0
4/24/19	9:30-1:00 PM	Low	-0.1
5/4/19	4:30-5:30 PM	Low	0.4

Macrophyte Density

Density of *Ulva* spp. was estimated as percent cover. At every 5 m mark on the transects, 0.5 m² quadrats were placed and photographed using a GoPro Hero 2 with a 14 mm focal longitude at a 170° angle. These photographs were taken from a distance of 0.75 m and later analyzed using ImageJ software to obtain estimates of *Ulva* spp. percent cover. In ImageJ, Images were

transformed using the binary function, and the threshold tool was used to adjust the pixel values to be highlighted and measured. Density of *Zostera marina* was estimated by counting the number of eelgrass shoots within the same 0.5 m² quadrats used to estimate percent cover of *Ulva* spp., placed along each transect across the ecotone.

Boundary Shift

At the beginning of the study, the ecotone boundary (mark zero on the transects) was established at the mid-point between the edge of the eelgrass bed and the nearest patch of *Ulva* spp. on each transect. The distance between this boundary and the edge of the eelgrass bed was calculated from the photographs taken for macrophyte density estimates. Similarly, the distance between the ecotone boundary and the edge of the nearest *Ulva* spp. patch on each sampling date was calculated. These values were used to estimate seasonal shift and variation in width of the boundary.

Water Quality

Changes in water quality were estimated using a multi-parameter recording instrument (YSI Professional Plus Multiparameter Meter) to take *in situ* measurements of temperature, salinity, pH, and dissolved oxygen across the ecotone. These measurements were taken during low tide, in the submerged section of the ecotone along the six transects, which included the marks at the boundary (0 m) and 5-15 m into the eelgrass bed, every two months. Additionally, surface water samples were collected in three arbitrary locations

within the eelgrass bed from May 2018 to November 2018, and analyzed for nutrient concentrations. Since the average monthly values obtained did not differ significantly from those collected at a nearby sampling station (Table 2), the data were only used for reference.

Table 2. Comparison of nutrient concentrations collected at Seal Bend and a nearby sampling station. These data show the mean concentration values of surface water samples collected at three arbitrary locations within the eelgrass bed at Seal Bend from May to November 2018.

Month	Nutrient	Seal Bend (μM)	Sampling Station (μM)
May 2018	Phosphate	0.571	0.421
May 2018	Nitrate	1.584	3.194
May 2018	Ammonium	10.951	9.982
July 2018	Phosphate	0.213	0.210
July 2018	Nitrate	1.336	2.083
July 2018	Ammonium	0.996	1.174
Sep 2018	Phosphate	0.289	0.316
Sep 2018	Nitrate	4.565	5.278
Sep 2018	Ammonium	3.971	4.697
Nov 2018	Phosphate	0.420	0.211
Nov 2018	Nitrate	4.528	5.000
Nov 2018	Ammonium	12.094	7.046

Sediment Characteristics

Porewater Nutrients: Push cores (5 cm diameter) were used to take sediment samples. The cores were sliced into two sections, transferred to 50mL Falcon tubes, and transported to the laboratory in a cooler. In the laboratory, as much volume of porewater as possible was extracted from the Falcon tubes by decantation after centrifuging them for five minutes at 5000rpm, following recommendations of Carignan et al. (1985) for porewater sampling techniques. Porewater samples were filtered through 0.7 μm Whatman glass fiber filters into acid-cleaned Falcon tubes and frozen until analysis. Preparation for analysis included thawing the samples and diluting them with Milli-Q water by 1:20 or 1:15, depending on the volume of sample available. Nutrient concentrations were measured on a Lachat QuickChem 8000 series autoanalyzer, yielding values for phosphate, ammonium, nitrite, and nitrate/nitrite concentrations.

Grain-Size Analysis: After extracting the porewater, sediment samples were used to test for differences in particle heterogeneity and grain size using a Beckman Coulter Laser Particle Sizer LS1230, an optical instrument that uses the Mie principle of light diffraction to measure particles between 0.04 μm and 2000 μm . Before doing grain size analysis, a small amount of each sample was transferred to a beaker. Approximately 7 mL of 30% hydrogen peroxide was added and left to react for 48 hours to break down the organic matter in the sample. The amount of sample that needed to be added to the aqueous module attached to the Laser Particle Sizer was initially determined by running a few

tests to find the obscuration range in which grain size measurements were repeatable. All samples were run at 12-15% obscuration and sonicated for 5-15 seconds when needed to insure the full disaggregation of the particles. Mean, median, mode and standard deviation of grain size were calculated using the proprietary Beckman Coulter software, and the standard deviation was used as an indicator of particle heterogeneity within each sample (McCave and Syvitski 1991).

Recruitment Observations

Artificial settlement surfaces were designed to determine if the distribution of *Ulva* spp. was driven by its inability to recruit to the eelgrass bed due to light availability or differences in sediment characteristics. The settlement surfaces were 0.75 m portions of nylon rope attached to 1 m PVC pipes that were vertically inserted in the mud. Following the general experimental setup, the PVC pipes were placed at seven different marks along each of the five 30m transects randomly distributed across the ecotone (Fig. 2). The lines of rope were checked two weeks later, and the presence or absence of *Ulva* spp. was recorded at each mark. For the ropes with successful recruitment, the percentage of the rope surface that was covered with algae was noted, as was the distance between the point of attachment of the rope at the top of the PVC pipe and the section of the rope where *Ulva* spp. stopped recruiting. After taking all measurements, the rope lines were detached from the pipes, put in labeled polyethylene bags, and transported back to the laboratory. The seaweed was scrapped off the rope,

separated from other plants and detritus, bubbled when needed, rinsed, dried at 27°C for 48 hours, and weighed on an analytical scale with 0.1 mg resolution to obtain estimates of *Ulva* spp. biomass.

Transplant Experiments

Transplant experiments were conducted to determine whether the distribution of *Ulva* spp. across the ecotone was a result of processes affecting adult individuals or early developmental stages. PVC pipes with attached nylon rope (same as recruitment experiments) were previously placed 15 m into the *Ulva* spp. side of the ecotone to allow *Ulva* spp. to recruit to them. Each time the PVC pipes were set up for transplanting, rope line portions with 100% *Ulva* spp. cover were selected and attached to the PVC pipes that were placed across the ecotone. These served as transplants that were checked after two weeks and transplant results were recorded as “successful” or “failed” to determine whether adult *Ulva* spp. could survive at each mark on the transect. For lines with transplant success, the percentage of the rope surface that was covered with algae was recorded, and the distance between the point of attachment of the rope at the top of the PVC pipe and the section of the rope where *Ulva* spp. was no longer present was also recorded. The presence or absence of mesograzers on the ropes was recorded, and the number of large mesograzers (>1 cm) within each of four groups (i.e. sea slugs, isopods, crabs, and sea snails) was counted. After taking all measurements, rope lines were detached from the pipes, placed in labeled polyethylene bags, and transported back to the laboratory. To obtain

small (<1 cm) mesograzer biomass estimates, ropes were scrapped; mesograzers were separated from the seaweed, rinsed, dried in an oven at 27°C, and weighed on a scale with a 10mg resolution.

Data Analysis

All data analysis was done using JMP Pro 13 statistical software. Table 3 shows the types of data produced, and the statistical variables and tests that were conducted on these data based on the main questions and experimental design. To test for differences between mean values of dependent variables at the different marks along transects, two different types of statistical tests were used: two-way analysis of variance (ANOVA) for normally distributed data, and Kruskal-Wallis test for non-normally distributed data. Generalized linear models (GLM) were used to test for associations between binomial dependent variables and distance from the ecotone throughout the year. Correlations between continuous variables were tested using the correlation test that best fit the data in each case.

Table 3. Summary of statistical analyses conducted.

Objective	Data produced	Variables		Statistical Test
		Independent	Dependent	
1	Macrophyte density	Distance from ecotone Month	<i>Zostera</i> density <i>Ulva</i> % cover	Two-Way ANOVA & One-Way ANOVA
		<i>Ulva</i> % cover	<i>Zostera</i> density	Nonlinear Regression
2	Boundary width	Month	Distance between macrophytes & boundary	Kruskal-Wallis
3	YSI measurements	Distance from ecotone Month	Temperature Salinity pH Dissolved oxygen	Two-Way ANOVA & One-Way ANOVA / Kruskal-Wallis
	Nutrient concentrations		Phosphate Nitrate Ammonium	
	Sediment characteristics		Mean grain size	
			Particle heterogeneity	
4	<i>Ulva</i> recruitment success	Distance from ecotone Month	Presence/absence of <i>Ulva</i>	Generalized Linear Model (Binomial)
	<i>Ulva</i> % cover on recruitment pipes		<i>Ulva</i> % cover	Two-Way ANOVA & One-Way ANOVA / Kruskal-Wallis
	<i>Ulva</i> biomass		<i>Ulva</i> biomass	
	Transplant success		Presence/absence of <i>Ulva</i>	Generalized Linear Model (Binomial)
	<i>Ulva</i> % cover on transplants Maximum length of <i>Ulva</i> cover		<i>Ulva</i> % cover	Two-Way ANOVA
			Length of <i>Ulva</i> growth	

4	Recruitment vs transplant success	Recruitment success	Transplant success	Fisher's Exact Test
5	Grazer abundance	Distance from ecotone Month	Small grazer biomass	Two-Way ANOVA
	Relative abundance of grazer groups		Large grazer counts % of slugs % of isopods % of crabs % of snails	
	<i>Ulva</i> abundance vs grazer abundance	<i>Ulva</i> % cover on transplants	Slug counts Isopod counts Crab counts Snail counts Small grazer biomass	Linear Regression

RESULTS

Macrophyte Density

As expected, abundance of *Ulva* spp. across the ecotone and across seasons (Fig. 3A; two-way ANOVA, Distance: $F_{6,196}=53.5$, $p<0.0001$, Season: $F_{6,196}=9.56$, $p<0.0001$, Distance x Season: $F_{36,196}=53.5$, $p=0.0242$). *Ulva* spp. cover increased with increasing distance away from the *Zostera* bed and the ecotone boundary. The highest macroalgal abundance was observed 15 m away from the boundary into the *Ulva* spp. zone. Percent cover of *Ulva* spp. was very low in quadrats placed at the boundary, and insignificant at every mark within the eelgrass bed. Overall *Ulva* spp. abundance differed significantly among sampling periods, peaking in the spring and summer relative to the fall and winter months. *Ulva* spp. abundance patterns across the ecotone were not consistent throughout the year, with stronger increase in abundance with increasing distance from the boundary in the spring than other seasons. Abundance of *Ulva* spp. varied significantly across the transect used as a control, outside of the eelgrass bed (Fig. 3A; one-way ANOVA, $F_{6,42}=2.75$, $p=0.0239$). Macroalgal cover in the control suffered seasonal fluctuations that were similar to the trends observed on the *Ulva* spp. side of the *Ulva*-*Zostera* ecotone, with the highest abundances detected in the summer (Fig. 3A; one-way ANOVA, $F_{6,42}=4.29$, $p=0.0019$).

Density of *Zostera marina* also changed spatially, but not seasonally (Fig. 3A; two-way ANOVA, Distance: $F_{6,238}=152.28$, $p<0.0001$, Season: $F_{6,238}=1.38$, $p=0.2235$, Distance x Season: $F_{36,238}=0.56$, $p=0.9782$). The highest density of

Zostera marina was observed 15 m away from the ecotone boundary and into the *Zostera* bed, and density values decreased with proximity to the boundary. Mean *Zostera marina* density values remained constant throughout the year, and spatial patterns across the ecotone were consistent through time.

Overall, there was a negative correlation between density of *Ulva* spp. and density of *Zostera marina* across the ecotone (Fig. 3B; Nonlinear Regression, $F_{1,243}=89.99$, $p<0.0001$, $R^2=0.61$), and both were found at similar densities at the boundary.

Figure 3. Macrophyte abundance across the ecotone. (A) Seasonal macrophyte abundance fluctuations across the ecotone. Green lines represent mean density of *Zostera marina* in shoots/m² across the ecotone (N=245). Continuous blue lines represent mean *Ulva* spp. cover in percentage across the ecotone (N=245). Discontinuous blue lines represent mean *Ulva* spp. cover in percentage across the control (N=49). Error bars represent standard error of the mean due to variability between transects. (B) Relationship between *Ulva* spp. abundance and *Zostera marina* abundance. There is a nonlinear correlation between *Zostera marina* abundance and *Ulva* spp. abundance. The green curve represents the best-fit model ($R^2=0.61$).

Boundary Shift

The relative abundance of macrophytes did not vary significantly across seasons at the boundary of the *Ulva-Zostera* ecotone. Proximity of *Ulva* spp. to the ecotone boundary was slightly greater in the summer and fall than in the winter and spring months but did not vary significantly with time (Fig. 4; Kruskal-

Wallis, $df=6$, $\chi^2 = 6.86$, $p=0.3340$). Proximity of *Zostera marina* to the mark initially designated as the ecotone boundary did not change throughout the duration of the study (Fig. 4; Kruskal-Wallis, $df=6$, $\chi^2 = 0.36$, $p=0.9992$). Subsequently, both the width of the transitional area and the placement of the boundary relative to tidal height remained constant throughout the year (Fig. 4; Kruskal-Wallis, $df=6$, $\chi^2 = 3.65$, $p=0.7237$). These trends were consistent with macrophyte density observations at other marks across the ecotone.

Figure 4. Seasonal changes in width of the ecotone boundary. Blue bars represent the distance between the ecotone boundary and the closest *Ulva* spp. patch in meters (N=35). Green bars represent the distance between the ecotone boundary and the edge of the *Zostera marina* bed in meters (N=35). Error bars represent standard error of the mean due to variability between transects. The black line represents the boundary width in meters (N=35).

Water Quality

Water quality varied significantly across the ecotone and throughout the year. Water temperature consistently decreased with increasing distance from the boundary through all sampling periods (Fig. 5; two-way ANOVA, Distance: $F_{3,112}=19.78$, $p<0.0001$, Season: $F_{6,112}=274.05$, $p<0.0001$, Distance x Season: $F_{18,112}=0.29$, $p=0.9981$). Average water temperature across the ecotone changed significantly throughout the year, with higher temperatures in the summer months.

Figure 5. Seasonal temperature fluctuations across the ecotone. Blue bars represent mean temperature values at the ecotone boundary and at distances of 5-15m away from the boundary throughout the year (N=140) in Celsius. Error bars represent standard error of the mean due to variability between transects.

Salinity suffered significant seasonal changes, but no spatial changes across the ecotone (Fig. 6; two-way ANOVA, Distance: $F_{3,112}=2.14$, $p=0.0993$, Season: $F_{6,112}=119.21$, $p<0.0001$, Distance x Season: $F_{18,112}=0.45$, $p=0.9732$). Lower salinity values were detected in the winter months, but there were consistently no

significant spatial differences in salinity across the ecotone at any sampling period.

Figure 6. Seasonal salinity fluctuations across the ecotone. Blue bars represent mean salinity values at the ecotone boundary and at distances of 5-15m away from the boundary throughout the year (N=140) in parts per thousand. Error bars represent standard error of the mean due to variability between transects.

Similarly, pH levels did not change significantly across the ecotone, but did change throughout the year (Fig. 7; two-way ANOVA, Distance: $F_{3,112}=0.75$, $p=0.5216$, Season: $F_{6,112}=20.89$, $p<0.0001$, Distance x Season: $F_{18,112}=0.49$, $p=0.9558$). Higher pH values were detected in the summer months than other seasons. However, pH values were not significantly different at different distances from the boundaty, a trend that was consistent through time.

Figure 7. Seasonal pH fluctuations across the ecotone. Blue bars represent mean pH values at the ecotone boundary and at distances of 5-15m away from the boundary throughout the year (N=140). Error bars represent standard error of the mean due to variability between transects.

On the other hand, dissolved oxygen values were significantly different across seasons and across the ecotone (Fig. 8; two-way ANOVA, Distance: $F_{3,112}=18.42$, $p<0.0001$, Season: $F_{6,112}=26.70$, $p<0.0001$, Distance x Season: $F_{18,112}=0.41$, $p=0.9835$). Dissolved oxygen concentrations were higher during the winter months, decreased with distance from the boundary, and spatial patterns were consistent over time.

Figure 8. Seasonal dissolved oxygen fluctuations across the ecotone. Blue bars represent mean dissolved oxygen values at the ecotone boundary and at distances of 5-15m away from the boundary throughout the year (N=140) in milligrams per liter. Error bars represent standard error of the mean due to variability between transects.

Sediment Characteristics

Porewater Nutrients: Phosphate levels were significantly different across the ecotone and throughout the year (Fig. 9; two-way ANOVA, Distance: $F_{2,81}=5.02$, $p=0.0088$, Season: $F_{6,81}=4.01$, $p=0.0015$, Distance x Season: $F_{12,81}=3.58$, $p=0.0003$). Phosphate concentrations ranged from 0-15 μM in both the *Zostera* bed and the ecotone boundary, and reached concentrations of up to 52 μM on the *Ulva* spp. side. There were also significant seasonal changes, with higher phosphate concentrations in the spring, and lower concentrations in the fall and winter. However, patterns in phosphate concentration along transects were not consistent across seasons, since the increase in concentration on the *Ulva* spp. side of the ecotone was much stronger in the spring and summer of 2018 than other seasons.

Figure 9. Porewater phosphate concentrations across the ecotone. Black points represent mean phosphate concentration values at the ecotone boundary and a distance of 10m away from the boundary on either side throughout the year (N=102) in micromolar. Error bars represent standard error of the mean due to variability between transects.

Nitrate concentrations were not significantly different across the ecotone, but did differ across seasons (Fig. 10; two-way ANOVA, Distance: $F_{2,81}=0.53$, $p=0.5878$, Season: $F_{6,81}=16.23$, $p<0.0001$, Distance x Season: $F_{12,81}=0.63$, $p=0.8071$). Nitrate concentrations ranged from 0-5 μM in the *Zostera* bed, the ecotone boundary, and the *Ulva* spp. side, a consistent pattern across seasons. However, greater concentrations of porewater nitrate were measured in the summer, and lower concentrations in the fall and winter.

Figure 10. Porewater nitrate concentrations across the ecotone. Black points represent mean nitrate concentration values at the ecotone boundary and a distance of 10m away from the boundary on either side throughout the year (N=102) in micromolar. Error bars represent standard error of the mean due to variability between transects.

Porewater ammonium levels differed significantly across the ecotone, although there were no significant seasonal differences detected (Fig. 11; two-way ANOVA, Distance: $F_{2,81}=24.78$, $p<0.0001$, Season: $F_{6,81}=1.88$, $p=0.0941$, Distance x Season: $F_{12,81}=1.56$, $p=0.1216$). Ammonium concentrations ranged from 50-490 μM in the *Zostera* bed, and from 0-150 μM in both the ecotone boundary and the *Ulva* spp. side. Although seasonal differences were not significant, there were slightly lower average ammonium concentrations across the entire ecotone in September 2018. The spatial patterns detected in ammonium concentrations were consistent through time.

Figure 11. Porewater ammonium concentrations across the ecotone. Black points represent mean ammonium concentration values at the ecotone boundary and a distance of 10m away from the boundary on either side throughout the year (N=102) in micromolar. Error bars represent standard error of the mean due to variability between transects.

Grain-Size Analysis: At Seal Bend, the sediment was mostly composed of fine-medium silt and clay. As expected, grain size differed significantly across the ecotone and across seasons (Fig. 12A; two-way ANOVA, Distance: $F_{2,84}=22.28$, $p<0.0001$, Season: $F_{6,84}=3.02$, $p=0.0101$, Distance x Season: $F_{12,84}=0.94$, $p=0.5106$). Mean grain size was not different between the ecotone boundary and the *Ulva* spp. side, ranging from 3.5-8 μm at both marks. Mean grain size was higher in the eelgrass bed, ranging from 3.8-11 μm . While the sediment was composed of clay and fine silt at the ecotone boundary and the *Ulva* spp. side, there was a large proportion of medium silt in the eelgrass bed consistently across sampling periods. There were also significant seasonal differences detected, with slightly higher grain sizes in the spring and summer than in the fall. Grain-size distribution across the ecotone did was not linked to hydraulic conditions (Fig. 12B).

Figure 12. Sediment composition across the ecotone.

(A) Grain size distribution across the ecotone. Black points represent mean grain size values at the ecotone boundary and a distance of 10m away from the boundary on either side throughout the year ($N=105$) in micrometers. Error bars represent standard error of the mean due to variability between transects. (B) Bivariate plot of mean grain size against sorting. Points within the ellipse represent mean grain size values against standard deviation at the ecotone boundary and a distance of 10m away from the boundary on either side ($N=105$). Green points were calculated from cores taken in the *Zostera marina* bed, red points from the ecotone boundary, and blue points from the *Ulva* spp. side. Measurements in micrometers were converted into the equivalent phi (ϕ) values and are plotted in a ϕ -scale. The bivariate plot incorporates the domains defined by Tanner (1991) and Lario (2002) to determine if grain-size distribution across the ecotone might be linked to hydraulic conditions. There is likely another explanation for the particle size distribution, since the majority of the larger particles (green points) fall in the low depositional energy section of the plot, which invalidates the hydraulic sorting theory.

Although there were no significant spatial differences in particle heterogeneity across the ecotone, there were significant seasonal differences (Fig. 13; two-way ANOVA, Distance: $F_{2,84}=1.30$, $p=0.2777$, Season: $F_{6,84}=2.92$, $p=0.0123$, Distance x Season: $F_{12,84}=1.19$, $p=0.3035$). Sediment composition was more heterogeneous in the fall and winter, and spatial patterns detected were consistent through the duration of the study.

Figure 13. Particle heterogeneity across the ecotone throughout the year. Black points represent mean particle heterogeneity values as a function of standard deviation of grain size at the ecotone boundary and a distance of 10m away from the boundary on either side throughout the year (N=105) in micrometers. Error bars represent standard error of the mean due to variability between transects.

Recruitment Observations

Presence of *Ulva* spp. (Y/N) on the nylon ropes attached to PVC pipes varied significantly across the ecotone, but it did not change throughout the year (Fig. 14; GLM, Distance: $\chi^2_{6,196}=256.55$, $p<0.0001$, Season: $\chi^2_{6,196}=0.02$, $p=1.0000$, Distance x Season: $\chi^2_{36,196}=17.27$, $p=0.9965$). Recruitment success was greatest 10-15m into the *Ulva* spp. zone, which was also where the greatest cover of *Ulva* spp. was calculated in the macrophyte density estimates. Recruitment success was approximately 20% on average at the boundary and there was no recruitment inside the eelgrass bed. There were no significant differences in recruitment success at the different distances from the boundary within each side of the boundary. On the other hand, recruitment success did not significantly vary spatially or seasonally in the control transect (Fig. 14; GLM, Distance: $\chi^2_{6,42}=0.002$, $p=1.000$, Season: $\chi^2_{6,42}=0.004$, $p=1.0000$, Distance x Season: $\chi^2_{36,42}=0.007$, $p=1.0000$). Recruitment success was extremely high at all marks on the control transect. Spatial trends in recruitment success remained constant throughout the year at the *Ulva-Zostera* ecotone and the control.

Figure 14. Recruitment and transplant success across the ecotone throughout the year. Blue bars represent mean recruitment success (binary response) across the ecotone as a percentage (N=245). Red bars represent mean transplant success (binary response) across the ecotone as a percentage (N=245). Error bars represent standard error of the mean due to variability between transects.

Percent cover of *Ulva* spp. on the surface of the rope varied significantly across the ecotone and across seasons (Fig. 15; two-way ANOVA, Distance: $F_{6,196}=79.35$, $p<0.0001$, Season: $F_{6,196}=7.14$, $p<0.0001$, Distance x Season: $F_{36,196}=2.19$, $p=0.0004$). Despite spatial differences along transects, percent cover values were similar between all distances from the boundary within each side of the ecotone. There was significantly greater percent cover of *Ulva* spp. on recruitment pipes in the spring and summer months. Spatial trends in *Ulva* spp. cover were not consistent across seasons, with stronger increase in percent cover on the *Ulva* spp. side of the ecotone in the spring and summer than other seasons. Macroalgal cover differed significantly among seasons in the control (one-way ANOVA, $F_{6,40}=3.02$, $p=0.0137$), with less cover during the fall and winter. Unlike what was seen across the *Ulva-Zostera* ecotone, *Ulva* spp. cover on recruitment pipes remained constant across the control (one-way ANOVA, $F_{6,40}=0.54$, $p=0.7746$).

Figure 15. Percent cover of *Ulva* spp. on recruitment and transplant pipes. Blue bars represent mean percent cover of *Ulva* spp. on recruitment pipes across the ecotone (N=245). Red bars represent mean percent cover of *Ulva* spp. on transplants across the ecotone (N=245). Error bars represent standard error of the mean due to variability between transects.

New *Ulva* spp. biomass on the recruitment pipes varied significantly across the ecotone and throughout the duration of the study (Fig. 16; two-way ANOVA, Distance: $F_{6,196}=30.37$, $p<0.0001$, Season: $F_{6,196}=6.12$, $p<0.0001$, Distance x Season: $F_{36,196}=1.53$, $p=0.0370$). The highest biomass values were recorded 15 m into the *Ulva* spp. zone, and in the spring and fall months. However, these spatial trends were not consistent throughout the year, with stronger increase in biomass with increasing distance from the ecotone boundary in the fall and winter than in the spring and summer months. Biomass of *Ulva* spp. that recruited to the lines of rope placed in the control showed similar trends to *Ulva* spp. percent cover on the control, with only significant seasonal (Fig. 16; Kruskal-Wallis, $df=6$, $\chi^2=33.87$, $p<0.0001$) but no spatial (Fig. 16; Kruskal-Wallis, $df=6$, $\chi^2=4.01$, $p=0.6759$) variability.

Figure 16. Change in *Ulva* spp. biomass on recruitment pipes across the ecotone. Filled bars represent daily change in *Ulva* spp. biomass across the *Ulva*-*Zostera* ecotone (N=245). Error bars represent standard error of the mean due to variability between transects. Bars with diagonal lines represent daily change in *Ulva* spp. biomass across the control (N=49).

Transplant Experiments

Survival rate of transplanted *Ulva* spp. (Y/N) varied with distance from the ecotone boundary and across seasons (Fig. 14; GLM, Distance: $\chi^2_{6,196}=112.7$, $p<0.0001$, Season: $\chi^2_{6,196}=15.99$, $p=0.0138$, Distance x Season: $\chi^2_{36,196}=27.29$, $p=0.8515$). On the *Ulva* spp. side, transplant success was higher than in the *Zostera* bed, but success rates were very similar within either side of the boundary. There were significant differences in survival of transplanted *Ulva* spp. throughout the year, with higher survival in the spring and summer than fall and winter months. Spatial trends in transplant survival remained constant throughout the year. In successful transplants, change in macroalgal percent cover after two weeks was significantly different across the ecotone and across seasons (Fig. 15; two-way ANOVA, Distance: $F_{6,117}=3.97$, $p=0.0023$, Season: $F_{6,117}=2.40$, $p=0.0413$, Distance x Season: $F_{36,117}=1.08$, $p=0.3649$). There was less cover on transplanted pipes in the eelgrass bed than at the boundary or on the *Ulva* spp. side. Additionally, there was slightly higher percent cover of *Ulva* spp. during the summer, and spatial patterns were consistent throughout the duration of the study. Distance from the top of the ropes to the portion at which *Ulva* spp. was no longer present remained fairly constant across the ecotone and throughout the year (Fig. 17; two-way ANOVA, Distance: $F_{6,117}=1.39$, $p=0.2316$, Season: $F_{6,117}=0.36$, $p=0.7823$, Distance x Season: $F_{36,117}=1.39$, $p=0.2316$). Spatial patterns observed in percent cover of *Ulva* spp. down the PVC pipes remained consistent across seasons.

Figure 17. Percent length of rope covered by *Ulva* spp. on transplants.

Filled bars represent percent length of rope covered by *Ulva* spp. on transplants across the *Ulva*-*Zostera* ecotone (N=245). Error bars represent standard error of the mean due to variability between transects. Bars with diagonal lines represent percent length of rope covered by *Ulva* spp. on transplants across the control (N=49).

Grazing

Biomass of small grazers differed significantly with distance to the ecotone boundary, but remained fairly constant throughout the year (Fig. 18; two-way ANOVA, Distance: $F_{6,196}=3.35$, $p=0.0036$, Season: $F_{6,196}=1.47$, $p=0.1916$, Distance x Season: $F_{36,196}=0.79$, $p=0.7914$). Higher biomass was measured at the ecotone boundary and 5 m into the eelgrass bed. Although mean small grazer biomass remained did not change significantly across seasons, slightly higher biomass was detected in the summer.

Figure 18. Biomass of small mesograzers across the ecotone. Filled bars represent small mesograzers biomass across the *Ulva-Zostera* ecotone (N=245). Error bars represent standard error of the mean due to variability between transects. Bars with diagonal lines represent small mesograzers biomass across the control (N=49).

Density of large mesograzers differed significantly both with distance to the ecotone boundary and across seasons (Fig. 19; two-way ANOVA, Distance: $F_{6,196}=5.75$, $p<0.0001$, Season: $F_{6,196}=4.45$, $p=0.0003$, Distance x Season: $F_{36,196}=0.88$, $p=0.6679$). Overall, grazer abundance was higher at the ecotone boundary, and 5-10 m into the eelgrass bed. Unlike small grazer biomass, density of large grazers changed significantly across sampling periods, with higher density in the spring and summer than in the fall and winter months. Spatial patterns in large grazer density remained consistent throughout the year. Grazer abundance followed a similar seasonal pattern in the control, but was only subject to small spatial changes across transects.

Figure 19. Density of large mesograzers across the ecotone. Filled bars represent large mesograzers across the *Ulva-Zostera* ecotone (N=245). Error bars represent standard error of the mean due to variability between transects. Bars with diagonal lines represent large mesograzers across the control (N=49).

The relative abundance of some common large mesograzer groups varied spatially and seasonally across the ecotone. Sea slugs (Fig. 20; two-way ANOVA, Distance: $F_{6,196}=4.97$, $p<0.0001$, Season: $F_{6,196}=2.52$, $p=0.0223$, Distance x Season: $F_{36,196}=0.72$, $p=0.8762$) and isopods (Fig. 20; two-way ANOVA, Distance: $F_{6,196}=5.09$, $p<0.0001$, Season: $F_{6,196}=0.4350$, $p=0.8549$, Distance x Season: $F_{36,196}=0.92$, $p=0.6096$) appeared to be more abundant at the boundary and inside the eelgrass bed than in the *Ulva* spp. side. On the other hand, crabs (Fig. 20; two-way ANOVA, Distance: $F_{6,196}=2.35$, $p=0.0322$, Season: $F_{6,196}=3.03$, $p=0.0074$, Distance x Season: $F_{36,196}=2.92$, $p<0.0001$) were more abundant in the *Ulva* spp. side, and sea snails (Fig. 20; two-way ANOVA, Distance: $F_{6,196}=1.47$, $p=0.1914$, Season: $F_{6,196}=1.18$, $p=0.3185$, Distance x Season: $F_{36,196}=F_{36,196}=0.65$, $p=0.9355$) were proportionally equally abundant across the ecotone. There were significant seasonal changes in relative abundance of sea slugs, with higher abundance in the spring and summer months. Density of crabs also changed seasonally, and no crabs were seen during the winter months. On the other hand, relative abundance of isopods and sea snails did not change throughout the year. Spatial patterns observed in relative abundance of sea slugs, isopods, and sea snails did not differ throughout the year. Spatial patterns detected in relative abundance of crabs were not consistent through time, with increases in density further from the ecotone boundary being stronger in the summer than other seasons.

Figure 20. Relative abundance of common large (>1 cm) mesograzers across the ecotone. Data shown represents mean percentage of sea slugs (blue), isopods (red), crabs (green) and sea snails (purple) relative to total large mesograzers density at each mark of the transect.

There was a significant relationship between small grazer biomass and percent cover of *Ulva* spp. on the pipes two weeks after being transplanted (Fig. 21; Linear Regression, $F_{1,163}=5.18$, $p=0.0243$, $R^2=0.03$), although it does not explain much variability. *Ulva* spp. cover was also negatively correlated with large mesograzer density (Fig. 22; Linear Regression, $F_{1,163}=6.37$, $p=0.0126$, $R^2=0.04$). More specifically, there was a significant relationship between percent cover of *Ulva* spp. and density of sea slugs (Fig. 23; Linear Regression, $F_{1,163}=5.17$, $p=0.0243$, $R^2=0.03$). This correlation was strongest in spring and summer, and was no longer significant after November 2018.

Figure 21. Correlation between small grazer biomass and *Ulva* spp. percent cover on transplants across the ecotone. Small grazer biomass is measured in grams and *Ulva* spp. cover in percentages (N=165). The blue line represents the best-fit line ($y=0.1059-0.0007x$).

Figure 22. Correlation between large mesograzer density and *Ulva* spp. percent cover on transplants across the ecotone. Large grazer density is measured in counts and *Ulva* spp. cover in percentages (N=165). The blue line represents the best-fit line ($y=1.1174-0.0091x$).

Figure 23. Regulating function of sea slugs in the eelgrass bed. Correlation between abundance of sea slugs and *Ulva* spp. cover on transplants across the ecotone (N=245). The blue line represents the best-fit line ($y=0.5551-0.0051x$).

DISCUSSION

This study described the *Ulva-Zostera* ecotone in Elkhorn Slough as a fairly stable feature that does not exhibit conspicuous seasonal changes. Ecotone dynamics were correlated with the biological and ecological traits of the habitat-forming species on either side of the boundary. The distribution of *Zostera marina* was likely limited by its tolerance to desiccation (Boese et al. 2003), which sets the upper limit of the eelgrass bed and the ecotone boundary. *Zostera* distribution appeared resilient to external processes associated with changes in the ecology of *Ulva* spp., possibly because *Zostera* is a slow-growing perennial species with a longer life span than *Ulva* spp (Kautsky 1988, Lyons 2014). On the other hand, *Ulva* spp. was extremely responsive to changing environmental conditions and mechanisms associated with other macrophytes (Schaadt 2005, Teichberg 2010). As a result, ecotone dynamics in Elkhorn Slough were driven by seasonality of *Ulva* spp.

Hessing-Lewis (2011) also found very low eelgrass variability that did not show response to high fluctuations in macroalgal production in two West Coast estuaries. She suggested that macroalgal blooms might have negative effects on eelgrass at large scales, but eelgrass is not affected by macroalgae within particular estuaries. Ultimately, Hessing-Lewis (2011) concluded that eelgrass density is more strongly affected by climate and nutrient loading than changes in the abundance of macroalgal taxa.

There appears to be an interaction between *Ulva* spp. and *Zostera marina* where their distributions overlapped at Seal Bend. The presence of *Zostera marina* may indirectly limit the distribution of *Ulva* spp. via modification of the environment, resulting in bottom-up controls on macroalgae (van Wesenbeeck et al. 2007). *Ulva* spp. is a morphologically plastic opportunistic species tolerant to a very wide range of environmental conditions (Valiela 1997), which allows its proliferation in diverse coastal areas around the globe (Teichberg 2010). *Ulva* spp. is also responsible for algal blooms that often have a negative effect on ecosystem health and productivity (Lyons 2014). For this reason, recent research studies have focused on identifying and quantifying the factors that facilitate these blooms (e.g. Teichberg et al. 2010, Hessing-Lewis et al. 2015) and have given little attention to factors that are responsible for limiting its growth. In Elkhorn Slough, the distribution of the species across the *Ulva-Zostera* ecotone might be influenced by processes taking place in its microscopic life stages.

Transplanted two week-old *Ulva* spp. had the ability to survive in the *Zostera* bed, yet *Ulva* spp. zoospores failed to recruit to that side of the ecotone (Fig. 14). This discrepancy can be explained by processes associated with microscopic life stages, such as the inability of zoospores to settle or develop (Fredesdorf 2009). Early life stages are more vulnerable to environmental stressors, with vulnerability being a factor of age, size, and time (Vadas et al. 1992). Early developmental stages of macroalgae, and especially post-settlement stages, have high mortality rates (Underwood & Fairweather, 1989). Spores and

germlings lack resistance mechanisms found in adults, which makes them delicate structures, critical to the macroalgal life cycle (Lubchenco 1983). It has been shown for a wide range of species that microscopic zoospores are more sensitive than adult macroscopic sporophytes to extreme abiotic conditions (Fredesdorf 2009). This is also true for bloom-forming macroalgae, where spores have experimentally shown a greater sensitivity than adult stages to both abiotic and biotic factors (Loetzel et al. 1999). These differences are due to several mechanisms that might also be responsible for seasonal variations in abundance of *Ulva* spp. in temperate estuaries (Sousa et al. 2007). The key processes that can suppress macroalgal recruitment are physical stress, competition, grazing, or a combination of these (Vadas et al. 1992). Settlement of *Ulva* spp. zoospores is influenced by biological, physico-chemical and topographic conditions that vary among species (Callow et al. 2000). *Ulva* spp. seem to prefer rough, fine granulated substrata to smooth surfaces (Luther 1976, Fletcher and Callow 1992). Although most studies have focused on the relationship between surface characteristics and *Ulva* spp. spore attachment for anti-fouling recommendations (e.g. Hoipkemeier-Wilson et al. 2004, Martinelli et al. 2016), there is evidence that nutrient availability is a major factor influencing development of *Ulva* spp. spores (Sousa 2007).

Porewater nutrient concentrations can affect spore development, especially if concentrations of toxic pollutants are high or conditions are hypoxic (Devinny and Volse 1978). Macroalgal spores can be chemotactically drawn to nutrients that

stimulate gametophytic growth and reproduction, but in eutrophic systems excess nutrients have indirect negative effects on development for most species (Coehlo 2000). These impacts on early life stages include the inhibition of sperm motility, fertilization, and embryo development, which results in high mortality rates (Coehlo 2000). The opposite effect is commonly observed in *Ulva* spp. and other opportunistic species, which have vegetative life cycles and thus are not affected by hormones-like molecules in the water that could otherwise inhibit sporulation (Coehlo 2000). *Ulva intestinalis* zoospores have been shown to be more sensitive to changes in external nutrient concentration than sporophytes, and to limited phosphate and excess ammonium in particular (Sousa et al. 2007). Regardless of salinity and light levels, recruitment is usually enhanced with phosphate enrichment and hindered by ammonium enrichment (Sousa et al. 2007). My data show lower phosphate and greater ammonium concentrations on the *Zostera marina* side of the ecotone, where *Ulva* spp. failed to recruit, possibly due to excretion of ammonia by organisms living in the eelgrass bed (Weihrauch and Allen 2018). Phosphate values were as high as 490 μM , which is above the 100 μM threshold value after which spore growth is hindered for many *Ulva* species (Sousa et al. 2007). This suggests that porewater nutrient concentrations, and specifically ammonium concentrations, had an influence on recruitment success of *Ulva* spp. across the ecotone.

Sediment characteristics have also been reported as important factors affecting macroalgal recruitment (Devinny and Volse 1978). Macroalgal

recruitment via sexual reproduction is generally unsuccessful in environments where less-consolidated sediments predominate (Park and Hwang 2010). Under eutrophic conditions, increased sedimentation negatively impacts recruitment by reducing the substratum available, and preventing firm adhesion of the spores, which prevents settlement and growth of early stages (Coehlo 2000).

Germination success of *Ulva* spp. zoospores decreases with decreasing particles size (Schories 1995, Park and Hwang 2010). At Seal Bend, larger grain sizes were observed inside the eelgrass bed than at the boundary or on the *Ulva* spp. side. These differences could be due to hydraulic sorting, if larger grain sizes were found towards the center of the channel, where there is higher depositional energy (Tanner 1991, Lario et al. 2002). However, the bivariate plot (Figure 12B) shows there is likely another explanation for the particle size distribution, since the majority of the larger particles fall where there is lower depositional energy, which invalidates the hydraulic sorting theory (Lario et al. 2002). Scouring due to more wave action could damage spores and gametophytes, as well as attenuate light and result in high *Ulva* spp. mortality (Coehlo 2000). Abrasion by movement of shoots on the eelgrass bed might also have a negative effect on *Ulva* spp. (Devinny and Volse 1978).

Grazing pressure is often the main factor controlling populations of opportunistic algal species (Lotze 1998). Species like *Ulva* spp. are especially vulnerable to grazing due to their lack of investment in chemical or structural defenses (Littler and Littler 1980). Consequently, they are a potential food source

for a wide variety of herbivores, including mesograzers without complex feeding structures. In addition to this, specialized grazers might change their preference if they have access to a less-defended alternative food source (Goecker 2003). For instance, amphipods and isopods have a preference for green filamentous algae even though they have strong mandibles for chewing tougher, morphologically defended species (Hickman 1967, Goecker 2003). On the other hand, nutrients generated by certain grazers have been reported to stimulate algal blooms (Porter 1976). Nutrient enrichment, along with other ecophysiological constraints and algal epiphyte consumption by grazers, cause grazing to have a non-controlling impact in certain environments (Kamermans et al. 2002, Goecker 2003).

Under eutrophic conditions, higher grazing pressure can result in a substantial loss of recruits for macroalgal populations (Coehlo 2000). In this study, the greatest density of grazers occurred where *Ulva* spp. had no recruitment success and transplanted *Ulva* spp. resulted in the lowest percent cover. Sea slug density in particular was significantly correlated with percent cover of *Ulva* spp. More than 90% of the individuals within this taxonomic group were of the species *Phyllaplysia taylori* (Taylor's sea hare), which was found almost exclusively on eelgrass (Hughes 2018). This highlights that *Ulva* spp. abundance might be regulated in *Zostera marina* habitat via top-down control by grazers that associate strongly with *Zostera*. Lotze (1998) found that germination and growth of *U. intestinalis* germlings decreased by approximately 96% in the

presence of crustacean mesograzers, and concluded that grazer presence plays a decisive role in regulating mass developments of early life stages. While grazer abundances could not explain much of the variability ($R^2=0.03$) in percent cover of *Ulva* spp. on transplants across the *Ulva-Zostera* ecotone, there was a strong correlation between grazer abundance and recruitment success of *Ulva* spp., suggesting that grazers regulate *Ulva* spp. recruitment at its early life stages.

Approximately 50-75% of the Elkhorn Slough water volume is flushed in and out of the estuary with each tidal cycle (Malzone 1999). Therefore, water quality parameters are not likely to affect the distribution of macrophytes across the ecotone. In opportunistic green macroalgae like *Ulva* spp., spore development and growth is strongly dependent on salinity (Sousa 2007). *Ulva* spp. spore recruitment is strongly constrained in salinities lower than 20ppt (Sousa 2007). Even though there were spatial differences in temperature (Figure 5), salinity (Figure 6), pH (Figure 7), and dissolved oxygen (Figure 8), all measurements were well within *Ulva* spp.'s tolerance range (Kjeldsen and Phinney 1972), and cannot explain why the macroalga was absent inside the eelgrass bed. Nutrient concentrations in surface water were very similar to those reported in a nearby site as part of the National Estuarine Research Reserve System (NERRS)'s water quality monitoring program (Elkhorn Slough Foundation). Again, no anomalies or extreme values were found outside of the usual fluctuations between dry and wet seasons.

Competition for light was predicted to be a key factor preventing the expansion of *Ulva* spp. to the *Zostera marina* side (Sand-Jensen 1988). However, the percent length down to which *Ulva* spp. survival was observed on ropes in the transplant experiments did not vary with eelgrass density (Figure 17). Determining how *Ulva* spp. recruitment is affected by light as an independent factor is a difficult task, since this correlation seems to strongly depend on a set of environmental factors (Sousa 2007). Light can be a relevant factor if paired with availability of nutrients and hydrodynamics of the estuarine system (Martins et al., 2001). *Ulva* spp. spores have been reported to survive more than 10 months (Schories 1995) and germinate (Santelices et al. 2002) in total darkness. These results suggest that there was enough light available throughout the water column at all distances from the boundary within the eelgrass bed, and that light does not affect the spatial distribution of *Ulva* spp. across the *Ulva-Zostera* ecotone in Elkhorn Slough. On the other hand, seasonal variability in macroalgal abundance can be attributed to lower hydrodynamics in the spring and summer that result in lower turbidity and more light available in the water column (Cardoso et al. 2004). These conditions favored the increase in *Ulva* spp. abundance during the spring and summer months relative to the fall and winter months.

Previous studies reported lower affinity of macroalgal zoospores for unstable substrates with highly heterogeneous particle composition (Devinny and Vorse 1978). These studies reported a relationship between sediment composition and

zoospore attachment in certain brown seaweeds exclusively (Lotze 1998). Park and Hwang (2011) described a relationship between density of *Ulva* spp. and ratio of sand to silt in the sediment. No differences in ecology of *Ulva* spp. across sediments with differing particle heterogeneity have been described on muddy substrates with grain size variances as small as found in our study. Sediment characteristics had limited effect on *Ulva* spp. in our study system, as there were no spatial or seasonal differences in particle heterogeneity across the ecotone (Figure 13). Thus, particle heterogeneity can also be ruled out as a relevant factor limiting *Ulva* spp. distribution in Seal Bend.

While the *Ulva-Zostera* ecotone in Elkhorn Slough meets the traditional definition of an ecotone (Attrill 2002), its spatial and seasonal dynamics are not driven by direct interspecific interactions as are implied in recent revisions of the ecotone concept. Changes in macrophyte abundance and distribution, and consequently the overall system ecology, seem to depend on spatial limitations in the distribution of *Ulva* spp. and seasonal fluctuations in the abundance of *Ulva* spp. Therefore, shedding light on the factors limiting the distribution of *Ulva* spp. and their relative importance is crucial to understanding the system as a whole. This study points to a combination of abiotic and biotic factors driving the *Ulva-Zostera* ecotone. More specifically, the presence of *Zostera marina* at Seal Bend has resulted in modified biogeochemical conditions that negatively impact settlement and development of *Ulva* spp.

Zostera marina was historically very abundant in Elkhorn Slough, but started declining in the 1920's (Van Dyke and Wasson 2005). In recent decades, the population has been rapidly recovering as a consequence of increased tidal flows within the slough (Broenkow and Breaker 2005), and increased sea otter density and foraging (Hughes 2013). In the lower slough region, *Zostera marina* has recovered approximately 100,000 m² of land (Zimmerman and Caffrey, 2002). During the last sampling period of this study (May 2019), an isolated patch of eelgrass was observed for the first time among the *Ulva* spp. mats in the control transect. This sighting highlights *Zostera marina*'s potential for rapid growth and expansion in Elkhorn Slough, a rare example of seagrass recovery in a highly eutrophied system (Grant 2009). At Seal Bend, eelgrass beds appear to have expanded to their tidal limit where dessication stress occurs. It is possible that *Ulva* spp. occurred deeper when *Zostera marina* was not present, and that the ecotone boundary has shifted to shallower waters with the recent recovery of *Zostera*.

The mechanisms associated with survival of early macroalgal developmental stages are understudied compared to those affecting adult individuals, but have been shown to be just as, if not more important (Vadas et al. 1992). Studies addressing production, development, growth and survival of early stages have focused on brown algae, and neglected mass-occurring filamentous algal groups like *Ulva* spp. In order to have a greater understanding of the key processes having an effect on the ecology of bloom-forming macroalgae, more research

needs to be conducted on the population dynamics of all life history stages. This study suggests that factors affecting microscopic stages of macroalgae might have a greater influence on species distribution than previously thought.

Abiotic and biotic factors limiting the distribution of *Ulva* spp. in Elkhorn Slough play an essential role in maintaining biodiversity of the ecosystem. These constraining factors associated with *Zostera marina* prevent the proliferation and overgrowth of *Ulva* spp., otherwise likely to predominate seasonally in shallow areas of the estuary due to its opportunistic nature. The presence of ecotones among multiple habitat-forming species translates into higher faunal diversity even at small scales, and an overall healthier system. For this reason, eelgrass meadows provide an additional ecosystem service by biomechanically modifying environmental conditions and ultimately limiting the spread of *Ulva* spp. Their ecological role in Elkhorn Slough is likely to become even more important with the effects of climate change, since conditions will be more favorable for the proliferation of opportunistic ephemeral macroalgae as a consequence of higher temperatures, large shifts in coastal productivity, and higher nutrient input.

The ecological value of ecotones as critical habitats, controls of nutrients and water flow, and indicators of environmental change at a global scale are well known. Management of these habitat boundaries requires a deeper understanding of their underlying ecological processes, along with informed predictions about the impact different management strategies might have on these processes. Ecotones are arguably a delicate balance of interacting abiotic

and biotic patterns, and are therefore considered indicators of widespread changes that can be helpful to predict the large-scale effects of climate change on ecosystem structure and functioning. In order to decide on the most appropriate management and conservation strategies, there is a need for more local research studies from a wide variety of ecotones.

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