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Eelgrass: factors that control distribution and abundance in Pacific Coast estuaries and a case study of Elkhorn Slough, California

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ABOUT THIS DOCUMENT

This document was written by Sherry L. Palacios, University of California, Santa Cruz. Eric Van Dyke, Elkhorn Slough National Estuarine Research Reserve conducted the analysis of historical distribution changes in Elkhorn Slough. The following experts have generously reviewed and greatly improved this document.

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This document is part of a series of reports on key species that use estuarine habitats on the Pacific Coast. Coastal decision-makers are setting habitat and water quality goals for estuaries worldwide and exploring restoration projects to mitigate the major degradation estuarine ecosystems have undergone in the past century. These goals can be informed by an understanding of the needs of key species that use estuarine habitats. To inform on-going restoration planning as a part of ecosystem-based management at Elkhorn Slough, an estuary in central California, we have selected eight species / groups of organisms that are ecologically or economically important to estuaries on the Pacific coast of the United States. The first five sections of each review contain information that should be broadly relevant to coastal managers at Pacific coast estuaries. The final sections of each review focus on Elkhorn Slough.

Kerstin Wasson served as Editor-in-Chief for this series of reports, with editorial and production assistance from Erin McCarthy and Quinn Labadie. They conducted this work as staff of the Elkhorn Slough National Estuarine Research Reserve, owned and managed by the California Department of Fish and Game in partnership with the National Oceanic and Atmospheric Administration (NOAA). Grants from the Packard Foundation, Resources Legacy Fund Foundation, and the Estuarine Reserves Division of NOAA supported this project.

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ABOUT THE ELKHORN SLOUGH TECHNICAL REPORT SERIES

The mission of the Elkhorn Slough Foundation and the Elkhorn Slough National Estuarine Research Reserve is conservation of estuarine ecosystems and watersheds, with particular emphasis on Elkhorn Slough, a small estuary in central California. Both organizations practice science-based management, and strongly support applied conservation research as a tool for improving coastal decision-making and management. The Elkhorn Slough Technical Report Series is a means for archiving and disseminating data sets, curricula, research findings or other information that would be useful to coastal managers, educators, and researchers, yet are unlikely to be published in the primary literature.

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A. Background

The submerged aquatic angiosperm, *Zostera marina* L (eelgrass), grows in shallow, protected waters, rooted in unconsolidated sediments (Fig. 2). Individual shoots are sessile, but plants can spread through rhizomatous growth and sexual reproduction. Under optimal conditions, eelgrass can form extensive mono-specific meadows and can be a dominant organism in the estuary. Eelgrass is considered a sentinel of estuarine ecosystem "health" because its survival on the seafloor depends on the sum of light availability, temperature, water flow, and grazing. Therefore, this species is the focus of various monitoring programs in North America and Europe (Short et al., 2006). Eelgrass was chosen as a key species in the Elkhorn Slough because of its importance as an "ecosystem engineer" and for the ecosystem services it provides (Bos et al., 2007; Hemminga and Duarte, 2000; Moore and Short, 2006).

- Eelgrass is an important primary producer, efficiently converting light energy, inorganic nutrients, and CO_2 into an organic form
- Eelgrass supplies organic matter to a variety of important food webs
- Eelgrass dampens wave energy and slows tidal velocities
- Eelgrass traps fine sediments and thereby enhances sediment accretion
- Eelgrass structures the seabed; creating a complex environment which provides habitat to a diversity of organisms (e.g. worms, mollusks, crustaceans, fish and birds).
- Eelgrass provides for direct utilization by organisms like waterfowl

On the Pacific coast of North America, eelgrass beds are critical nursery habitat for commercially harvested fish species, e.g. California halibut, Pacific herring, northern anchovy, starry flounder, and several species of rockfish (Yoklavich et al., 2002), and support other animals, including nudibranchs, geoduck, isopods, amphipods, pipefish, and Brant (Harvey and Connors, 2002; Phillips, 1984; Wasson et al., 2002). Eelgrass beds on this coast have been shown to increase infaunal (Ferraro and Cole, 2007) and epifaunal (Reed and Hovel, 2006) invertebrate diversity in estuaries.

B. Trends in distribution and abundance

Eelgrass is widely distributed in the temperate northern hemisphere (Fig. 3) (den Hartog and Kuo, 2006; Hartog, 1970). Populations are distinct between the northern and southern range in the eastern Pacific. Eelgrass populations in the eastern Pacific continue to have gene flow with populations in the Atlantic, suggesting an Arctic connection (Olsen et al., 2004). In the eastern Pacific, the species is distributed from the Kotzebue Sound, Alaska southward to the San Ignacio Lagoon on the Baja California peninsula, Mexico (Green and Short, 2003).

Eelgrass grows primarily in calm, soft sediments of embayments and estuaries. Its depth distribution is determined by localized factors, where light availability is the limiter for maximum depth and desiccation tolerance limits shallower depths (approximately the high intertidal to shallow sub-tidal) (Alberte and Zimmerman, 1991; den Hartog and Kuo, 2006). Large mono-specific beds may form, and there is little overlap with other *Zostera* species, although the phylogenetics of eelgrass species are complicated and cryptic species have been detected (Talbot et al. 2006, Coyer et al. 2008). In British Columbia, Washington, and Oregon, a non-native eelgrass species, *Zostera japonica* co-occurs extensively with the native species. *Zostera japonica* grows at shallower depths (0 to -1.8m MSL) than *Z. marina* (-0.9m to -6m MSL (den Hartog and Kuo, 2006)). *Z. japonica* is not typically found south of Oregon (Phillips, 1984), although some beds have recently been detected from the Eel River estuary in northern California. The seagrass genera, *Phyllospadix* and *Ruppia*, are also found along the US west coast, but occupy different niches and so are not considered in this review.

Throughout its range, eelgrass has experienced a significant decline in distribution and abundance principally due to anthropogenic disturbance (Hemminga and Duarte, 2000; Short and Wyllie-Echeverria, 1996; Short et al., 2006). Over the last century, 50-90% of eelgrass habitat along the west coast has been lost due to this disturbance (Green and Short, 2003). The most immediate threat to eelgrass survival on the Pacific coast is declining water quality with associated reduction in light availability (Dennison et al., 1993; Hemminga and Duarte, 2000; Zimmerman, 2006; Zimmerman et al., 1995). Typical reasons for light limitation include sediment loading from terrestrial run-off, eutrophication induced algal blooms, re-suspension of sediments within the estuary, and dredging (Moore and Short, 2006; Moore et al., 1997; Zimmerman and Caffrey, 2002). Additional declines in density and distribution are due to physical habitat destruction for development of residences, industry, bridges and harbors along this coast.

C. Factors affecting eelgrass abundance

A number of factors can influence eelgrass biomass, growth and persistence (Table 1). Shoot density is a useful metric to evaluate eelgrass health for a particular area over time (Fonseca et al., 1998; Palacios and Zimmerman, 2007). As with other species, both bottom-up factors (e.g., availability of nutrients or light) and top-down control (e.g., grazing) can control eelgrass populations (Borowitzka et al., 2006; Jorgensen et al., 2007; Zimmerman et al., 2000).

Light Availability

Light limitation affects carbon balance between emergent photosynthetic shoots and below ground biomass (Zimmerman, 1995). Seasonally reduced light levels or episodic turbidity events during the spring and summer can drastically reduce the amount of carbon fixed and translocated to belowground tissues. Prolonged light limitation causes plant death and thinning of the eelgrass canopy (Palacios and Zimmerman, 2007). Reduced shoot density results in greater sediment exposure, increased erosion, and reduced water clarity—a feedback that has a negative impact on eelgrass abundance (Koch, 1994; Moore, 2004; Short and Wyllie-Echeverria, 1996; Zimmerman et al., 1991). Conversely, the eelgrass canopy alters the local hydrography, which facilitates the export of water column sediments to the benthos. Thus eelgrass provides its own water quality services by trapping water column sediments and promoting water clarity.

Inorganic Nutrients

Photosynthesis by eelgrass is limited by the availability of dissolved aqueous carbon dioxide (CO_2), or CO_2(aq), in seawater (Beer, 1996; Beer and Rehnberg, 1997; Invers et al., 2001;

Zimmerman et al., 1997; Zimmerman, 1995). Up to 50% of dissolved inorganic carbon used by seagrass is in the form of CO_2(aq) (Beer and Rehnberg, 1997). Yet, the concentration of CO_2(aq) in seawater is only 1% of the total dissolved inorganic carbon pool compared to the more abundant bicarbonate (HCO_3) at normal seawater pH, 8.3 (Morel and Hering, 1993). Nitrogen, phosphorous, and other inorganic nutrients are obtained through the roots while most CO_2(aq) exchange occurs through the leaves. Eelgrass roots are buried in sediments rich in the nutrients; nitrogen, phosphorus, and iron (Romero et al., 2006) and are typically not limited by their availability (Zimmerman et al., 1987). Eutrophication may cause toxic concentrations of nitrate and ammonium that threaten eelgrass survival (Touchette and Burkholder, 2000).

Eutrophication poses a major threat to seagrass abundance and distribution because of its effect on algal growth (Short et al., 2006). Seagrasses encounter a double loss against algae. Algae are not limited by carbon availability because they efficiently dehydrate HCO_3 for photosynthesis (Beer and Koch, 1996). Secondly, nutrient enrichment induces noxious algal blooms and increased epiphyte growth on seagrass leaves, which decreases light penetration to the seagrass leaves (Borowitzka et al., 2006; Moore et al., 1996; Ralph et al., 2006).

Disease, Grazing and Bioturbation

In the 1930s and 1940s eelgrass beds in the North Atlantic (along both Europe and North America) experienced a catastrophic decline in abundance due to "wasting disease." Up to 90% loss was reported (Moore and Short, 2006). Causes were initially attributed to temperature, salinity, anthropogenic influences, or disease. Another outbreak in the 1980s and 1990s revealed that the cause was due to the pathogen, *Labyrinthula zosterae*, a slime mold. This pathogen essentially digests the eelgrass leaves from within and can kill the plant within a matter of days (Moore and Short, 2006). The outbreak of the 1930s and 1940s occurred in the North Atlantic, not the North Pacific, but illustrates the potential for dramatic changes to density that can result from pathogens. Natural disturbance such as population decline due to *L. zosterae* may be exacerbated by human –induced disturbances such as light limitation due to sediment loading and eutrophication (Short and Wyllie-Echeverria, 1996; Vergeer et al., 1995).

Invertebrate and vertebrate species occasionally graze directly on the *Zostera marina* plant, and occasionally may exhibit top-down control over eelgrass populations (Jorgensen et al., 2007; Zimmerman et al., 1996; Zimmerman et al., 2000). For instance, Brant geese are conspicuous consumers of eelgrass; targeting eelgrass beds along their migratory routes. Brant populations have shown declines in response to eelgrass degradation (Moore and Short, 2006).

Burrowing and bioturbation may also negatively affect eelgrass. For instance experimental decreases in ghost shrimp with pesticides can lead to expansion of eelgrass beds (Dumbauld and Wyllie-Echeverria 2003).

Recruitment Limitation

Eelgrass reproduces sexually and asexually. Life histories of this species can be either annual or biennial. Sexual and asexual reproduction occur and in populations with mixed life histories (both annual and biennial), vegetative propagation by biennial plants can play a significant role in colonizing new areas (Moore and Short, 2006). Eelgrass morphology consists of three growth modules: leaves; a single, segmented rhizome buried horizontally in the sediment; and pairs of root bundles that grow at each node separating the rhizome segments (Kuo and den Hartog, 2006). Vegetative expansion occurs through sympodial propagation of new shoots from the rhizome at approximately a 45° angle from the apical shoot on the parent rhizome (Kuo and den Hartog, 2006). Further horizontal propagation from the meristem is in the forward direction causing clones to grow laterally away from the parent shoot. Patches expand and fill in during the spring, summer, and early fall, and thin over the winter.

Sexual reproduction increases genetic diversity within eelgrass beds and provides a long-lived seed bank. Although sexual reproduction can have only a 5 to 10% success rate (Orth et al., 2006), the resulting genetic recombination is valuable to ensure high genetic diversity and long-term persistence of eelgrass beds. Seeds are negatively buoyant, thus are not transported far beyond the parent shoot (Orth et al., 1994; Pickerell et al., 2005). Flowering shoots are occasionally dislodged from the rhizome and transported beyond the localized beds. Rafting of flowering shoots is one valuable mechanism of long distance transport of seeds (Koch et al., 2006) by supplying seeds to uncolonized areas or new genotypes to established beds. Eelgrass seeds can remain dormant in the sediment for over two years (Greve et al., 2005). A long dormancy period improves eelgrass bed persistence by providing seedling germination following an acute period of disturbance or disease (Greve et al., 2005).

Natural recruitment by seagrasses may not be sufficient to replace populations destroyed by human disturbances, and so restoration efforts have been used to increase recruitment. Natural recruitment via seed germination is quite variable, dependent on environmental conditions (e.g. light and current velocity), and may take several growing seasons for seedlings to become established. Vegetative propagation tends to be slower and occurs over several growing seasons to many years (Fonseca et al., 1998). In regions dominated by annual life history populations, restoration via seed germination is required. Because of the positive feedback between eelgrass beds and the local environment, especially water clarity, habitat conditions for recruitment may have to be better that those required for continued persistence of established beds (Moore, 2004).

D. Factors that determine estuarine distribution

The main factors that affect eelgrass distribution within the estuary are water quality, tidal elevation, water temperature, and water motion (Table 1).

Water Quality

The lower depth limit of eelgrass is primarily controlled by the availability of light, which in turn is affected by water quality and tidal elevation. Survival is impeded at light levels less than 11% of surface irradiance (Duarte, 1991). The instantaneous light quantity that saturates eelgrass photosynthesis ranges from 40-70 μmol photon m^{-2} s^{-1} (Zimmerman et al., 1994). The minimum number of hours of exposure to photosynthetically saturating irradiance (H_{sat}) ranges from 3 to 10 hours per day (Dennison and Alberte, 1982). This range is variable depending on other environmental influences such as temperature, seasonal variability in metabolic activity, distribution of biomass between shoots and belowground tissue, and genetically determined adaptive characters (Alberte and Zimmerman, 1991).

Photosynthetically available radiation (PAR) is the quantity of light integrated over the visible range that is available to submerged aquatic vegetation (Kirk, 1994). PAR is regulated by the inherent optical properties such as light absorption (by particles, epiphytes, and chromophoric dissolved organic matter (CDOM)) and scattering; and by the apparent optical properties such as diffuse attenuation through the water column, which is strongly influenced by sun angle. Absorbing and scattering material in the water column exponentially reduces light levels according to Beer's Law,

$$E_d = E_0 \times e^{-kz}$$

Where downwelling light (E_d), at a specific depth, is a function of the exponential decay of surface light (E_0) controlled by the diffuse light attenuation coefficient (k), and water depth (z). The depth limit of eelgrass is directly related to the diffuse attenuation coefficient with higher values resulting in shallower depth limits (Duarte, 1991).

Sediment loading is, by far, the major contributor to the total loss of light in seagrass habitat (Moore et al., 1997). However, other constituents in the water column filter light unevenly across the visible spectrum so that light quality as well as quantity can be changed from sea-surface to the top of the seagrass canopy (Moore et al., 1997). For example, CDOM absorbs light strongly between 400nm and 500nm, which is also where chlorophyll absorbs light. In regions of high CDOM loading, typical in calm estuarine environments, photosynthesis by seagrass can become light limited. Epiphyte growth on seagrass leaves can reduce light penetration by up to 30% or more (Kemp et al., 2004; Tomasko and Lapointe, 1991), again absorbing light in regions of the visible spectrum where chlorophyll absorbs strongly, further starving the seagrass plant of light. Therefore, it is more accurate to measure photosynthetically used radiation (PUR) as the metric for a suitable eelgrass light environment (Borowitzka et al., 2006; Zimmerman, 2003a) when proposing eelgrass habitat restoration. Because PUR is determined by seagrass species and is influenced by external pressures such as turbidity and eutrophication stimulated epiphyte loading, frequent monitoring of the spectral quality and quantity of light is needed in restored habitat.

Tidal Elevation

The upper depth limit of eelgrass is a function of tidal elevation. It is defined by desiccation tolerance due to exposure to air on the low tide (Koch and Beer, 1996). Eelgrass shoots growing in the high intertidal had a higher blade turn-over rate than shoots in the lower intertidal and desiccation stress was likely the most important factor in structuring eelgrass habitat in the intertidal (Boese et al., 2005).

Water Temperature

Optimal water temperatures range from 10-20° C (Phillips, 1984). Temperature modulates net production to respiration rates, and strongly influences carbon balance (Marsh et al., 1986). Net production is defined as carbon fixed through photosynthesis minus the carbon cost due to respiration. If carbon balance is positive, more photosynthesis is occurring relative to respiration and the plant will increase in biomass. If carbon balance is negative, then the carbon cost of survival is greater than photosynthesis can provide. Eelgrass can survive brief periods of negative carbon balance, but cannot survive under prolonged periods of negative carbon balance precipitated by high temperatures or prolonged low light (Kraemer and Alberte, 1995; Zimmerman et al., 1989).

Temperature may also influence the timing of sexual reproduction and the distribution of plants with annual or biennial life histories (Ackerman, 2006). Presently, we do not have a thorough understanding of the driving mechanisms favoring annual plants, some possible factors include: thermal stress and bio-turbation (e.g. bat rays; K. Boyer, pers. comm.). For example, selection for an annual life history strategy in some regions of Baja California, Mexico has been attributed to extreme summer temperatures that exceed eelgrass tolerance levels (Moore and Short, 2006). These annual plants reach maturity and release seeds by late spring, and then die off through the summer and late fall. In polar regions, annuals may be favored because of losses due to grounding by sea ice (Phillips, 1984). While annual beds have been found in more temperate regions, eelgrass meadows are more often composed of both annual and biennial plants (Moore and Short, 2006). The non-native species *Zostera japonica* which has invaded the Pacific coast of North America thrives at much higher temperatures than *Z. marina*, and so temperature increases associated with global climate change may favor the non-native (Shafter et al. 2008).

Water Motion

Seagrasses require water flow over leaves to breakdown boundary layers and facilitate gas exchange from the water to the leaf (Koch, 1994). Without water flow, gas exchange is slow because the boundary layer across the leaf is too thick for passive diffusion of CO_2 to occur efficiently (Koch, 1994). The optimum rate of flow is 0.2 to 0.4 m s^{-1} for eelgrass survival (Phillips, 1984; Thom et al., 2001; Zimmerman and Caffrey, 2002). Water velocities above 0.8 m s^{-1} can facilitate erosion and threaten eelgrass survival (Koch et al., 2006). The impact of direct wave action, regardless of its velocity, has the potential to destroy eelgrass beds.

Eelgrass meadows dampen flow, and can reduce erosion. By dampening flow, current velocity decreases, and particles in the water column have time to settle. Therefore beds can act as sediment filters in estuaries (Bos et al., 2007; Koch et al., 2006; Moore et al., 1997), and can reduce the re-suspension of sediments when eelgrass cover increases to above 50% (Moore, 2004). Eelgrass growing in patches or meadows will persist over time while plants growing singly, in small patches, or in sparse patches have the tendency to vanish over time because of erosion pressures (Wyllie-Echeverria and Fonseca, 2003) (Wyllie-Echeverria and Fonseca, 2003).

E. Predicted changes in estuary-wide abundance in response to estuarine restoration projects

The goals of large-scale estuarine restoration projects generally fall into two major categories, changes to water quality and changes to habitat extent. Expected response to such restoration projects is reviewed below.

Changes to water quality

Changes to water quality resulting from restoration projects are likely to significantly affect eelgrass populations. As described above, both eelgrass density and distribution are typically a direct function of light availability, which in turn is affected by turbidity and algal blooms. Restoration projects that decrease water column turbidity or eutrophication are likely to increase eelgrass populations and eelgrass community health. Robust models based on empirical data can be used to predict changes in eelgrass populations resulting from physical changes in light availability or nutrients (Zimmerman and Mobley, 1997), and are an effective tool for designing restoration projects (Zimmerman, 2003b; Zimmerman, 2006).

Changes to habitat extent

Large-scale eco-engineering projects that alter the near-shore and subtidal landscape may result in both gains and losses of eelgrass coverage. Eelgrass occupies a narrow elevation range from the intertidal to the shallow subtidal. Increase in extent of low intertidal-shallow subtidal mudflats resulting from restoration projects may increase estuary wide eelgrass abundance if other physiological requirements are met with respect to light, temperature, nutrients, substrate, water motion, and desiccation stress.

Ecosystem-wide changes in water quality, benthic elevation, and water motion may lead to increases in eelgrass abundance and distribution if surrounding eelgrass patches or seed banks are sufficient to colonize the open space. However, if surrounding eelgrass coverage is lacking, restoration efforts may be recruitment limited (Fonseca et al., 1998). In such cases, time and resources will be needed to replant and monitor new eelgrass patches.

F. Status and trends of Elkhorn Slough populations

Present distribution and abundance

Extensive, dense eelgrass beds are currently found only in a few areas along the lower main channel of Elkhorn Slough, with the largest bed near Seal Bend (Fig. 4). Sparse growth occurs at various places in the mouth area, the lower main channel, and the entrance channel to the Parsons Slough complex. Sediment type varies considerably in Elkhorn Slough eelgrass beds, from very fine muds in Seal Bend to coarse shell hash in the lower main channel (K. Hammerstrom, pers. obs.). While flowering and seed production is common in Seal Bend, eelgrass growing in the lower main channel has not been observed to flower or set seed (K. Hammerstrom, pers. obs.). The first comprehensive survey of eelgrass beds in Elkhorn Slough was conducted in 2000 (Palacios and Zimmerman, 2001). The average shoot density measured *in* *situ* at Seal Bend was 110 shoots m^{-2} (Palacios and Zimmerman, 2001). Dense eelgrass beds that can be detected in aerial imagery have continued to be monitored (E. Van Dyke, unpublished data). Despite significant inter-annual variability in vegetation density; overall distribution appears relatively similar between 2000-2007.

Eelgrass is absent from tidally restricted sites, the upper main channel of Elkhorn Slough, and from the Parsons Slough complex. Restoration attempts were made in the South Marsh portion of the Parsons Slough complex during the 1980s by Richard C. Zimmerman, Randall S. Alberte, and others. Eelgrass transplant mortality was high in intertidal and stagnant sites. However, eelgrass in sites with sufficient water flow (0.2 -0.3 m s^{-1}) and depths not exceeding -2m MLLW survived and in some cases expanded their range before ultimately failing (Zimmerman and Caffrey, 2002). It is unclear why recruitment failed in the Parsons Slough complex in the 1980s or what processes may be limiting survival in this region of the Slough. Further study is needed to determine what pressures are controlling eelgrass survival in this region.

Other studies by this group explored how genetic diversity might influence eelgrass survival. These studies included DNA fingerprinting of eelgrass along the US west coast to determine genetic similarity (Alberte et al., 1994). Another study assessed how eelgrass from other estuaries along the west coast would fare in the Elkhorn Slough (Alberte and Zimmerman, 1993). While it appears that distinct sub-groups of eelgrass occupy its northern or southern range in the eastern Pacific, eelgrass survivorship in Elkhorn Slough was not strongly associated by sub-group (Zimmerman and Caffrey, 2002).

Temporal trends in distribution and abundance

The prehistoric distribution of eelgrass in the Elkhorn Slough area is unknown. Archeological records suggest the presence of nomadic peoples in the region of Elkhorn Slough who were dependent on the sea for food. Midden data for this area reveal the presence of flatfish species often found abundantly in eelgrass beds, but there is no direct evidence for the presence of eelgrass beds (Jones, 2002). The earliest historical records for the region, from the mid- to late 1800s, suggest that the main Slough channel was relatively deep and narrow, and thus appropriate shallow subtidal habitat for eelgrass may have been limited to channel edges.

MacGinitie (1935) conducted pioneering surveys of Elkhorn Slough in the late 1920s to early 1930s in what is now the Moss Landing Harbor area. He defined eight regions from the Old Salinas River Mouth in the north, southward to the region shoreward of Moss Landing Marine Laboratories, spanning a distance of approximately 4 km. Eelgrass was present in all but one of these regions. MacGinnitie's study ended at the Highway 1 bridge, but he noted ".....along the north side above the Hwy bridge *Zostera* extends in an area several feet in width..."

Analysis of aerial photographs from 1931 to the present reveals a decline in eelgrass coverage (Fig. 4). In images from 1931 and 1937, there were dense eelgrass beds throughout much of the lower Slough, including the north and south harbor and eastward to western Seal Bend (Fig. 4a). The lower Elkhorn Slough channel, both east and west of the Highway 1 Bridge, appeared almost choked with eelgrass in 1931 and 1937. No eelgrass was visible east of Seal Bend. A band of submerged aquatic vegetation is apparent on the NW bank of Seal Bend in both 1931 and 1937, and a similar band is apparent on the SE bank in 1937 (E. Van Dyke, unpublished data).

In images from the first decades after the harbor mouth was opened in 1947 (Fig. 4b), eelgrass was largely gone from the north harbor and greatly reduced in the main channel of the Slough. Only scattered bands of eelgrass were present on the north and south sides of the main channel as far east as Rubis Creek. By 1980, only a few patches of eelgrass were present at the Highway 1 bridge (Zimmerman and Caffrey, 2002).

In images from the 1980s forward, a new shoal appeared in the region of Seal Bend, and eelgrass colonized it (Fig. 4c). The shoal has been a persistent feature of the Elkhorn Slough. The flood of 1995 transported a tremendous amount of sediment into the Slough from the Pajaro River, and since that time the shoal and accompanying eelgrass bed have continued to expand (Fig. 4d).

Aerial image analysis is a useful tool in tracking eelgrass coverage, in addition to marsh plant and upland vegetation. Under-sampling, or sampling during different times of the tidal cycle and in different years can compromise the utility of such data. Because of high intra- and inter-annual variability in eelgrass coverage, consistent aerial sampling is needed to better understand trends in coverage in the Slough.

Factors affecting abundance and distribution at Elkhorn Slough

Major factors that may have influenced the distribution and abundance of eelgrass at Elkhorn Slough over the past 150 years are reviewed below.

Restriction of tidal exchange

More than 50% of Elkhorn Slough's estuarine habitats were diked and removed from natural tidal influence to support human land uses over the past 150 years (Van Dyke and Wasson, 2005). Tidal exchange has been restored to some of these wetlands, but about a third of estuarine habitats still remain behind water control structures. Eelgrass is not present in any areas with restricted tidal exchange (K. Wasson, unpublished data), including areas near the mouth (e.g., Bennett Slough) where it was historically present (MacGinnitie, 1935). Restriction of tidal exchange has thus almost certainly decreased the estuary-wide abundance of eelgrass.

One extensive wetland area, the Parsons Slough complex, was diked and drained for decades and then returned to tidal exchange in the 1980s. This area had been historically dominated by marsh, but subsided below the tidal elevation that supports marsh vegetation and evolved into intertidal and subtidal mudflats following the return of tidal exchange (Van Dyke and Wasson, 2005). Attempts at eelgrass restoration in this area were initially successful, but ultimately failed (Zimmerman and Caffrey, 2002), and no eelgrass has colonized naturally. Despite early failures of natural colonization, the complex represents a promising region for eelgrass restoration because of frequent tidal exchange and appropriate benthic elevation. High water transparency in this region may allow for successful restoration of eelgrass habitat.

Opening of harbor mouth

In 1947, the Army Corps of Engineers created a new, larger mouth to the Elkhorn Slough estuarine system to accommodate Moss Landing Harbor. The mouth was directly in-line with the axis of the Slough, and water flow into and out of the Slough was dramatically changed. Water velocity increased with coincident increases in tidal scour that continue to alter the topography of the Slough today. The lower Slough has changed from a shallow embayment to a more fjord-like benthic environment. Intermittent storms and flood events in the decades since the mouth opening have moderated this transition.

The effect of harbor construction and mouth maintenance on eelgrass coverage is complicated. Though baseline data on the natural tidal range are lacking, there is evidence that harbor development and intensive land use (e.g. diking and draining) may have increased tidal range and the net amount of intertidal mudflats along the main channel of the Elkhorn Slough (Eissinger, 1970). By 1945, the tidal prism had been substantially decreased due to sedimentation. Changes to tidal inundation patterns resulting from the opening of the harbor mouth have contributed to the conversion of salt marshes to mudflats along the main channel of the Slough (Van Dyke and Wasson, 2005). Most of the extensive new areas of mudflat are far from the mouth and at a high intertidal elevation; and thus do not represent appropriate mudflat habitat for eelgrass. Eventually, conversion of lower elevation salt marsh to mudflat may create new and appropriate habitat. The harbor mouth may also have benefited eelgrass by decreasing temperatures (through greater tidal exchange and depth in the main channel) in the lower Slough (Figure 6).

Conversely, harbor development has also led to a decrease in suitable habitat for eelgrass. Harbor construction led to substantial losses of eelgrass beds formerly present near the mouth (MacGinnitie, 1935). Harbor construction also increased tidal velocities to levels exceeding the optimum for eelgrass in some areas (Figure 5). These tidal velocities have led to deepening of the main channel, and thus conversion of areas formerly shallow enough to support eelgrass beds to depths beyond their limit. Anecdotal evidence suggests that some eelgrass beds near the harbor mouth are being undercut as sediment is eroded out from under the eelgrass, leaving rhizomes extending out into the water column (K. Hammerstrom, pers. comm.). In Elkhorn Slough, the lower light limit corresponds roughly with the -2m MLLW level (Zimmerman and Caffrey, 2002). Overall it therefore appears that there has been a net loss of appropriate habitat for eelgrass resulting from the construction and maintenance of the harbor mouth, although some gains have also resulted.

Water quality

Water quality in the estuarine habitats of Elkhorn Slough has decreased over time as a result of changes in human land use (Caffrey et al., 2007). In particular, high concentrations of pesticides and nutrients (e.g. up to 5000μM nitrate) occur during the rainy season, especially in the southwestern portion of the estuary and near the harbor mouth (Caffrey, 2002; Caffrey et al., 2007; Phillips et al., 2002). Extremely high nitrate concentrations that occur during storms may result in direct toxicity to eelgrass (Caffrey et al., 2007; Touchette and Burkholder, 2000). There are no baseline data on macroalgae abundance from periods preceding intensive agricultural land use, but it is likely that it has increased as a function of nutrient loading. Macroalgae mats composed primarily of *Ulva* spp. (formerly *Enteromorpha*) are common in the Elkhorn Slough and may impede light penetration or smother eelgrass shoots. The absence of eelgrass from putative habitat in the Slough (e.g., the upper main channel of Elkhorn Slough and the restored Parsons Slough complex) may be a result of increased eutrophic symptoms in these areas, such as higher chlorophyll concentrations (Figure 7) resulting in decreased water clarity, and more frequent supersaturation of dissolved oxygen (Figure 8), which might lead to carbon limitation during photosynthesis.

G. Predictions for Elkhorn Slough

Overview

Four large-scale management alternatives for Elkhorn Slough were developed with the goal of decreasing rapid rates of subtidal channel scour and salt marsh conversion to mudflat habitat that have been documented over the past decades (Largay and McCarthy, 2009; Williams et al., 2008). Changes to physical processes and water quality in response to these management alternatives vs. a "no action" alternative have been modeled and summarized (Williams et al. 2008, Largay and McCarthy 2009). To determine which management alternative best optimizes estuarine ecosystem health, the coastal decision-makers involved in this process of wetland restoration planning require at minimum some basic information about how species that play major ecological or economic roles are likely to respond to the different management alternatives. In the absence of detailed demographic data and rigorous quantitative modeling, it is impossible to obtain robust quantitative predictions about response of these key species. Instead, the goal of the preceding review of factors affecting density and distribution of the species across their range and the evaluation of trends at Elkhorn Slough is to provide sufficient information to support qualitative predictions based on professional judgment of experts. These predictions represent informed guesses and involve a high degree of uncertainty. Nevertheless, for these species the consensus of an expert panel constitutes the best information available for decision-making.

Biological predictions based on habitat extent

Our assessment of the management alternatives has multiple components. First, we predict how population sizes will respond to alternatives based only on extent of habitat of the appropriate tidal elevation. This assessment was based on the predictions of habitat extent at Year 0, 10, and 50 under the five alternatives (as summarized in Largay and McCarthy 2009 and shown in part A Figure 9). Note that all alternatives involve major loss of salt marsh and concurrent gain of other habitat types at year 50; this is due to an assumption of 30 cm of sea level rise after 50 years, which largely overshadows effects of the alternatives. A significant change in habitat area was defined as an increase or decrease of 20% or greater over year 0, No Action (Alternative 1) acreages. Likewise, a significant change in population size of the species was defined as an increase or decrease of 20% or greater over the average population size of the past decade (1999-2008). For the habitat and species predictions, the geographic boundaries are all the fully tidal estuarine habitats of Elkhorn Slough excluding the Parsons complex (predictions do not include tidally restricted areas). For this first component, we made a very simplified assumption that population size is a linear function of area of habitat of appropriate tidal elevation. Thus for example a significant increase in habitat extent translates directly into a significant increase in population size.

Eelgrass occupies the shallow subtidal zone on soft, unconsolidated sediments, so we used the habitat predictions for ‘shallow subtidal’ area (Part B of Table 2) to assess potential aerial coverage of eelgrass. As a first order, a linear relationship between shallow subtidal area and suitable eelgrass habitat was assumed. Predictions based on this habitat model alone are indicated with the letter ‘H’ and presented in blue in Figure 9. Multiple factors such as light, temperature, and nutrient availability interact so that this linear relationship provides a weak correlation estuary-wide. However at local scales, the relationship is robust with subtidal depth a strong indicator of eelgrass distribution. This is due to light availability being the major factor controlling eelgrass distribution and abundance in the slough. Light availability is a function of the diffuse attenuation coefficient (k) and depth. K integrates several water quality parameters (e.g. eutrophication and sedimentation), and may vary throughout the slough so that some regions are favorable to eelgrass growth and others are not.

Factors other than habitat extent that may be altered by management alternatives

Clearly the assumption of a strictly linear correlation between population size and extent of habitat of appropriate tidal elevation is overly simplistic and unlikely to accurately describe population response to the alternatives. Habitat quality or environmental conditions other than habitat extent are also important drivers of estuary-wide population size. Indeed, habitat quality appears more important than quantity in explaining eelgrass distribution in the estuary, since the majority of the subtidal in the estuary (i.e. the upper estuary and Parsons complex) lacks eelgrass, presumably due to habitat quality problems. Unfortunately, we lacked quantitative predictions for most parameters relevant to habitat quality for these species. In order to address this shortcoming, we attempted to identify key aspects of each management alternative that might affect habitat quality or critical environmental conditions. Consideration of these aspects led to characterization of “best case” and “worst case” scenarios for each alternative, indicated by arrows in Figure 9. These arrows represent qualitative assessments; the exact length or location of the arrow has no quantitative significance. Each arrow is marked with a letter; abbreviations are described below. The description of the range of possible outcomes may be as important for decision-makers as the rough predictions of changes to population sizes based on habitat extent. Moreover, we indicate what sort of measures might be taken to avoid or mitigate the worst-case scenario. This information will provide important guidance on future design or refinement of management alternatives. Identification of important parameters other than habitat extent which may be altered by the management alternatives may also lead to future physical modeling and predictions of these parameters, funding permitting, which would enable more robust biological predictions to be made in future iterations of this process, as management alternatives are refined. Here we review the factors invoked in the development of worst and best case scenarios for each of the alternatives.

The main factors, other than habitat extent, which control the distribution and abundance of eelgrass and are likely to be affected by these alternatives are:

a. Water velocity

b. Water temperature
c. Water quality, especially symptoms of eutrophication

Water velocity of about 0.2-0.4 m/sec is considered optimal for eelgrass – velocities lower than this do not provide sufficient mixing, while high velocities can dislodge plants from the sediments. Current peak velocities are about 0.75 m/sec in the lower Slough (Williams et al. 2008), and average velocities are often above the optimum (Figure 5). These high velocities appear to have direct negative impacts such as uprooting eelgrass plants, as well as indirect impacts by scouring away fine sediments that are best for rooting of eelgrass, leaving behind coarse rocks and shell hash that are not appropriate eelgrass substrate (K. Hammerstrom, pers. com.). Under management alternatives 2-3, peak and average velocities would decrease significantly in all years except for year 0 of alternative 3a (Figure 5, most substantial slowing under Alternative 2, least under 3a). Even under the no action Alternative (1) and Alternative 4 (Parsons restoration), velocities are predicted to decrease over time, with significant decreases by year 50 (Figure 5), due to equilibrium gradually being reached. All of these significant decreases in velocity may improve habitat quality for eelgrass and thus may increase eelgrass abundance; such potential increases are indicated with an arrow marked "-v" (for decreased velocity) in Figure 9.

Water temperature between 10-20° C is considered optimal for eelgrass. Temperature influences both the partial pressure of CO_2 in seawater and the metabolic rate of living things. Warmer water holds less gas, according to Henry's Law, so $CO_{2(aq)}$ is available at a time when biological demand for organic carbon is elevated. Increased temperatures accelerate metabolism so that carbon fixed during photosynthesis would be used more rapidly than under lower temperatures. This would decrease carbon storage in the rhizome, an important organ the eelgrass shoot accesses to mitigate episodic carbon starvation. Under current conditions in the lower Elkhorn Slough, where eelgrass is found, temperatures rarely exceed 20° C (Figure 6). However in the upper Slough, where eelgrass is absent, temperatures often exceed 20° C in summer. Under Alternatives 2 and 3b, decreased tidal flushing may result in temperatures in the lower Slough becoming somewhat more like they currently are in the upper Slough. Potential decreases in habitat quality and abundance of eelgrass due to this factor are shown with an arrow marked "+t" for increased temperature in Figure 9. More complex temperature effects, such as changes in flowering or seed production period or shift from biennial to annual life cycles, or increased invasibility by *Zostera japonica*, are not considered here, but are certainly possible (Lee at al. 2007, Shafer et al. 2008).

Water quality, specifically water transparency, is one of the most important factors structuring eelgrass distribution and abundance in the Elkhorn Slough. Under current conditions, chlorophyll conditions in the lower Slough where eelgrass occurs are highly variable, but in some periods of the year, are markedly lower than in the upper Slough where no eelgrass occurs (Figure 7). High water column productivity may be limiting water transparency. Macroalgal mats may also grow or persist more in the upper Slough; algal mats can compete with eelgrass for light. Dissolved oxygen shows much stronger diurnal variation in the upper Slough than lower Slough, particularly on sunny summer days (Figure 8). Supersaturated oxygen conditions can result in oxygen competing for $CO_{2(aq)}$ in photosynthesis, leading to carbon starvation of eelgrass. Increased chlorophyll and macroalgal growth and greater fluctuation in oxygen are symptomatic of eutrophic conditions. All of these differences between the lower and upper Slough may be the result of the much greater residence time of water in the upper Slough (many weeks) vs. lower Slough (one tidal cycle). Indeed, a rough correlation between eelgrass success and estuarine residence time has been observed – eelgrass on this coast can thrive in areas with residence time of a week or less, and tolerate conditions in areas with residence times between 1-2 weeks, but is not found in areas with residence times greater than 2 weeks (M. Josselyn, pers. com.). Under management alternatives 2-4, symptoms of eutrophication might increase in the lower Slough due to decreased tidal flushing. Increased chlorophyll concentrations, increased growth or persistence of macroalgae, or increased frequency of dissolved oxygen supersaturation could lead to decreased abundance of eelgrass. These potential effects are shown by arrows marked "+e" (for increased eutrophication) in Figure 9.

Biological predictions under different management alternatives

Each alternative is evaluated below. The assessment for each includes a) predictions based on extent of habitat of appropriate tidal elevation alone (summarized by the "H" and blue font in Figure 9) consideration of other factors (habitat quality, environmental conditions) related to the management alternatives that might alter these predictions, leading to "best" and "worst" case scenarios shown by arrows in Figure 9, and c) suggestions for how worst case scenarios could be avoided or mitigated.

Alternative 1 – No action

By definition, there will be no significant change in Year 0. Based on habitat extent changes alone, we predict no change at 10 or 50 years either, as area of shallow subtidal habitat is not expected to change significantly. These habitat-based trends are supported by trends over the past decades, which may serve as a proxy for "no action" trends in the future. In the best case scenario, eelgrass distribution in the slough may increase beyond what is predicted by habitat alone due to decrease in water velocity, which is predicted to become significant by Year 50 (decrease of peak velocity from 0.79 to 0.50 m/sec, Williams et al. 2008). This decrease in velocity, which results in velocities more close to the optimum for eelgrass, translates to the potential increase in eelgrass shown with the arrow marked "-v" for Year 50, Alternative 1 (Figure 9). No other major habitat quality changes are associated with this alternative, so no worst case scenarios are considered.

Alternative 2 – Re-route of estuary mouth to create new inlet and decrease tidal prism

Based on habitat predictions alone, we predict a significant increase in eelgrass coverage beginning in Year 0 which is expected to persist through to Year 50. Shallow subtidal area is expected to double by the end of this period, which could translate to a doubling of eelgrass coverage. These habitat-based predictions are supported by the approximate similarity of this alternative to 1943 conditions before opening of the harbor mouth, a period when eelgrass extent was much greater in the estuary (Figure 4). However since nutrient-loading and eutrophication was much lower in the 1940s than now, it is hard to make direct comparisons between these conditions.

In the best case scenario, decreased water velocity under this alternative will increase eelgrass abundance beyond what is predicted by habitat alone, as shown by the arrows marked “-v” in Figure 9. In particular, high velocity areas near the mouth where eelgrass currently settles but appears to become dislodged by high current speeds may sustain substantial eelgrass beds under this alternative. In the worst case scenario, symptoms of eutrophication (high chlorophyll concentrations decreasing water clarity, high macroalgal cover competing for light, and supersaturated daytime oxygen concentrations leading to carbon starvation) will increase in the lower slough, making conditions more like those currently observed in the upper slough where eelgrass is absent. Decreases in eelgrass abundance resulting from increased eutrophication are shown with arrows marked “+e” for this alternative in Figure 9. To mitigate this worst case scenario, implementation of this alternative could occur concurrently with improvement of land use practices to decrease nutrient loading to the estuary.

The temperature profile of the lower Slough might also become more similar to the upper Slough, with the upper limit of optimal conditions (20° C) more often exceeded than currently. Decreases in eelgrass abundance resulting from increased temperature are shown with arrows marked “+t” in Figure 9. No obvious options are available to mitigate the effects of increased temperature.

<u>Alternative 3a – Low sill under Highway 1 bridge to slightly decrease tidal prism</u>

Based on habitat changes alone, we predict a significant increase in eelgrass coverage beginning in Year 10 which will be sustained to Year 50.
Tidal velocities are expected to decrease significantly in Years 10 and 50. This may lead to increases in eelgrass beyond what is expected from habitat area alone; this best case scenario is illustrated with arrows marked “-v” for this alternative in Figure 9.

Symptoms of eutrophication (increased chlorophyll concentrations, macroalgal cover, supersaturation of oxygen) may increase in the lower slough in this alternative due to decreased tidal flushing relative to the no action alternative. This leads to the worst case scenarios, potential decreases in eelgrass related to increased expression of one or more symptoms of eutrophication, illustrated by arrows marked “+e” for this alternative in Figure 9. Since the low sill (Alternative 3a) reduces tidal exchange less than does the mouth re-route (Alternative 2) or the high sill (Alternative 3b), increase in symptoms of eutrophication should be less pronounced. To mitigate the worst case scenario, implementation of this Alternative could occur concurrently with improvement of land use practices to decrease nutrient loading to the estuary.

We predict no significant change in temperature under this scenario, since tidal exchange is affected much less than in the other two mouth-shrinking alternatives. We thus do not predict temperature-related changes to eelgrass abundance for this alternative.

<u>Alternative 3b – High sill under Highway 1 bridge to strongly decrease tidal prism</u>

The predictions for this alternative are identical to those for Alternative 2.

Alternative 4 – Decreased tidal prism in Parsons Complex

The predictions for this alternative are identical as those for Alternative 1.

Synthesis: ranking management alternatives for this taxon

Overall, it appears that Alternatives 1 and 4 are the ones most likely to favor continued eelgrass persistence and expansion in the estuary. Of these, Alternative 4 might be the best for eelgrass, because tidal velocities in the lower estuary would slow somewhat more than in Alternative 1 due to the decreased contribution of the Parsons complex to the tidal prism. Extent of habitat of appropriate tidal elevation (shallow subtidal) increases under other alternatives. But since the majority of the estuary's subtidal is currently not occupied by eelgrass (i.e., the upper estuary and Parsons complex), habitat extent does not appear to be the major factor limiting eelgrass. Rather, eelgrass in this estuary is limited by habitat quality – some combination of decreased water clarity, increased macroalgal cover, increased summer temperatures, and increased supersaturation with dissolved oxygen appear to prevent it from colonizing much of the estuary except for the most strongly marine-influenced areas in the lower estuary. Management Alternatives 2-3 might increase the extent of these unfavorable habitat conditions in the estuary, making the lower estuary more like the upper estuary and decreasing potential eelgrass habitat. This is a matter of degree and concerns are greatest for Alternative 3b and 2, which involve fairly substantial decreases in tidal prism. Under Alternative 2 (mouth re-route), eelgrass might be able to colonize the new mouth area receiving strong marine influence. Alternative 3a (low sill) might have slight enough changes in water quality or macroalgal cover to allow eelgrass to persist where it does currently, or even expand due to increased subtidal habitat extent. Thus the ranking of alternatives from the perspective of eelgrass is:
Alternative 4 > 1 > 3a > 2> 3b.

External factors affecting population trends and importance relative to management alternatives

In addition to changes induced by the above management alternatives, eelgrass distribution and abundance may be significantly affected by other factors in the coming decades. Rising sea level may have an impact, though it is unclear to what degree. Eelgrass survival in current locations may be impeded by rising sea level as the lower extent of the subtidal area becomes deeper, limiting light penetration to eelgrass beds. This loss of habitat may be offset by the conversion of collapsing salt marsh first to intertidal mudflat then to subtidal habitat.

Another external factor affecting population trends is the management of land use practices in the watershed. Decreases in nutrient loading should eventually lead to decreased organic enrichment and symptoms of eutrophication, including improved water clarity and less fluctuation in dissolved oxygen concentrations. This should lead to increased eelgrass extent in the estuary in the long term, and could have an effect greater than that of the hydrological management alternatives under consideration, many decades from now.

Human induced CO_2 increases in the atmosphere will lead to an increase in $CO_{2(aq)}$ and increases in ocean acidification. While this may have a negative impact on calcium carbonate shell forming organisms like oysters or clams, eelgrass will survive and possibly even double in aerial coverage if water transparency is favorable (Palacios and Zimmerman, 2007). However, increases in temperature could have negative effects on eelgrass. The combined effects of rising CO_2 and rising temperature are not well resolved and therefore, predictions to that effect cannot be made at this time.

Targeted restoration actions for these species at Elkhorn Slough

Targeted restoration actions could be undertaken to enhance populations of eelgrass in Elkhorn Slough. It is plausible that large restoration areas with appropriate shallow subtidal habitat depths such as the Parsons complex have appropriate conditions of water clarity and temperature but are recruitment limited due to distance from existing beds. Early attempts to restore eelgrass to the Parsons complex were made by Zimmerman and colleagues and showed promise, although they ultimately proved unsuccessful. Small pilot experiments deploying seeds in buoys are currently being tested in the Parsons complex (K. Hammerstrom, pers. com.)

Extensive restoration efforts have been initiated along the west coast. Over 100,000m^2 of *Zostera marina* plantings have been attempted with varying success in British Columbia, Washington, Oregon, and California (Fonseca et al., 1998). Restoration projects that had the most success met a handful of conditions: a larger acreage was planted; biennial life history donor plants were used; donor bed locations were nearby; planted shoot densities were similar to those found in extant beds nearby; and shoot biomass included the photosynthetic shoot, at least 6 rhizome internodes, and intact root bundles (Fonseca et al., 1998). Germination of seedlings can also be an important method of restoration (Orth et al., 2006), with between 5 and 10% of seedlings successfully germinating (Orth et al., 2006; Pickerell et al., 2005). However, planting shoots or broadcasting seedlings on bare mud may be ineffective. Seedlings may need ripples or burrows in the mud to survive high currents during large wind events (Orth et al., 1994), and shoot survival may be greater with "in-fill" plantings (where "in-fill" includes plantings in bare mud surrounded by eelgrass beds) (Moore, 2004). In San Francisco Bay, deployment of seeds from buoys has recently proven successful (K. Boyer, pers. com.).

Restoration of eelgrass in Elkhorn Slough could be guided by measurements of light availability in potential restoration sites. The light requirements of eelgrass are well documented for populations from Del Monte Beach, near Monterey and the San Francisco Bay (Zimmerman et al., 1996; Zimmerman et al., 1995). A first approach would be to monitor water column transparency (i.e. the downwelling diffuse attenuation coefficient, k_d) in the slough at either moorings or existing sample stations. These k_d values could be used in the eelgrass bio-optical model (Zimmerman, 2003a) to evaluate locations where restoration is most feasible. Following this, sediment or eutrophication to these locations would need to be mitigated. One example, which has been used in the Chesapeake Bay, would be to establish artificial reefs of native filter feeders adjacent to- or even integrated with- eelgrass restoration sites. The filter feeders may improve water quality in regions that may be marginal and do not presently support eelgrass. Once established, eelgrass beds can facilitate sediment trapping, further improving water quality.

Importance of Elkhorn Slough population sizes

Eelgrass beds are important nursery habitat for many invertebrate and vertebrate species of the estuary and coastal ocean. The aerial extent of eelgrass coverage is directly proportional to the benefit to the species served. Elkhorn Slough hosts relatively small beds compared to Morro Bay or Humboldt Bay. However it is important as a biogeographic link among the estuaries of the US West Coast. At Elkhorn Slough, eelgrass beds also serve an important function in providing refuge and pupping habitat for sea otters, which anchor themselves to the vegetation when resting. Infaunal samples collected at Seal Bend have higher biomass and species richness than infaunal samples collected from unvegetated sediment in Elkhorn Slough (K. Hammerstrom, unpublished data). Epifaunal invertebrate and fish densities, including juvenile surfperch and rockfish, are higher in eelgrass than in surrounding unvegetated habitat in Elkhorn Slough (N. Grant, unpublished data).

Table 1 - Habitat ranges for eelgrass growth (adapted from Phillips 1984 with additions from Hemminga and Duarte 2001)

	Range	Optimum	Notes
Light			
as % surface irradiance	> 11%	> 15%	
as H_{sat}	3 to 10 hrs d^{-1}	> 5 hrs d^{-1}	
Depth	high intertidal to 10m	MLLW to 6m	depends on water clarity and latitude
Temperature	6°C to 40°C	10°C to 20°C	
Substrate	mud to sand	mixed mud and sand	
Salinity	0 to 42	20 to 30	
Water motion	Waves to still water	0.2 – 0.3 m s^{-1}, little wave action	

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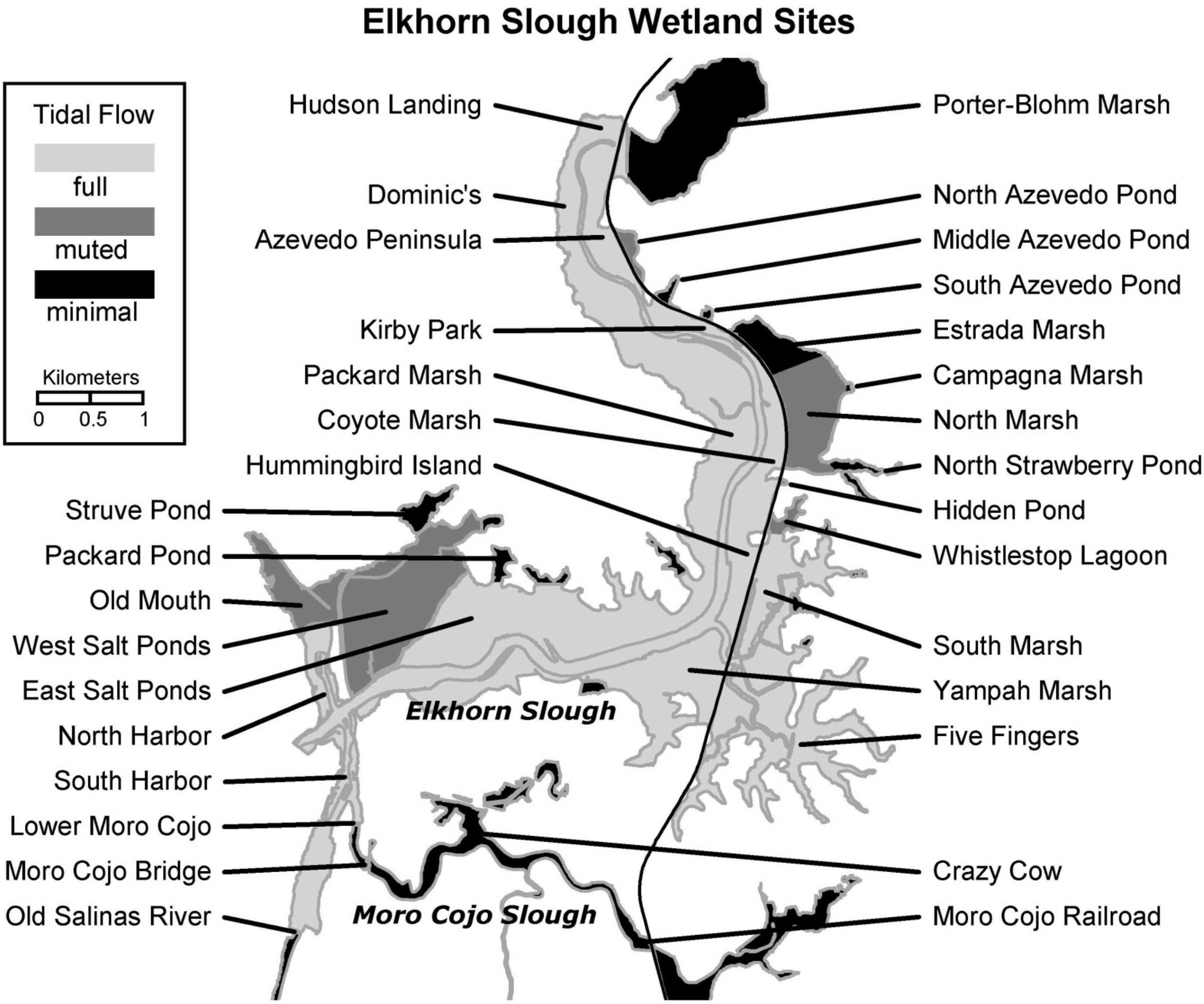

Figure 1. The Elkhorn Slough estuarine complex.

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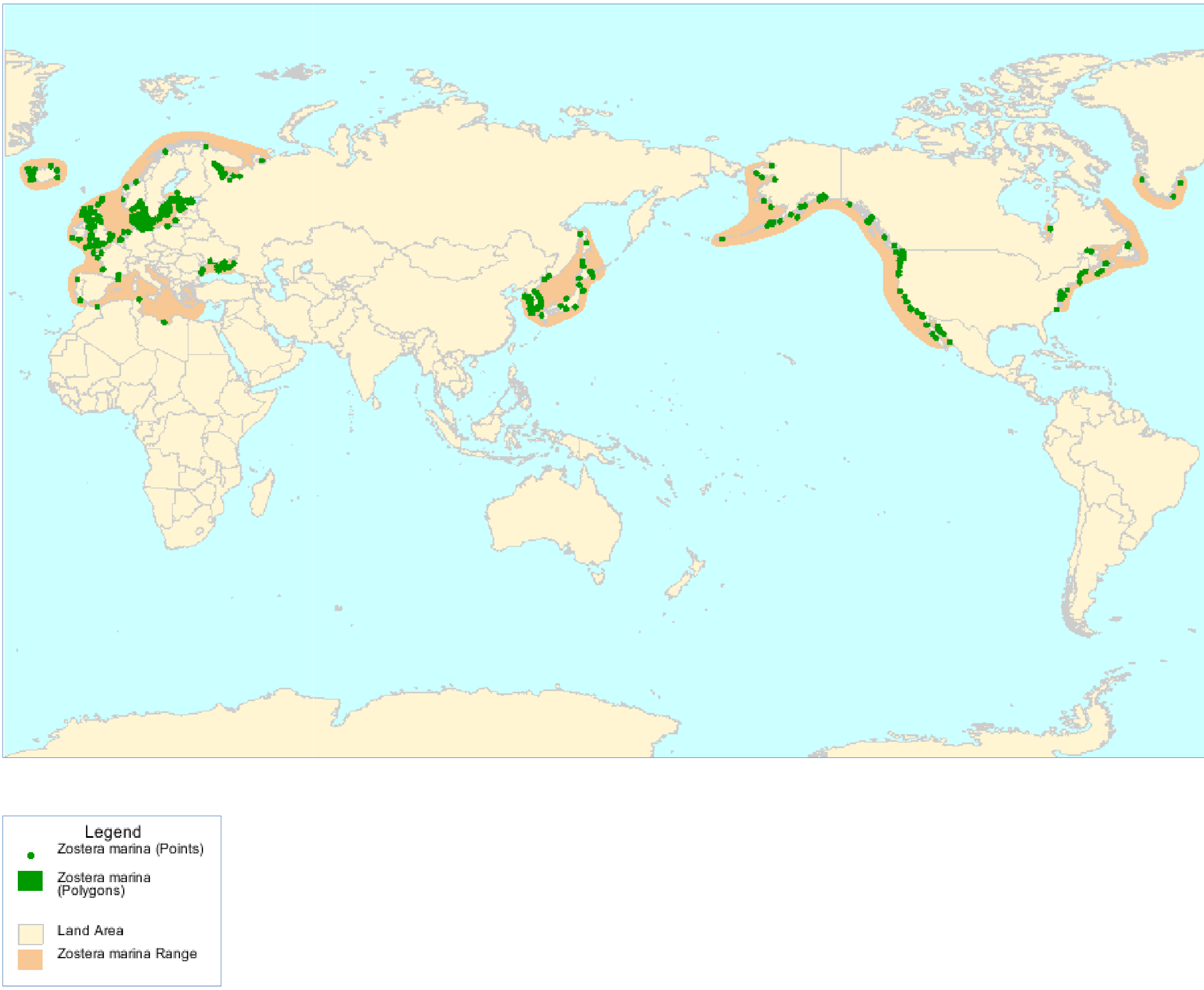

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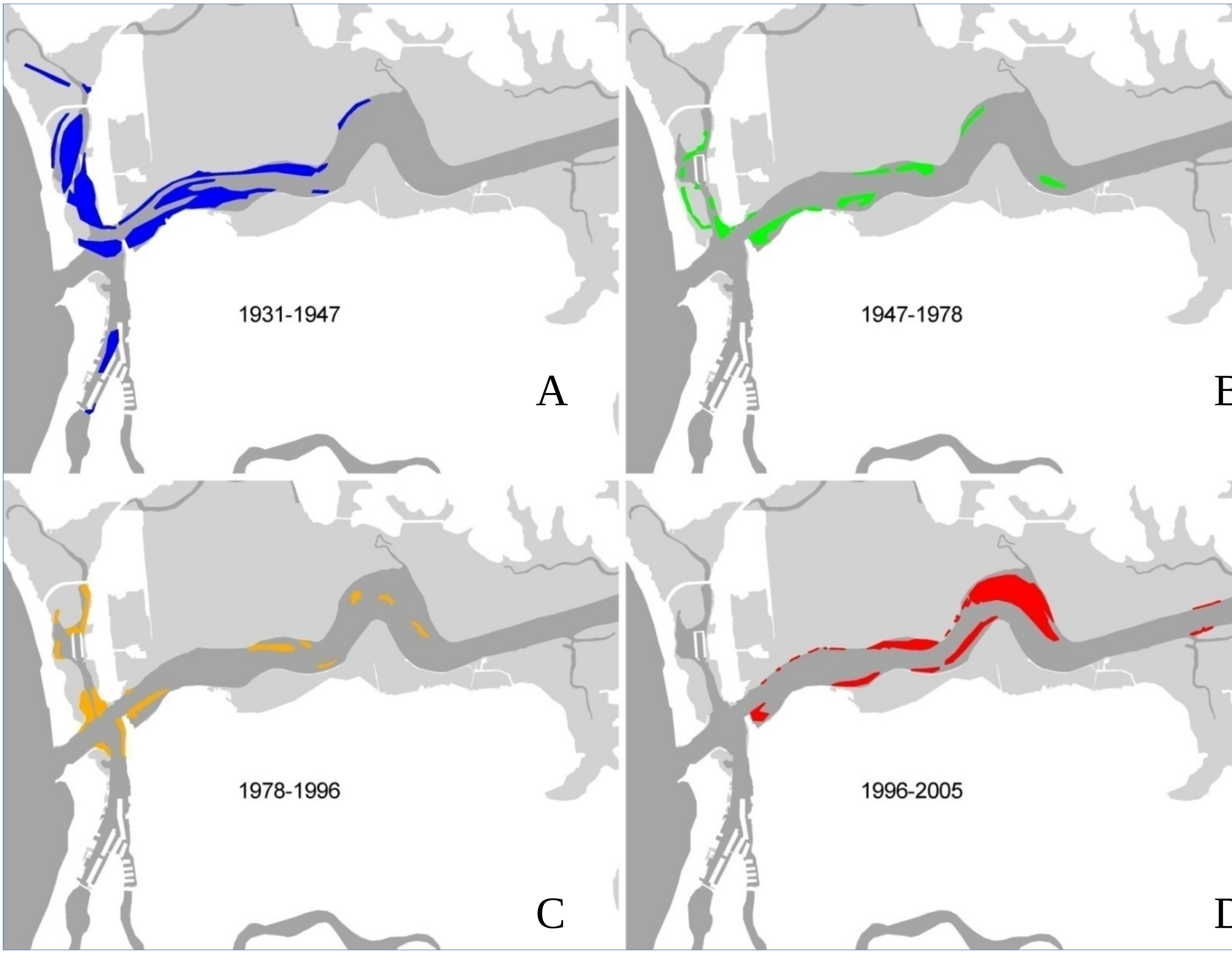
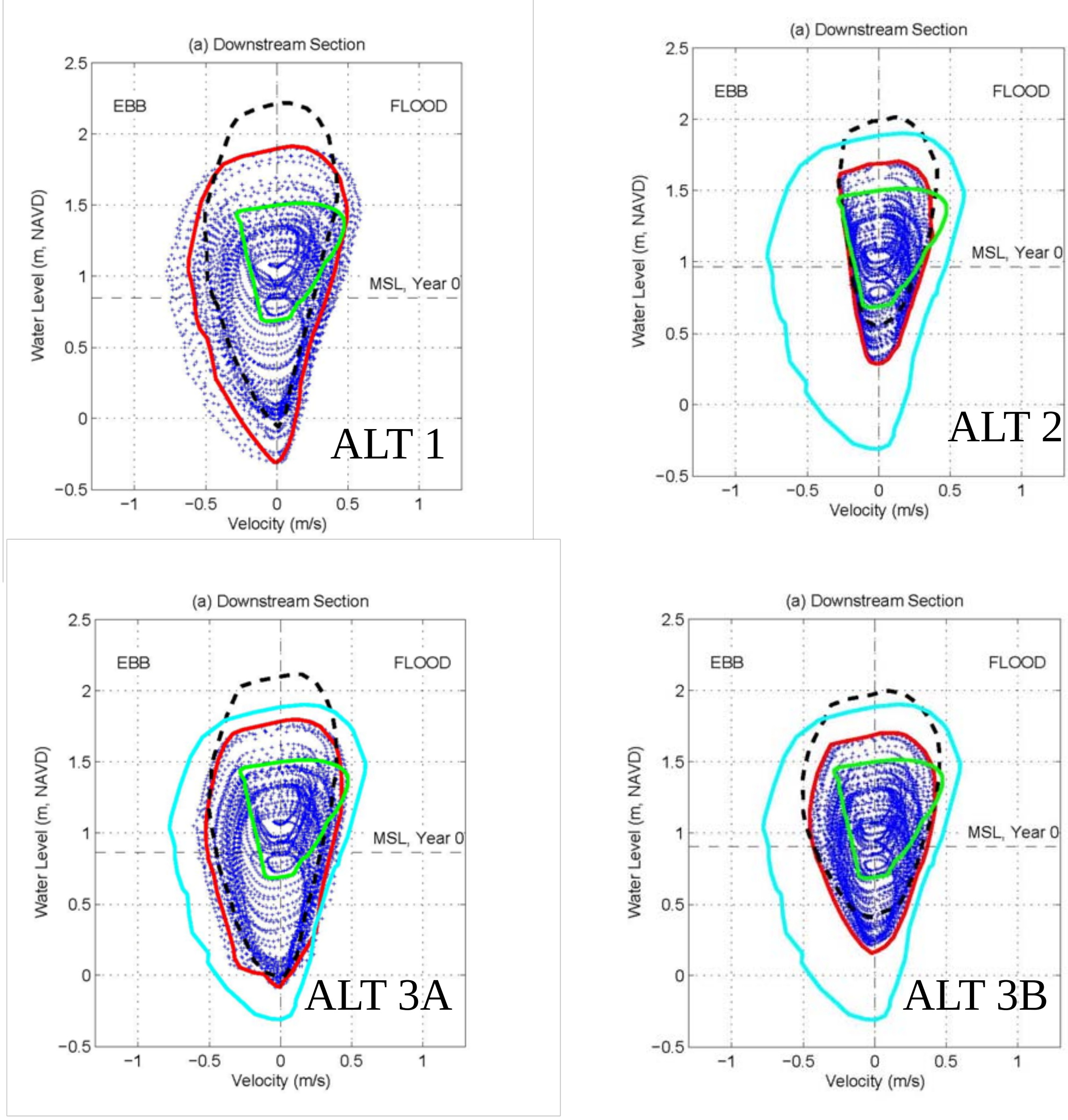
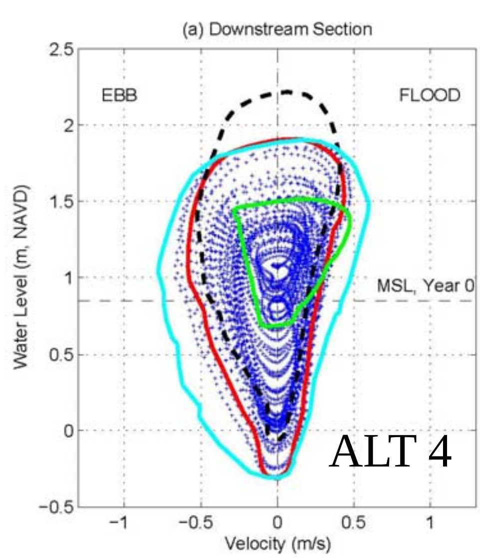


Figure 4. Eelgrass extent in Elkhorn Slough in different periods. (A) 1931 to 1947 (B) 1947 to 1978 (C) 1978 to 1996 (D) 1996 to 2007. These diagrams are based on analysis of multiple aerial photographs from each period. This synthetic approach is more robust than analysis of single photographs and construction of a year-by-year time series, because available photographs (especially from earlier periods) differ in season, tidal height, image quality and type. Averaging based on multiple photographs per period thus led to better representation of the period.





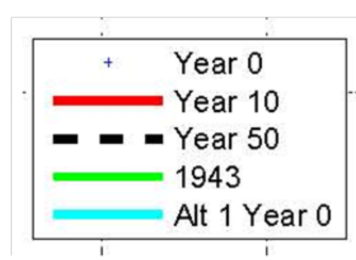


Figure 5. Predicted velocities (X axis) in lower Slough under different management alternatives, from Williams et al. 2008. Eelgrass optimum is 0.2-0.4 m/s.

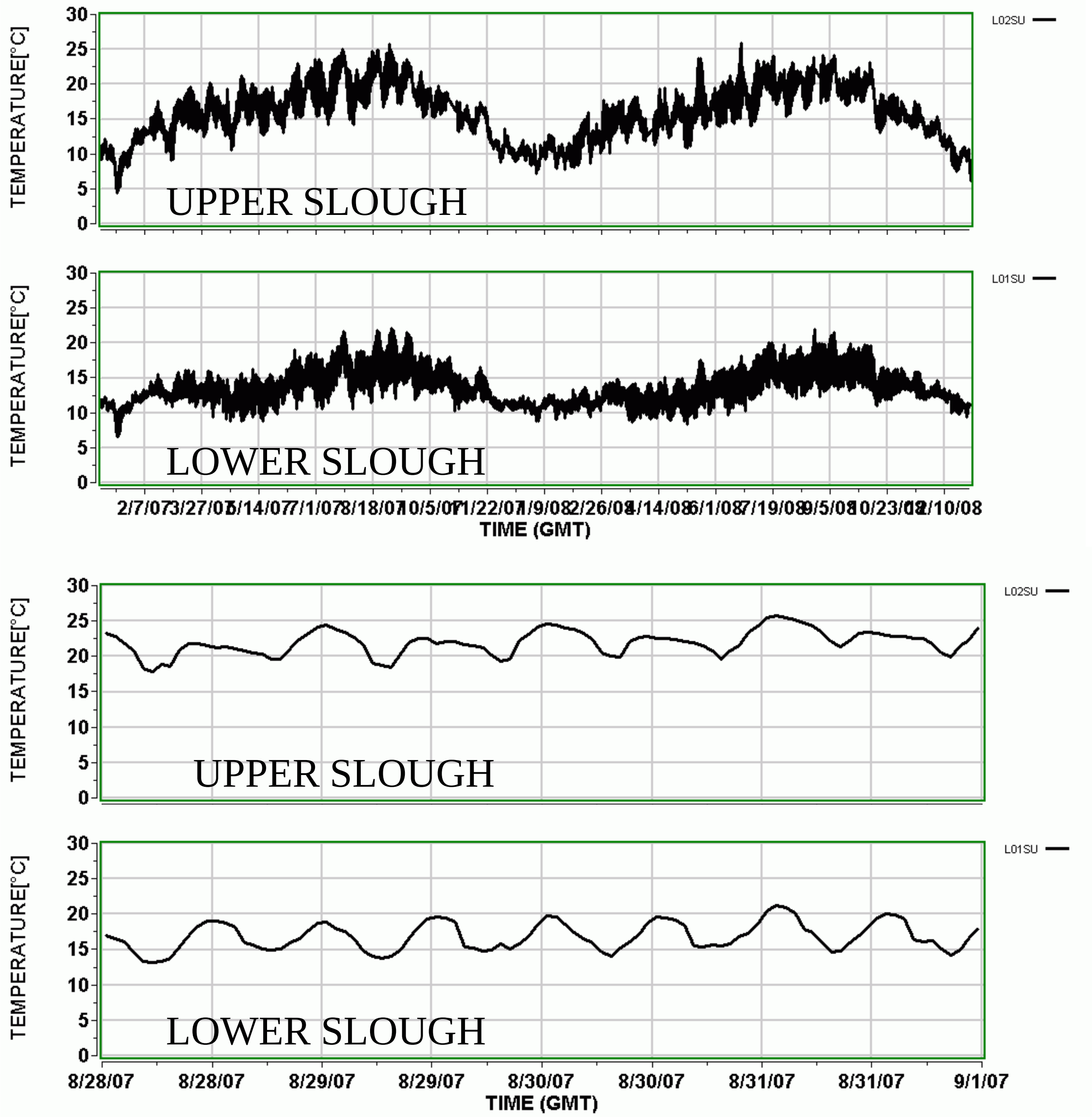
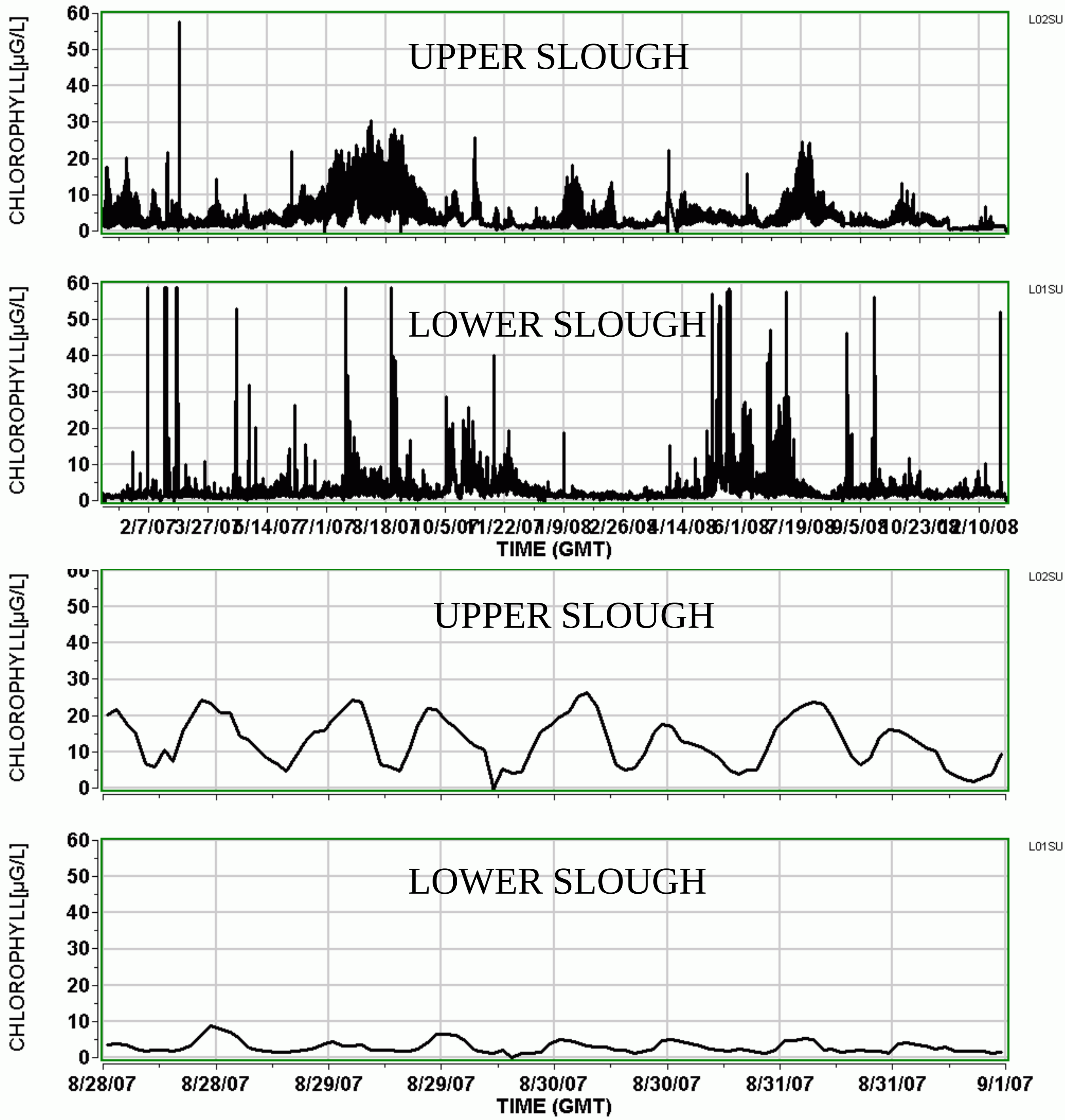


Figure 6. Water temperature in the upper Slough (Kirby Park) and lower Slough (station between Hwy 1 and Seal Bend), courtesy of Ken Johnson (www.mbari.org/lobo). Top panels: 2 years of temperature data; lower panels; 5 summer days. Eelgrass beds in Elkhorn Slough occur at and around the lower Slough station where measurements were made. Under Alternatives 2 and 3b, temperature conditions might shift somewhat towards the profile currently found in the upper Slough. The optimum for eelgrass is 10-20° C; this is surpassed often in the upper Slough in summer months.



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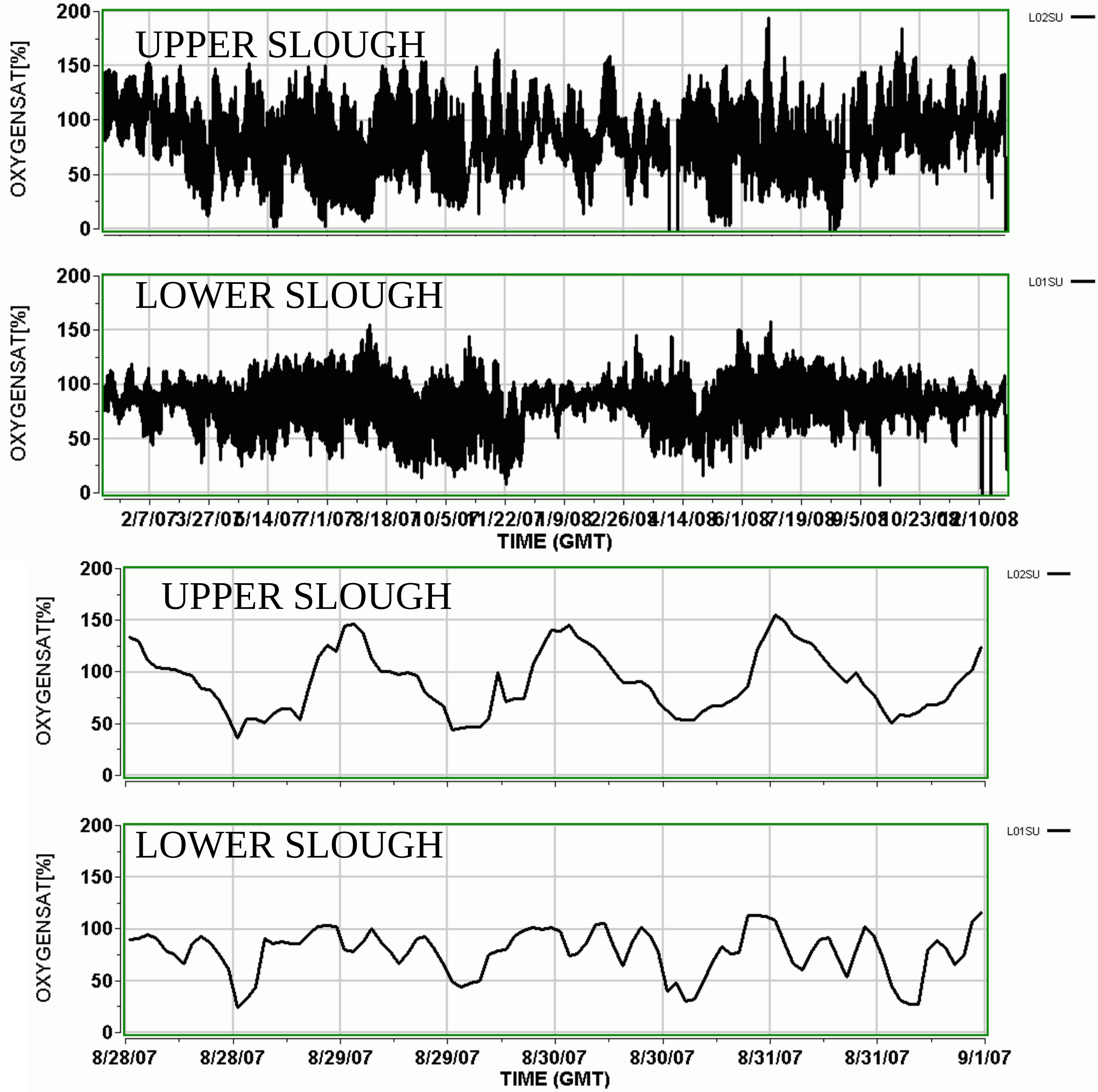

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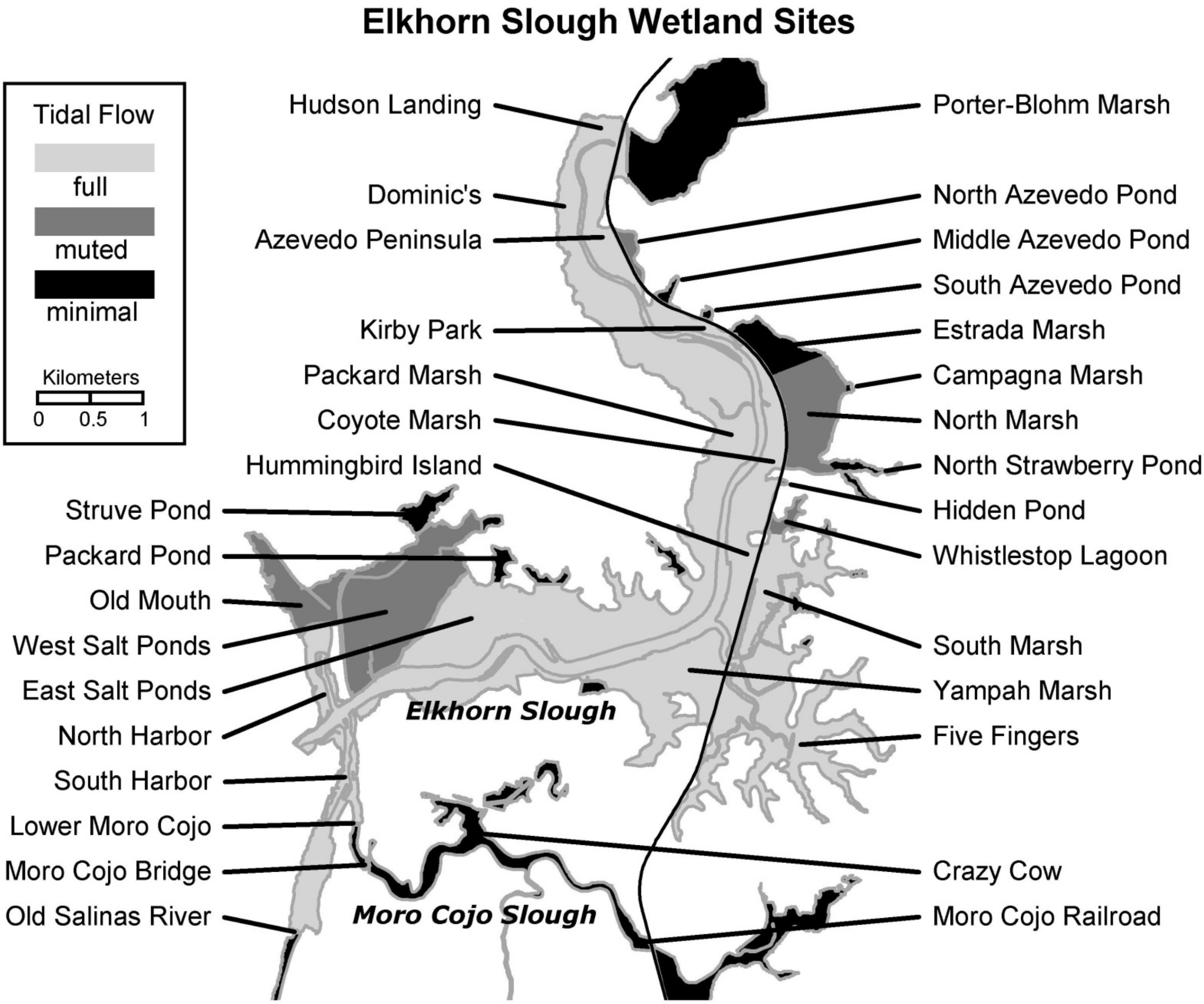

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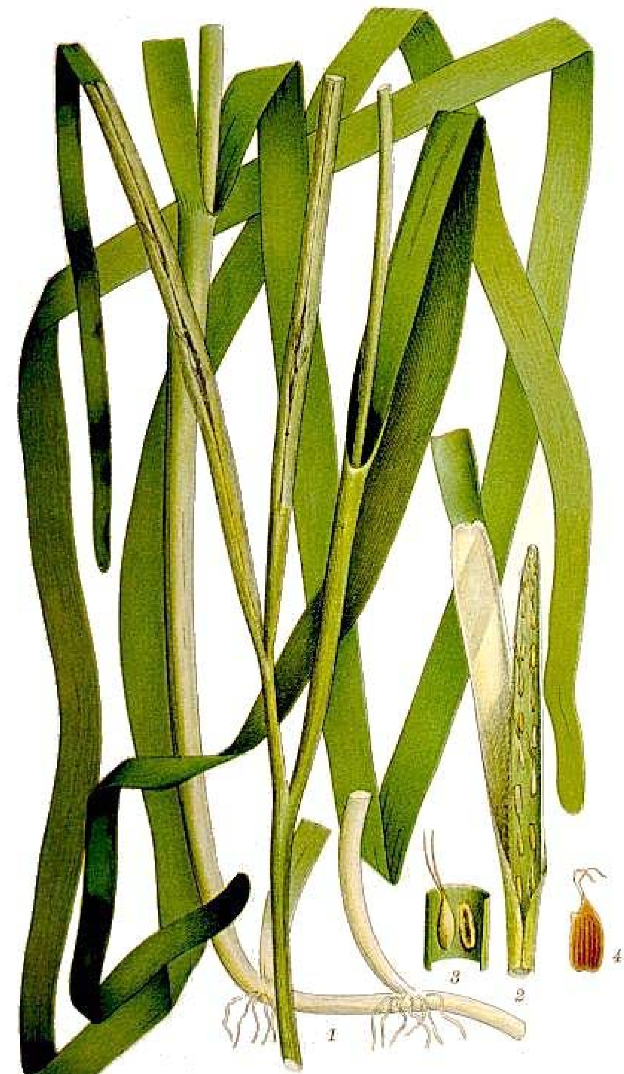

BANDTÅNG, ZOSTERA MARINA L.

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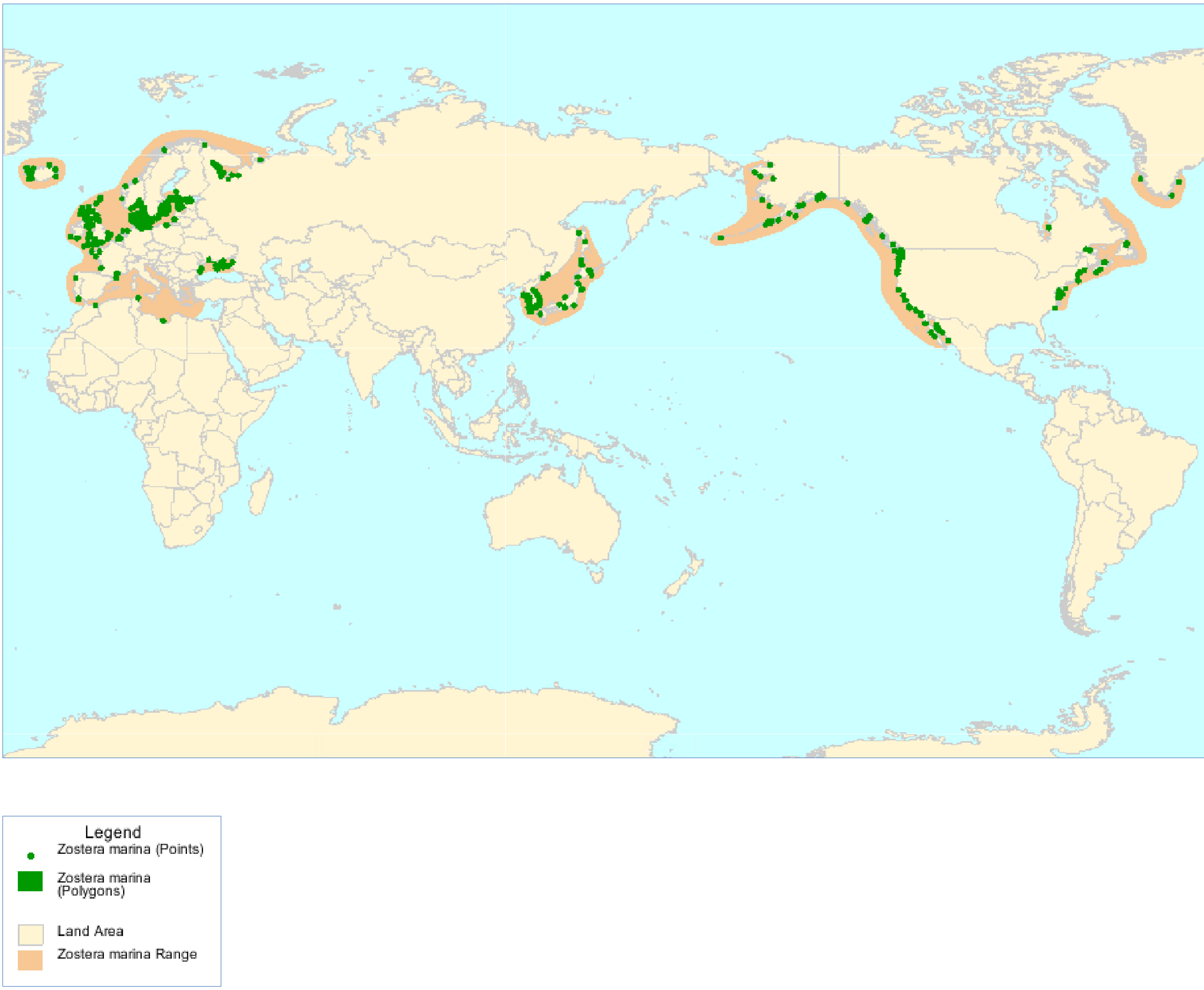

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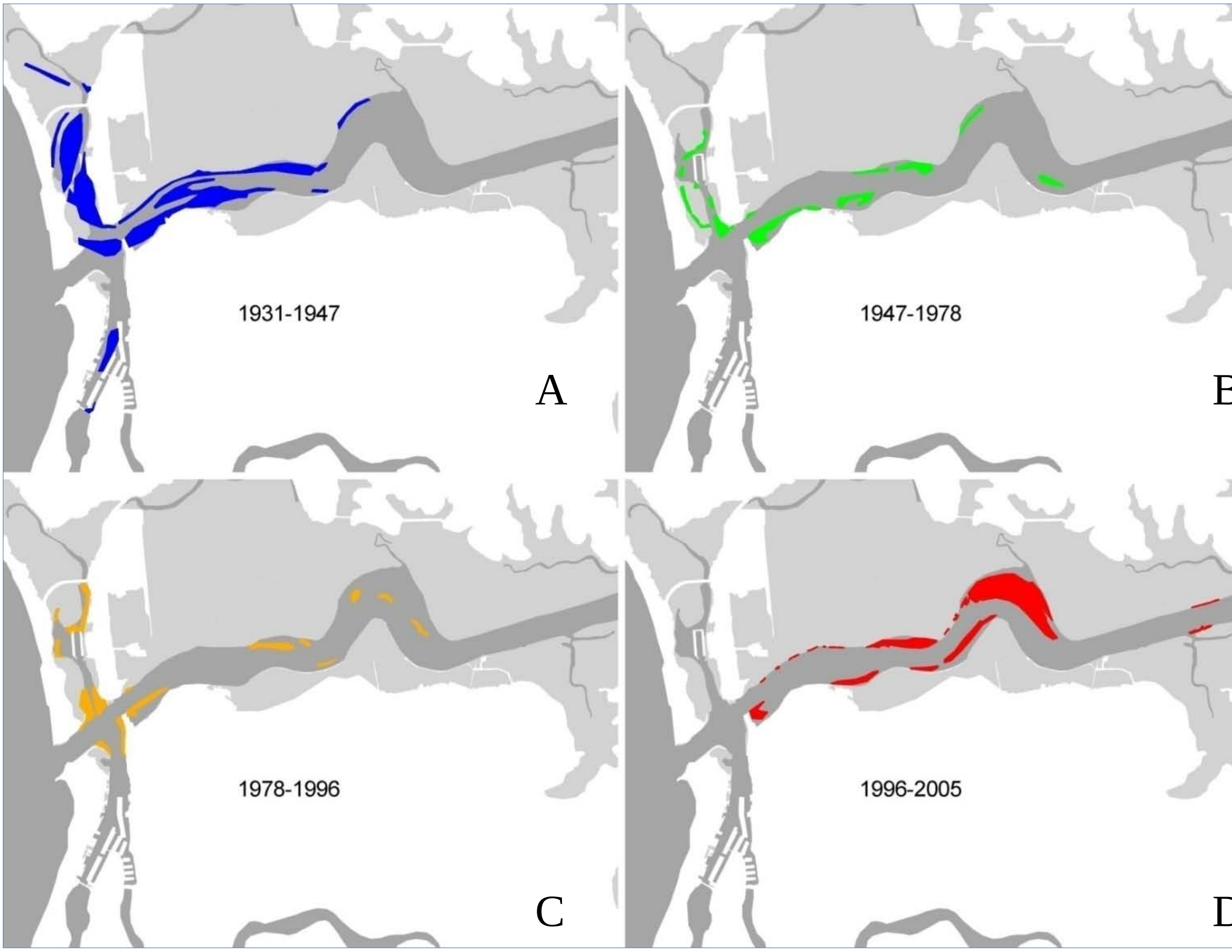

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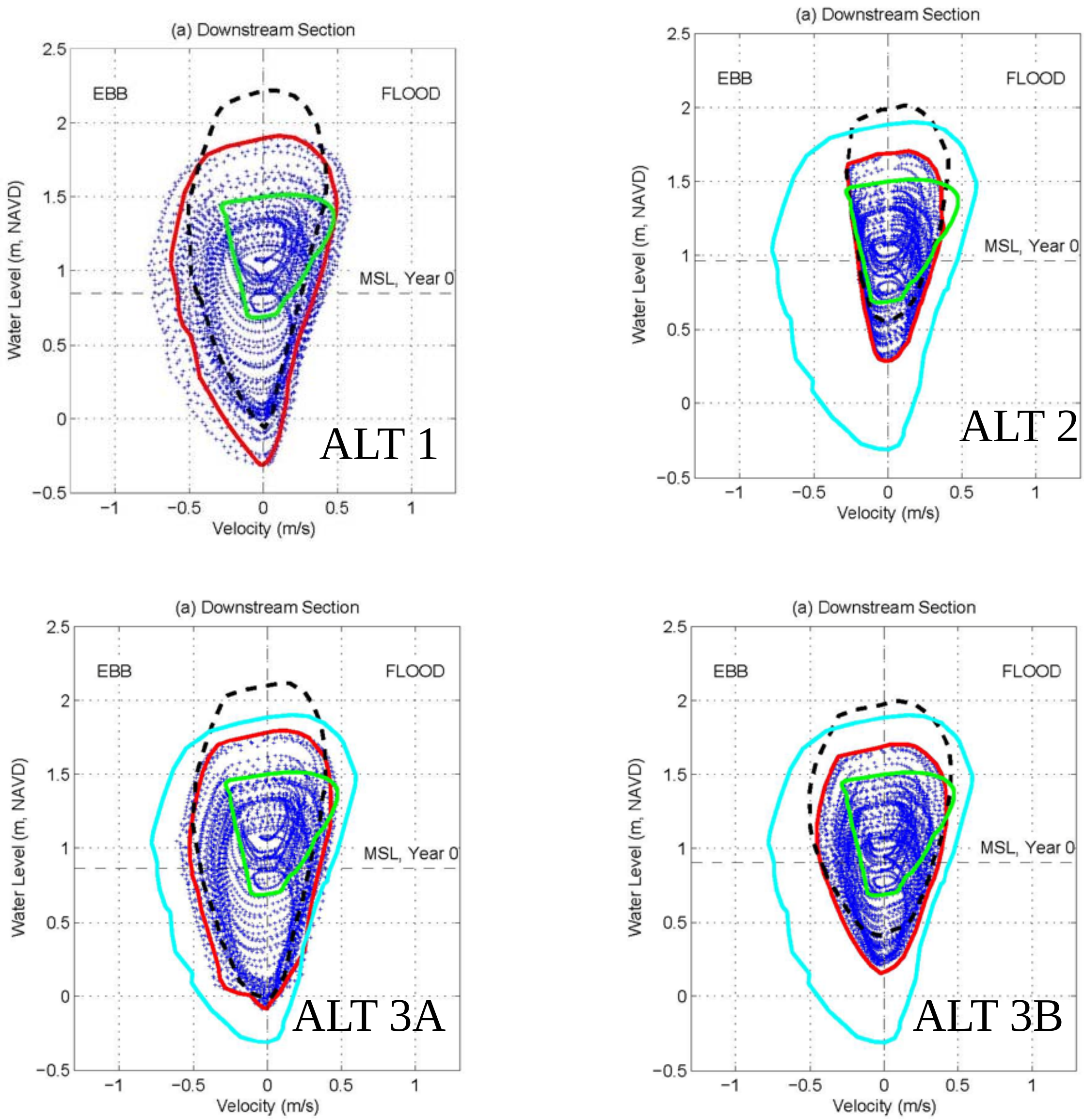

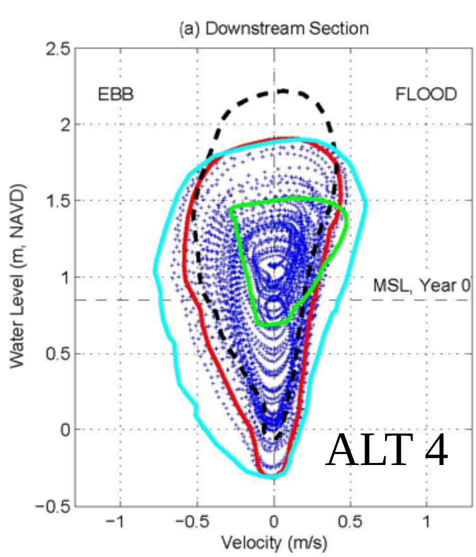

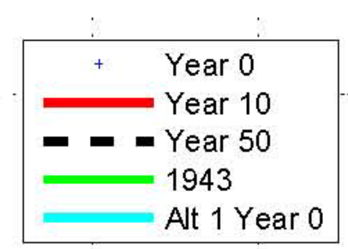

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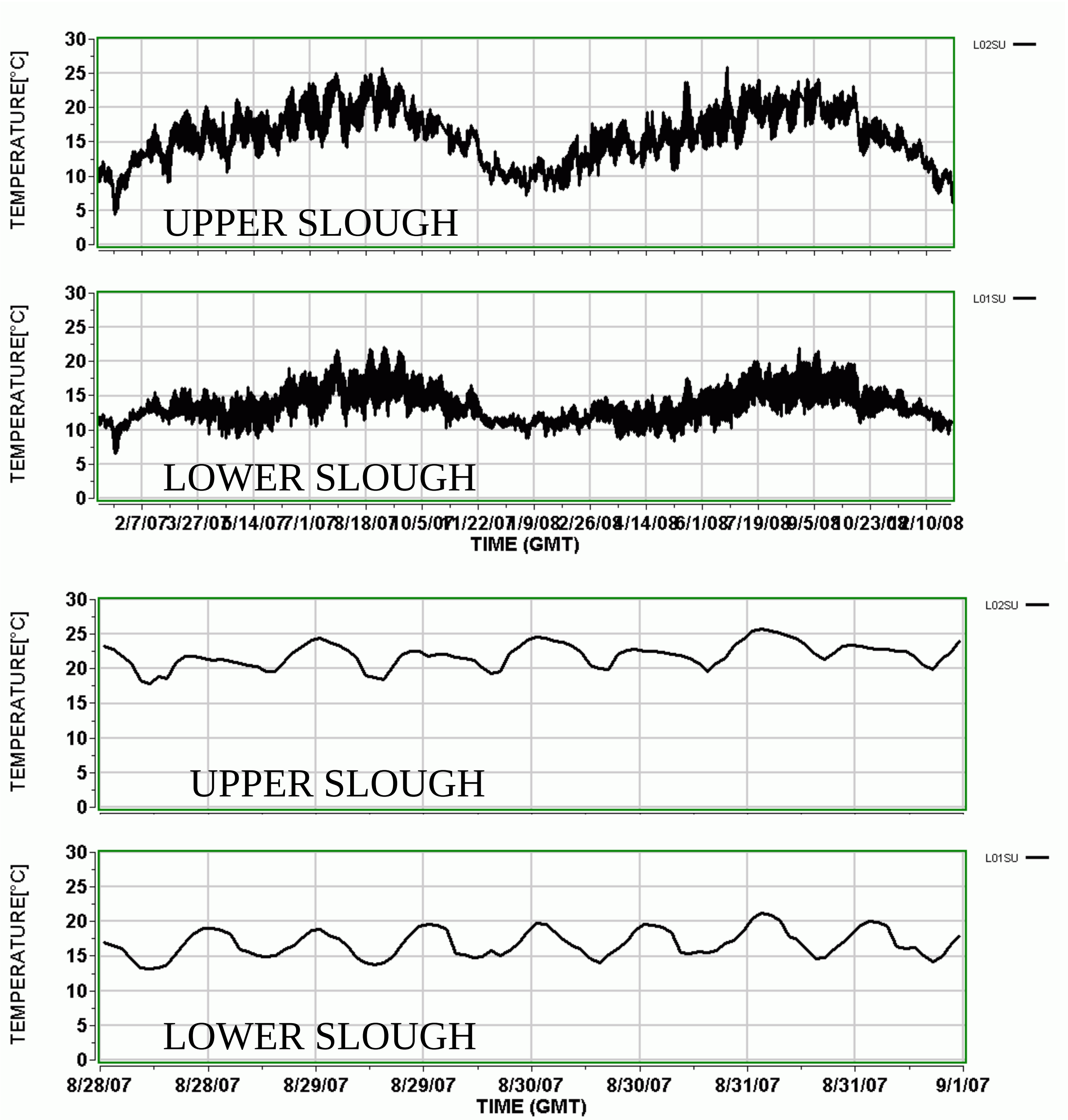

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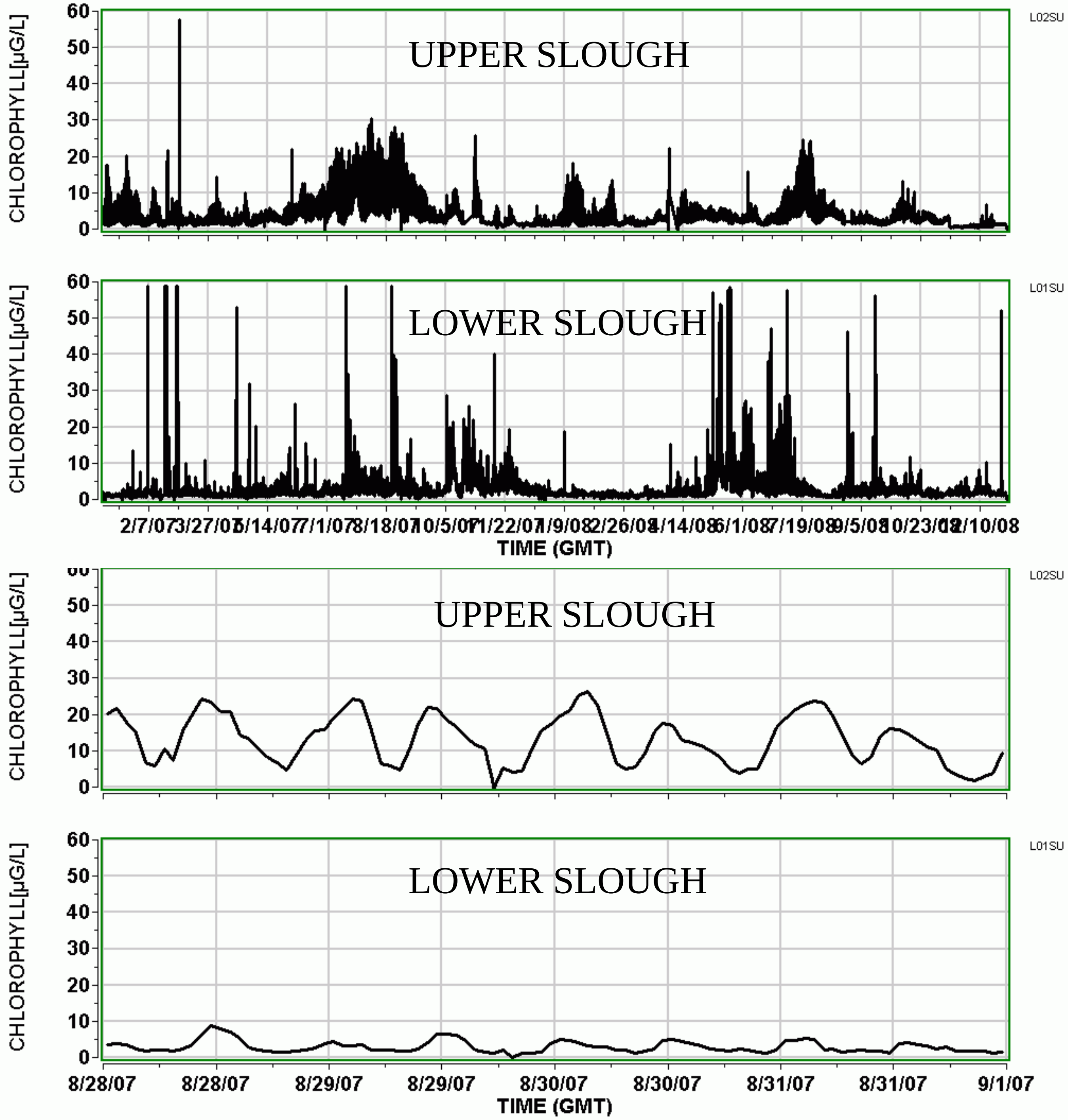

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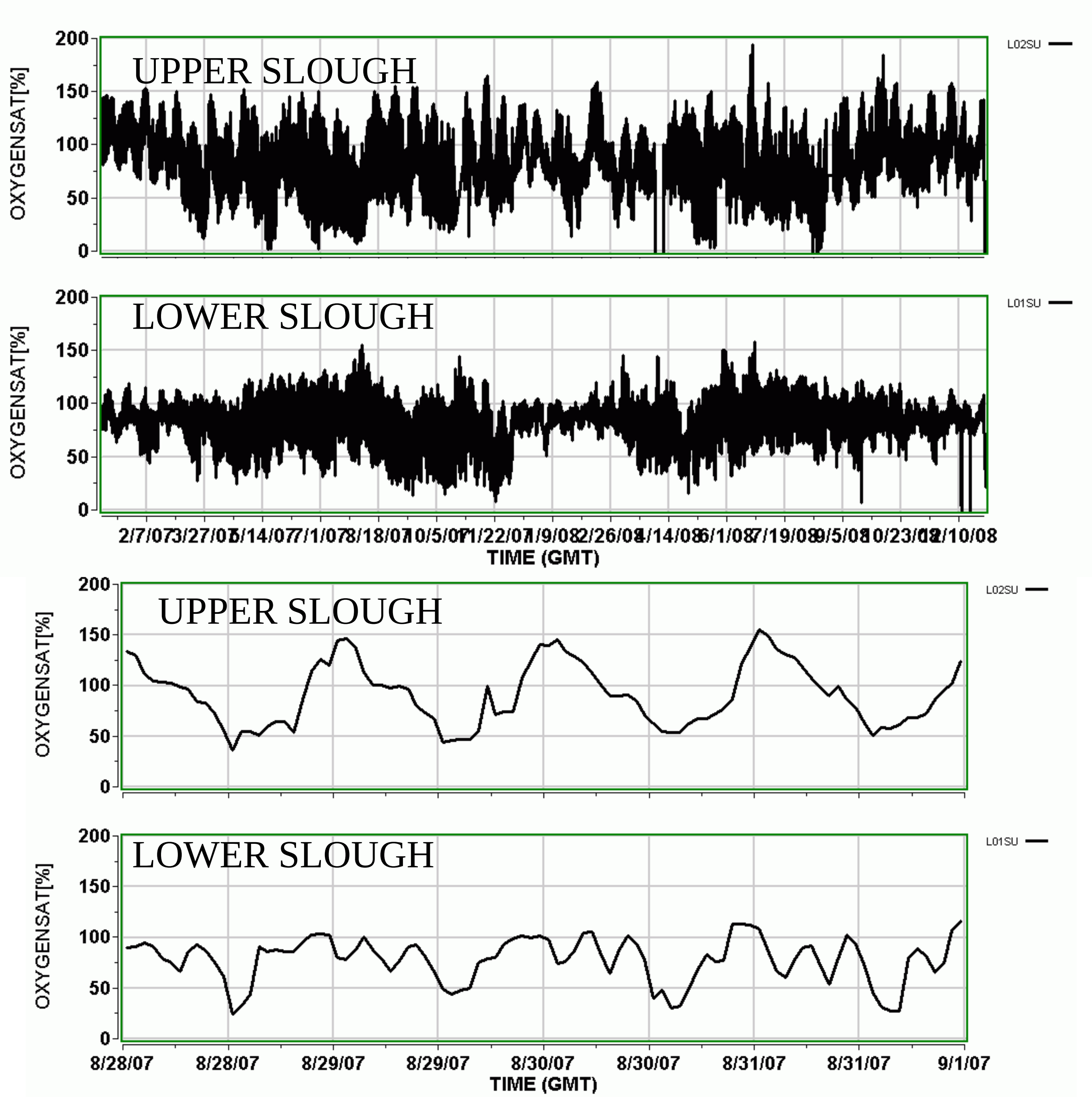

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TABLE 2. Predicted habitat extent under management alternatives.

The numbers represent percent change from baseline conditions (Year 0, No Action alternative) as predicted by H.T. Harvey and Associates and summarized in Largay and McCarthy 2009. Habitats were defined based tidal elevation zones. The area of habitat considered excludes the Parsons Slough complex and all wetlands behind water control structures.

To facilitate perusal of trends, significant increases are coded with warm colors (20% or greater = orange, 50% or greater = red). Significant decreases are coded with cool colors (20% or greater = light blue, 50% or greater = dark blue).

HABITAT PREDICTIONS FOR SINGLE HABITAT TYPES

	A. Deep (>2 m) subtidal			B. Shallow subtidal			C. Intertidal mudflat			D. Salt marsh		
ALTERNATIVE	yr 0	yr 10	yr 50	yr 0	yr 10	yr 50	yr 0	yr 10	yr 50	yr 0	yr 10	yr 50
1 - No Action	0%	9%	42%	0%	8%	15%	0%	3%	22%	0%	-7%	-65%
2 - New Inlet	54%	65%	105%	53%	70%	108%	-39%	-36%	-32%	18%	6%	-40%
3a - Low Sill	9%	12%	20%	8%	22%	72%	-10%	-3%	14%	9%	0%	-55%
3b - High Sill	39%	28%	6%	39%	75%	182%	-34%	-28%	-16%	22%	18%	-36%
4 - Parsons	1%	6%	38%	0%	5%	10%	0%	3%	19%	-1%	-6%	-61%

HABITAT PREDICTIONS FOR COMBINED HABITAT TYPES

	E. Total mud (A+B+C)			F. Shallow mud (B+C)			G. Subtidal (A+B)			H. Intertidal (C+D)		
ALTERNATIVE	yr 0	yr 10	yr 50	yr 0	yr 10	yr 50	yr 0	yr 10	yr 50	yr 0	yr 10	yr 50
1 - No Action	0%	5%	25%	0%	4%	21%	0%	8%	32%	0%	-1%	-12%
2 - New Inlet	-8%	-1%	15%	-24%	-19%	-9%	53%	67%	106%	-17%	-20%	-35%
3a - Low Sill	-4%	3%	23%	-7%	1%	23%	8%	16%	40%	-2%	-2%	-13%
3b - High Sill	-9%	-3%	14%	-22%	-11%	16%	39%	45%	72%	-12%	-10%	-24%
4 - Parsons	0%	4%	22%	0%	4%	18%	1%	6%	27%	0%	0%	-12%