Changes in the Abundance of the Seagrasses *Zostera marina* L. (eelgrass) and *Ruppia maritima* L. (widgeongrass) in San Diego, California, Following an El Niño Event

Megan R. Johnson*, Susan L. Williams†, Carolyn H. Lieberman, and Arne Solbak

Department of Biology, San Diego State University, San Diego, California 92182-4614

ABSTRACT: **Changes in environmental conditions can be accompanied by shifts in the distribution and abundances of organisms. When physical factors become unsuitable for growth of *Zostera marina* (eelgrass), which is a dominant seagrass species in North America, other more ruderal seagrass species, including *Ruppia maritima* (widgeongrass), often increase in abundance or replace the dominant species. We report the proliferation of widgeongrass into eelgrass beds in Mission Bay and San Diego Bay in San Diego, California, during the 1997 to 1998 El Niño Southern Oscillation (ENSO). Widgeongrass persisted in these eelgrass beds at least one year after a return to non-ENSO conditions and an increase in eelgrass density. We suggest that a warming of the water in two bays in San Diego by 1.5–2.5°C could result in a permanent shift in the local seagrass vegetation from eelgrass to widgeongrass. This shift could have substantial ecosystem-level ramifications.**

Introduction

Shifts in the distributions of species are major consequences of environmental change (Kareiva et al. 1993; Holbrook et al. 1997), and estuaries are experiencing rapid changes in environmental conditions (Pulich and White 1981; Robblee et al. 1991; Walker and McComb 1992; Short and Wyllie-Echeverria 1996). The effects of anthropogenic changes such as eutrophication and resultant anoxia, hydrologic modifications, dredging and filling, introduction of non-native species, and loss of wetlands have been well documented. The effects of global climate change that are being superimposed upon these other effects are poorly understood. Increasing sea surface temperature and rising sea level have been predicted to have important effects on estuarine ecosystems (Michener et al. 1997). Under global climate change, a shift in the distribution of a foundation plant species could have major implications for ecosystem function because such plants play dominant roles in marine biogeochemical cycles and in providing habitat support for living resources. Effects of climate change on submersed plant species such as seagrass beds and salt marshes are of particular concern because of the current extent of their loss and continued degradation and the importance of the ecological functions they provide. Almost no research has considered the effects of global climate change, or its implications, on seagrasses (Thom 1990; Beer and Koch 1996; Williams and Davis 1996; Short and Neckles 1999).

El Niño Southern Oscillation (ENSO) events are associated with conditions predicted to occur during global climate change (Schneider 1993), e.g., increases in sea surface temperature and storm frequency and a rise in sea level (Tegner and Dayton 1987). ENSOs provide scientists with an opportunity to study ecological effects anticipated as the climate continues to change. An ENSO event in 1983 received public attention in southern California due to the costly damage to coastal ecosystems and developments. Since the ENSO of 1983 there have been ENSOs in 1987, 1992, and 1997. The 1997 ENSO is referred to as May 1997–April 1998 in this manuscript because National Oceanic and Atmospheric Administration data indicate that early signs of the ENSO (including high sea-surface temperatures) were observed in the summer of 1997 and lasted until early 1998 (http://www.elnino.noaa.gov). Based on ocean temperature anomalies, the 1997 ENSO was the strongest of this century and was twice as intense as the ENSOs of 1987 and 1992 (http://www.elnino.noaa.gov).

This study describes the expansion of *Ruppia maritima* (widgeongrass) into *Zostera marina* (eelgrass) beds in San Diego, California, during the 1997 ENSO. An emerging scenario in seagrass habitats is the replacement of well-studied dominant species, such as eelgrass, with marginal ones, such as widgeongrass, for which there is limited infor-

* Current address: Merkel and Associates, Inc., 5434 Ruffin Road, San Diego, California 92123.

† Corresponding author; current address: Bodega Marine Laboratory, University of California at Davis, P. O. Box 247, Bodega Bay, California 94923; e-mail: slwilliams@ucdavis.edu.

TABLE 1. Sampling dates, variables, techniques, frequencies, and sample sizes used at two sites in San Diego Bay and one in Mission Bay. Sampling dates for water temperature data were during either El Niño Southern Oscillation (ENSO) or non-ENSO logging periods. Shoot density was measured for eelgrass. Seed crop and % cover were measured for wideongrass.

Bay/Site	Variable	Date	Technique	Frequency	n
San Diego					
Coronado Cays	Seed Crop	Jul 1998–Mar 2000	0.04-m² cores	Monthly	10
Silver Strand	Water Temperature	May 19–Jul 18, 1997 (ENSO); May 19, 1998–Jul 31, 1999 and Aug 20–Nov 18, 1999 (non-ENSO)	HOBO	Every 70 min	
	Shoot Density	Jun 1993–Dec 1999;	0.25-m² quadrats	Monthly	40
Mission					
Kendall-Frost	Water Temperature	Jan 1–Mar 3, 1996 (non-ENSO); Sep 11, 1997–Feb 9, 1998 (ENSO); Feb 10, 1998–Apr 9, 1998 and May 30, 1998–Feb 9, 2000 (non-ENSO)	HOBO	Every 70 min	
	Shoot Density	Jun 1993–Dec 1999;	0.25-m² quadrats	Monthly	40
	% Cover	Feb 1999–Aug 2000	0.5-m² grided quadrats	Monthly	10

mation. Environmental conditions in many coastal areas have changed or been degraded so severely that formerly abundant and dominant seagrasses like eelgrass and turtlegrass (*Thalassia testudinum*) have declined greatly in abundance and have been replaced by species that formerly were subdominant or ruderal (Lukatelich et al. 1987; Orth and Moore 1988; Powell et al. 1991; Robblee et al. 1991; Fourqurean et al. 1995). Until environmental conditions again become favorable for the dominant seagrasses, only subdominant or ruderal seagrass species might be able to tolerate changed or degraded environments (Thorne-Miller et al. 1983; Burkholder et al. 1994; Dunton 1996).

Widgeongrass is a ruderal or opportunistic species with wide environmental tolerances associated with a virtually cosmopolitan distribution from the arctic to the tropics (Setchell 1924; Anderson 1972; Verhoeven 1979; Kantrud 1991). Widgeongrass typically exists in more marginal seagrass habitats or as a subdominant species when conditions favor growth of the dominant seagrass species in North America (Orth 1977; Pulich 1985; Lazar and Dawes 1991). When environmental conditions are unfavorable for the dominant seagrasses, widgeongrass can proliferate. Broad environmental tolerances also account for the observation that widgeongrass was the only species of the diverse aquatic angiosperm community to remain in the mesohaline to tidal freshwater portions of the upper Chesapeake Bay in 1990, after the major degradation of water quality bay-wide (Dennison et al. 1993).

We present 6 years of monthly census data for eelgrass in two bays in San Diego, California, and describe the previously unobserved proliferation of widgeongrass into local eelgrass beds during the 1997 ENSO.

Materials and Methods

This study was conducted at three eelgrass beds and with various sampling techniques (Table 1). The Kendall-Frost Reserve site is located in Mission Bay (32°47′29″N, 117°13′24″W), and the Silver Strand (32°38′08″N, 117°08′16″W) and Coronado Cays (32°37′15″N, 117°07′36″W) are in south San Diego Bay, San Diego, California. Prior to and throughout the ENSO these three eelgrass beds were healthy and persistent, and Silver Strand was the largest and most genetically diverse eelgrass population in San Diego County (Williams and Davis 1996). Before 1997, widgeongrass had not been quantified at Silver Strand or the Coronado Cays, and was observed only in the intertidal mudflat areas of Kendall-Frost. Our study was necessarily opportunistic because we had not anticipated that widgeongrass, which had been so limited within local bays, would change so obviously in distribution and abundance.

At Kendall-Frost, Silver Strand, and the Coronado Cays widgeongrass typically grew from 0 to −1 m MLLW, which exposed the shallowest portion of its distribution. The distribution of eelgrass began at the lower depth limit of the widgeongrass and extended to approximately −3 m MLLW. Eelgrass and widgeongrass coexisted within a small zone where the two species met. In San Diego, the period of maximum growth for widgeongrass and eelgrass is from approximately May to October (Ewanchuk 1995; Lieberman 2002).

The Kendall-Frost and Silver Strand study sites were part of a long-term eelgrass monitoring project, which documented eelgrass leaf shoot density and water temperature for over 6 years. From June 1993 to December 1999, we censused the shoot

density of eelgrass at Kendall-Frost and Silver Strand each month, except when weather or water conditions prevented diving. Eelgrass shoots were counted in 0.25-m^2 quadrats (n = 40) placed randomly from a haphazardly chosen starting point in the center of the bed. Within the eelgrass quadrats, the presence of widgeongrass was noted but shoot density was not counted. We present the percent of all quadrats containing widgeongrass.

In order to assess the recruitment potential of widgeongrass, we present data on the seed bank and germination success collected at Coronado Cays during a separate but concurrent study. Seeds were collected on 5 dates between December 1999 and June 2000 using cores (400 cm^2 to 10 cm sediment depth, n = 10) and seed density and germination status were measured. The average number of seeds (± 1 SD) is presented.

We began to monitor changes in the abundance and distribution of widgeongrass at Kendall-Frost because its proliferation was noted during a monthly eelgrass survey. Widgeongrass at Kendall-Frost was monitored on 11 sampling dates, separated by at least 1 month, between February 1999 and August 2000. In order to describe the distribution of widgeongrass, permanent census sites (n = 10) were established every 5 m along two 50-m transects. These transects extended across the depth range of the widgeongrass-eelgrass bed and were centered at the widgeongrass-eelgrass transition zone. At each census site along the transects a grided quadrat (0.5 m^2) was used to estimate seagrass percent cover. Percent cover was used as an estimate of seagrass abundance because widgeongrass shoots are too dense and fine to count efficiently in situ. The mean percent covers (± 1 SD) of census Stations 1–5 (n = 5) and 6–10 (n = 5) were calculated for each sampling date. Transect 2 was not censused from May 1999–August 2000 because it was lost due to human interference, but it was re-established in August 2000. The measurement of widgeongrass percent cover was conducted only at the Kendall-Frost site for logistic reasons.

Throughout the eelgrass monitoring project, water temperature near the edge of each eelgrass bed was logged (HOBO XT and Optic Stowaway, Onset, Pocasset, Massachusetts 02559-3450) every 70 min at Kendall-Frost and Silver Strand (Table 1). The water temperature at the Coronado Cays was assumed to be similar to Silver Strand because of close proximity (Johnson 2000). In order to compare water temperature between ENSO and non-ENSO years, we calculated the 95% confidence intervals (CI) for monthly means of daily maximum water temperature at both study sites. The ENSO time period was May 1997–April 1998 (12 mo) but,
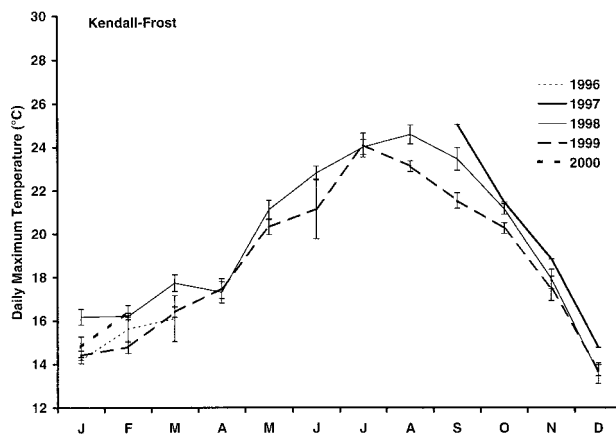

Fig. 1. Monthly average (± 95% CI) of the daily maximum water temperature in the eelgrass bed at the Kendall-Frost Reserve, Mission Bay, California. The graph displays temperatures for the years 1996–2000. The ENSO period is May 1997–April 1998.

due to a lack of data, water temperature was not available for every month. Water temperature was compared at Silver Strand between ENSO (May–July 1997, n = 3) and non-ENSO years (May–July 1998 and 1999, n = 6) and at Kendall-Frost between ENSO (September 1997–February 1998, n = 6) and non-ENSO years (September 1998–February 1999 and September 1999–February 2000, n = 12), where monthly averages were available for all years. Because this study opportunistically investigated the effects of the ENSO, water temperature data before 1997 are discontinuous, necessitating the comparison of water temperatures in the months during the ENSO to the temperatures in the same months of the following years. Average monthly rainfall data were obtained from the National Weather Service for Lindberg Field, San Diego, which is located on San Diego Bay roughly halfway between Kendall-Frost in Mission Bay and Silver Strand in San Diego Bay.

Results

Our data indicate an increase in the daily maximum water temperature of 1.5–2.5°C, depending on the month, during the 1997 ENSO (May 1997–April 1998) in San Diego and Mission Bays (Figs. 1 and 2). There was little overlap between CIs around the average daily maximum water temperature calculated for each month. The grand mean (± 95% CI) of the daily maximum water temperature in Mission Bay (Kendall-Frost) averaged each month that data were available during the ENSO (September 1997–February 1998) was slightly higher (18.7°C ± 3.1, n = 6) than during the same months of the non-ENSO years 1998 and 1999
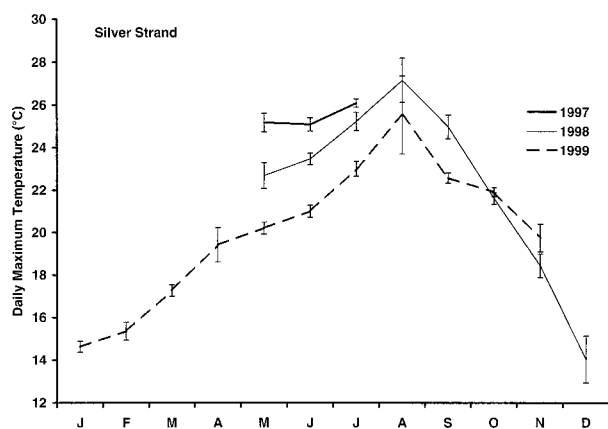
Fig. 2. Monthly average (± 95% CI) of the daily maximum water temperature in the eelgrass bed at Silver Strand, San Diego Bay, California. The graph displays temperatures for the years 1997–1999. The ENSO period is May 1997–April 1998.

TABLE 2. The number of days during which daily maximum water temperatures exceeded critical thermal limits for eelgrass in San Diego during 1997 (ENSO) and 1998 (non-ENSO). Data represent the following time periods when temperature data were available for both years: Kendall-Frost, Mission Bay: September 11–November 25, December 2–8, December 10–April 9 (total = 204 d); Silver Strand, San Diego Bay: May 20–July 18 (total = 60 d).

Critical Thermal Limits[1]	Kendall Frost		Silver Strand	
	ENSO	Non-ENSO	ENSO	Non-ENSO
>21°C	44	45	60	60
>25°C	21	1	38	10
>30°C	2	0	0	0

[1] <20°C is considered favorable for growth of *Z. marina* in this region; >25°C is stressful; 30°C can result in shoot declines (Phillips 1984; Thayer et al. 1984; Zimmerman et al. 1989).

(17.4°C ± 1.9, n = 12). The grand mean (± 95% CI) of the daily maximum water temperature in San Diego Bay (Silver Strand) during the ENSO (May–July 1997) was higher (25.4°C ± 0.6, n = 3) than the same months in 1998, 1999, and 2000 (23.3°C ± 1.6, n = 6). Although water temperatures increased in both bays during the ENSO, the increase was greater in San Diego Bay (2.1°C) than in Mission Bay (1.3°C). Although our temperature records are discontinuous, they suggest that bay water temperatures were affected by the ENSO event much like the ocean waters off San Diego, where records are more continuous (http://meteora.ucsd.edu/wx_pages/scripps.html). During ENSO, eelgrass was exposed to daily maximum water temperatures above 25°C for 20–30 d longer than during a normal year (Table 2). This temperature represents a threshold above which eelgrass typically exhibits stress (see Discussion).

Precipitation data for Lindbergh Field, on San Diego Bay, (www.wrh.noaa.gov/sandiego/prec.html) reveal that the average annual rainfall was 25.17 cm from 1950 to 2001 and 45.67 cm during the ENSO period in 1997–1998. Precipitation was approximately 81% greater than the 50-yr average during the period of time we refer to as the 1997 ENSO.

Eelgrass density in both bays varied seasonally with minima typically occurring in late summer and early fall when bay temperatures, macroalgae, and epiphytic anemones are highest (Ewanchuk 1995; Sewell 1996) and in winter during periods of intense storms and rains and high turbidity (Sewell 1996; Fig. 3, e.g., 1995). Superimposed upon such seasonal cycles were longer-term trends, such as recovery from the severe winter in 1995 and also declines during and following the ENSO (Fig. 3). Starting with Kendall-Frost, the lowest densities observed in the study occurred during the winter of 1995 (21 shoots m^{-2} ± 36, mean ± 1 SD, n = 40) when winter storms were very severe. Eelgrass density recovered from the 1995 winter minimum only to decline again during ENSO to a similar minimum and for a longer period (Fig. 3). The ENSO-associated decline in eelgrass density lagged slightly behind the rise in water temperature and continued through the summer of 1998. We compared mean densities in summer months (Figs. 4 and 5) when water temperatures can exceed critical thresholds for eelgrass stress (Table 2). Prior to the ENSO, the lowest monthly shoot density (125 shoots m^{-2} ± 45, n = 40) observed during a sum-
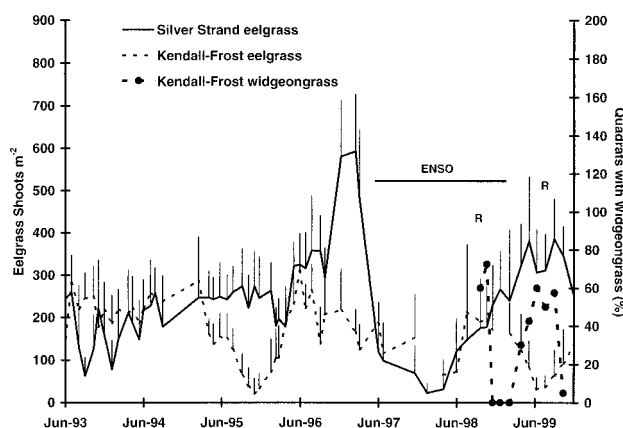

Fig. 3. Eelgrass leaf shoot density (mean + 1 SD, n = 40) at Kendall-Frost Reserve, Mission Bay and Silver Strand, San Diego Bay, California, from June 1993 to December 1999. The presence of widgeongrass (percent of quadrats with widgeongrass) within the eelgrass bed at Kendall-Frost was censused from June 1998 to December 1999. Widgeongrass was observed in census quadrats at Silver Strand on two dates, indicated by R on the graph. A line indicates the approximate duration of the ENSO.
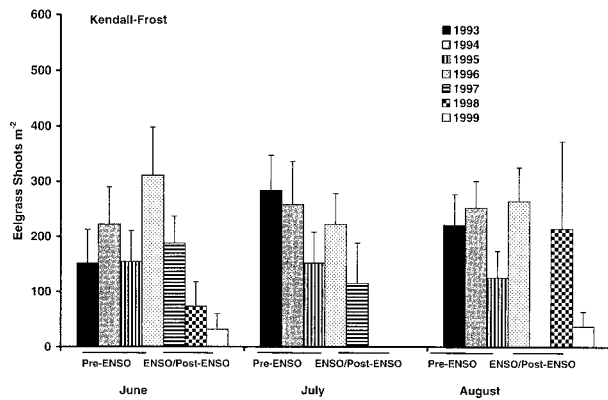
Fig. 4. Comparison of eelgrass leaf shoot density (mean + 1 SD, n = 40) during the summer in years prior to, during, and following the ENSO at Kendall-Frost Reserve, Mission Bay, California.
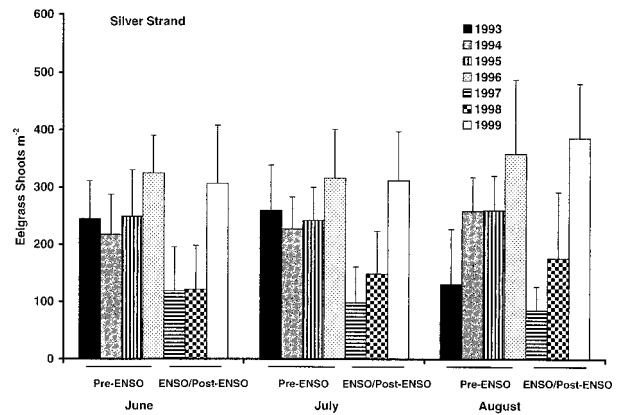

Fig. 5. Comparison of eelgrass leaf shoot density (mean + 1 SD, n = 40) during the summer in years prior to, during, and following the ENSO at Silver Strand, San Diego Bay, California. The eelgrass bed was sampled in September rather than August during 1998.

mer month (June, July, and August) at Kendall-Frost occurred in August 1995 when eelgrass was rebounding from a bad winter (Fig. 4). During the 6 years of observation, the lowest summer eelgrass density (32 shoots m^{-2} ± 28, n = 40) occurred following the ENSO in August 1999, a value 75% less than the previous summer minimum, which occurred in August 1995. By the end of the study, the monthly average densities in each season had not yet recovered to pre-ENSO values (Fig. 3). Lack of a strong rebound in eelgrass after ENSO was associated with a proliferation of widgeongrass in the bed (Fig. 3, results to follow).

Similar declines in eelgrass shoot density were observed at Silver Strand during the ENSO. Prior to the ENSO, eelgrass shoot densities tended to decline during the summer months when bay temperatures were maximum. Compared to Kendall-Frost, shoot densities at Silver Strand were not as strongly affected by the winter conditions of 1995. Prior to the ENSO, the lowest eelgrass shoot densities (63 shoots m^{-2} ± 49, n = 40) at Silver Strand occurred in September 1993 (Fig. 3). The lowest density (23 shoots m^{-2} ± 23, n = 40) in this eelgrass bed over 6 yr of monitoring was observed in January 1998 during the ENSO. Eelgrass declined by 96% from the highest observed density in February 1996 (593 shoots m^{-2} ± 189, n = 40), which represented the most severe decline in eelgrass density we observed in this study. During the ENSO, the minimum summer density observed (85 shoots m^{-2} ± 42, n = 40) at Silver Strand occurred in August 1997 and was 35% less than the lowest pre-ENSO summer density (130 shoots m^{-2} ± 96, n = 40), which occurred in August 1993 (Fig. 5). Eelgrass at Silver Strand recovered to pre-ENSO densities within two years (Fig. 3).

During the ENSO at Kendall-Frost, widgeongrass was observed in the eelgrass bed for the first time in our long-term subtidal census areas (Fig. 3). Its abundance, measured as the percent of censused quadrats that contained widgeongrass, was high during October and November 1998 but after producing flowering shoots in the fall, the bed began to die back in December. The occurrence of widgeongrass began to increase again in March 1999. Although widgeongrass had been observed growing in the adjacent salt marsh (Talley personal communication), it had not previously been reported from this subtidal or intertidal eelgrass habitat.

Following our initial observations of widgeongrass in the eelgrass bed at Kendall-Frost, we assessed the extent to which widgeongrass proliferated into the eelgrass bed by monitoring transects at this site. During the ENSO, widgeongrass displaced eelgrass at water depths of approximately 0 to −1 m MLLW (Stations 1–5) and was mixed with eelgrass at the center of the bed (Figs. 6 and 7); eelgrass dominated the areas at approximately 1 to −3 m MLLW (Stations 6–10). For the 11 sampling dates that widgeongrass was measured, the grand mean (± 1 SD) of widgeongrass percent cover at Stations 1–5 (34.2% ± 33.7, n = 55) was about 6 times greater than eelgrass cover (5.7% ± 13.5, n = 55), but percent cover was highly variable for both species. At Stations 6–10, the grand mean (± 1 SD) of widgeongrass percent cover (11.8% ± 28.0, n = 55) was about one third that of eelgrass (31.2% ± 38.5, n = 55), but percent cover was also highly variable for both species at these stations.
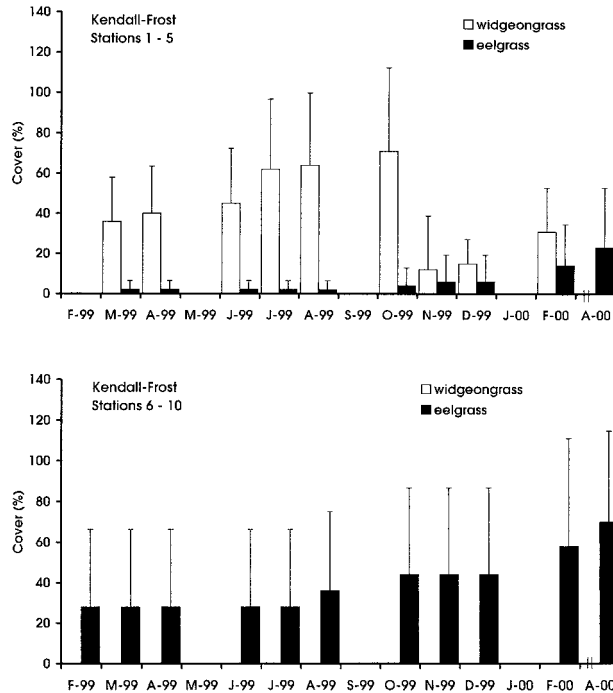
Fig. 6.   Seasonal relative abundance (mean percent cover + 1 SD, n = 10) of eelgrass and widgeongrass along Transect 1 at Kendall-Frost Reserve, Mission Bay, California. Stations 1–5 are the shallow depths (approximately 0 to −1 m MLLW) and Stations 6–10 are the deeper depths (approximately −1 to −3 m MLLW).
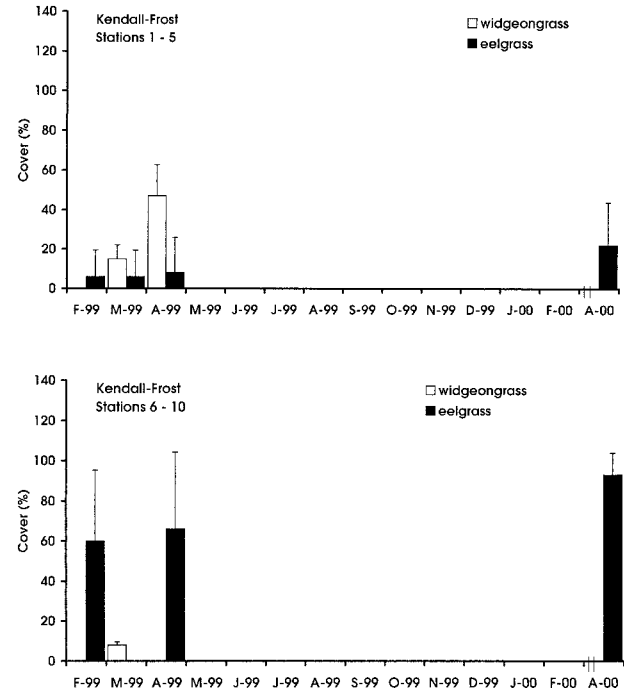

Fig. 7.   Seasonal relative abundance (mean percent cover + 1 SD, n = 10) of eelgrass and widgeongrass along Transect 2 at Kendall-Frost Reserve, Mission Bay, California. Stations 1–5 are the shallow depths (approximately 0 to −1 m MLLW) and Stations 6–10 are the deeper depths (approximately −1 to −3 m MLLW). No data were collected from April 1999–August 2000 due to human interference.

The widgeongrass canopy died back dramatically at the shallower stations in November, at the end of the growing season for both seagrass species. The eelgrass canopy persisted over the winter and began to increase in August when widgeongrass had not yet begun to grow back. Although our qualitative observations indicated that widgeongrass dominated the shallow portions of the transect at Kendall-Frost (Transect 1; Fig. 6), its overall dominance along this transect might have been specific to that site. On the replicate transect that was lost during the sampling period (Transect 2; Fig. 7), widgeongrass was more abundant than eelgrass in the shallow depths in the spring of 1999 but had declined by August, based on the few sampling dates. This and our qualitative observations at the site suggest the pattern along Transect 1 was general at Kendall-Frost.

Widgeongrass persisted at Kendall-Frost through the summer of 2000 (Lieberman personal observation), despite increasing eelgrass abundance (Fig. 3). At one point in the sampling, widgeongrass was observed beyond the lower depth limit of eelgrass (−3 to −4 m MLLW). Widgeongrass did not continue to propagate into the eelgrass bed, at least along the transect. On the last sam-

pling of our established transect through the eelgrass bed, widgeongrass had completely died off along the transect, which was totally dominated by eelgrass (Figs. 6 and 7). In February 2000 we also observed eelgrass seedlings in the widgeongrass bed above the mixed widgeongrass-eelgrass zone, suggesting that eelgrass was beginning to regain this habitat.

Prior to the ENSO, widgeongrass was observed only once in the Silver Strand eelgrass bed in the intertidal portion of the bed (June 1992, Williams personal observation). During the ENSO, widgeongrass was observed in eelgrass census quadrats on two occasions in the Silver Strand eelgrass bed (Fig. 3). Widgeongrass established better in the shallower subtidal and intertidal portions of the bed, where we did not census eelgrass (Johnson 2000).

When we began the study, we did not know whether widgeongrass would survive the winter in San Diego. Although it did die back dramatically in winter, it recovered in spring due to a combination of vegetative proliferation (Lieberman personal observation) and possibly seedling recruitment. We found a large seed crop of widgeongrass

TABLE 3. Total seed crop and seed germination of widgeon-grass (mean [± 1 SD], n = 10) at Coronado Cays, San Diego Bay. Seed crop is both germinated and ungerminated seeds.

Date	Total Seed Crop (seeds m^{-2})	Seed Crop that Germinated (seeds m^{-2})
December 8, 1999	2,103.4 (1,113.9)	0
January 10, 2000	915.7 (370.9)	73.1 (31.7)
March 26, 2000	2,506.1 (1,454.1)	23.5 (43.1)
May 1, 2000	1,715.3 (893.0)	11.0 (23.1)
June 1, 2000	1,151.0 (660.0)	0

at Coronado Cays and a small percentage of germinated widgeongrass seeds (Table 3).

Discussion

Coincident with ENSO conditions, eelgrass declined and widgeongrass increased in some areas sampled in two bays in San Diego. Previous to this ENSO, widgeongrass was restricted to its typical habitats, including salt marsh pans, on intertidal flats of a commercial salt plant, and in the warm-water effluent from a power plant (Williams personal observation). Although we have insufficient environmental and experimental data to conclude that the shifts in distributions and abundance were due to ENSO, water temperatures increased well beyond the typical summer temperatures when eelgrass in San Diego is subject to chronic declines (Ewanchuk 1995; Sewell 1996). Eelgrass grows well between 10–20°C and reaches maximum photosynthetic rates between 19–22°C, although both acclimation and adaptation to local conditions are important (reviewed in Phillips 1984 and Thayer et al. 1984; Zimmerman et al. 1989). Zimmerman et al. (1989) suggested that temperatures > 25°C represented stressful conditions for eelgrass growth and temperatures near 30°C could exceed the capacity for acclimation, resulting in eelgrass decline. During ENSO, the duration of exposure to temperatures stressful to eelgrass was substantially longer than a non-ENSO year (Table 2).

We have since confirmed experimentally that the temperatures reached during the ENSO event stressed San Diego eelgrass. When grown outdoors in temperature-regulated mesocosms and allowed to acclimate for several months, local eelgrass produced 15–30% fewer shoots under ENSO water temperatures than in waters 2–4°C cooler (Williams 2001). These results were supported when a similar experiment was conducted in another year (Lieberman 2002).

To proliferate in eelgrass habitat, widgeongrass would have to recruit after dispersing from its typical habitats or from a seed bank. Reduced competition from diminished eelgrass (Orth 1977; Bird et al. 1994; Lieberman 2002) and more favorable environmental conditions could have contributed to the increased abundance of widgeongrass. Widgeongrass can maintain a maximum photosynthetic rate at higher temperatures, and has a higher temperature optimum for growth, than eelgrass (Setchell 1924; Verhoeven 1979; Wetzel and Penhale 1983; Evans et al. 1986). These optima are reported to occur around 25°C and widgeongrass can apparently flourish in 36°C (Edwards 1978) and tolerate 43°C in some cases (Koch and Seeliger 1988). Widgeongrass, like eelgrass, exhibits acclimation and adaptation to local conditions (Koch and Seeliger 1988; Koch and Dawes 1991), and these limits should be considered as relative and average for this region. Results from experiments conducted in San Diego on the relative growth of widgeongrass and eelgrass in response to temperature along with field tests of interspecific competition revealed that the ability of eelgrass to outcompete widgeongrass was compromised under ENSO temperatures (Lieberman 2002).

There are other factors that limit the distribution of widgeongrass, which we did not investigate. Widgeongrass can tolerate a wide range of salinities, but it tends to germinate and grow best in low-salinity waters (Setchell 1924; Seeliger et al. 1984; Kantrud 1991; Koch and Dawes 1991). Unusually high rainfall resulting in lowered salinity observed in south San Diego Bay during the ENSO (Merkel unpublished data) might have been a factor in the local expansion of widgeongrass through enhanced seed germination and subsequent recruitment. The limits of widgeongrass distribution are also influenced by competition from other species, light, nutrients, and sea level (studies above; Orth and Moore 1988; Burkholder et al. 1994), factors not addressed in this study.

Widgeongrass abundance might increase in many areas as the oceans warm, a premise based on the temperature tolerance and geographic distribution of this species as well as the observations we report here. Widgeongrass is distributed more widely than other ruderal and subdominant seagrasses, including *Halodule* spp. and *Halophila* spp., which are restricted to warmer waters. Studies of seasonal dynamics in seagrass communities where widgeongrass is present indicate that it becomes abundant in summer months (Nixon and Oviatt 1973; Richardson 1980; Harrison 1982; Evans et al. 1986; Kinnery and Roman 1998), and widgeongrass has an annual growth cycle in locations where ambient temperatures are too cool (Harrison 1982; Pulich 1985; Flores-Verdugo et al. 1988; Dunton 1990). These studies support the

expectation that the distribution of widgeongrass could increase with increasing ocean temperatures. Widgeongrass recruits would be expected to recruit relatively rapidly to new areas because it has many vectors for dispersal as waterfowl and fishes consume its seeds (Martin et al. 1961; Agami and Waisel 1988). It also recruits very well from seeds (Van Vierssen et al. 1984; Koch and Seeliger 1988). The increase in the distribution of widgeongrass might be evident already (Bortulus et al. 1998).

If the proliferation of widgeongrass and the decline of eelgrass during the 1997 ENSO indicates the future under a global warming scenario, then there is an important need to understand the consequences for seagrass ecosystems. The larger dominant species in the Northern Hemisphere, e.g., eelgrass and turtlegrass, tend to have higher areal biomass and biomass-specific rates of primary production than the subdominant species, which tend to have thinner leaves and higher orders of branching (McRoy and McMillan 1977; Zieman and Wetzel 1980; Williams and McRoy 1982; Thorne-Miller and Harlin 1984). The community structure of associated fauna also can differ among seagrass species (Stoner 1980; Middleton et al. 1984; Jernakoff and Nielsen 1998; Williams and Heck 2001). In order to assess differences in ecosystem function between eelgrass and widgeongrass beds, the proliferation of widgeongrass was studied at two additional sites in San Diego Bay during a concurrent but separate study that compared trophic support functions of eelgrass and widgeongrass beds (Johnson 2000). This study indicated that widgeongrass maintained biomass equivalent to that of eelgrass, but only in summer, and also provided nutritious food to benthic detritivores. Results from this study and ones cited above indicate that displacements of dominant species by subdominants, like widgeongrass, could have complex effects on seagrass ecosystem functions.

Acknowledgments

Literature Cited

Agami, M. and Y. Waisel. 1988. The role of fish in distribution and germination of seeds of the submerged macrophytes *Najas marina* L. and *Ruppia maritima* L. *Oecologia* 76:83–88.

Anderson, R. R. 1972. Tentative outline for inventory of submerged aquatic vascular plants: *Ruppia maritima* L. (ditchgrass). *Chesapeake Science* 13:S172–S174.

Beer, S. and E. W. Koch. 1996. Photosynthesis of marine macroalgae and seagrasses in globally changing CO_2 environments. *Marine Ecology Progress Series* 141:199–204.

Bird, K. T., J. Jewett-Smith, and M. S. Fonseca. 1994. Use of in vitro propagated *Ruppia maritima* for seagrass meadow restoration. *Journal of Coastal Research* 10:732–737.

Bortulus, A., O. O. Iribarne, and M. M. Martínez. 1998. Relationship between waterfowl and the seagrass *Ruppia maritima* in a southwestern Atlantic Coastal Lagoon. *Estuaries* 21:710–717.

Burkholder, J. M., H. B. Glasgow, Jr., and J. E. Cooke. 1994. Comparative effects of water-column nitrate enrichment on eelgrass *Zostera marina*, shoalgrass *Halodule wrightii*, and widgeongrass *Ruppia maritima*. *Marine Ecology Progress Series* 105: 121–138.

Dennison, W. C., R. J. Orth, K. A. Moore, J. C. Stevenson, V. Carter, S. Kollar, P. W. Bergstrom, and R. A. Batiuk. 1993. Assessing water quality with submersed aquatic vegetation. *Bioscience* 43:86–94.

Dunton, K. H. 1990. Production ecology of *Ruppia maritima* L. s.l. and *Halodule wrightii* Aschers. in two subtropical estuaries. *Journal of Experimental Marine Biology and Ecology* 143:147–164.

Dunton, K. H. 1996. Photosynthetic production and biomass of the subtropical seagrass *Halodule wrightii* along an estuarine gradient. *Estuaries* 19:436–447.

Edwards, R. R. C. 1978. Ecology of a coastal lagoon complex in Mexico. *Estuarine and Coastal Marine Science* 6:75–92.

Evans, A. S., K. L Webb, and P. A. Penhale. 1986. Photosynthetic temperature acclimation in two coexisting seagrasses, *Zostera marina* L. and *Ruppia maritima* L. *Aquatic Botany* 24: 185–197.

Ewanchuk, P. J. 1995. Population growth of eelgrass (*Zostera marina* L.): The relative importance of sexual versus asexual reproduction. M.S. Thesis, San Diego State University, San Diego, California.

Flores-Verdugo, F. F., J. W. Day, L. Mee, and R. Briseño-Dueñas. 1988. Phytoplankton production and seasonal biomass variation of seagrass, *Ruppia maritima* L., in a tropical Mexican lagoon with an ephemeral inlet. *Estuaries* 11:51–56.

Fourqurean, J. W., G. V. N. Powell, W. J. Kenworthy, and J. C. Zieman. 1995. The effects of long-term manipulation of nutrient supply on competition between the seagrasses *Thalassia testudinum* and *Halodule wrightii* in Florida Bay. *Oikos* 72: 349–358.

Harrison, P. G. 1982. Seasonal and year-to-year variations in mixed intertidal populations of *Zostera japonica* Aschers. and Graebn. and *Ruppia maritima* L. *Aquatic Botany* 14:357–371.

Holbrook, S. J., R. J. Schmitt, and J. S. Stephens. 1997. Changes in an assemblage of temperate reef fishes associated with a climate shift. *Ecological Applications* 7:1299–1310.

Jernakoff, P. and J. Nielsen. 1998. Plant-animal associations in two species of seagrasses in Western Australia. *Aquatic Botany* 60:359–376.

JOHNSON, M. R. 2000. Investigating functional equivalency: Trophic support provided to benthic detritivores by the seagrasses *Ruppia maritima* and *Zostera marina*. M.S. Thesis, San Diego State University, San Diego, California.

KANTRUD, H. A. 1991. Widgeongrass (*Ruppia maritima* L.): A literature review. *Fish and Wildlife Research* 10:1–58.

KAREIVA, P. M., J. G. KINGSOLVER, AND R. B. HUEY. 1993. Biotic Interactions and Global Change. Sinauer Associates Inc., Sunderland, Massachusetts.

KINNERY, E. H. AND C. T. ROMAN. 1998. Response of primary producers to nutrient enrichment in a shallow estuary. *Marine Ecology Progress Series* 163:89–98.

KOCH, E. W. AND C. J. DAWES. 1991. Ecotypic differentiation in populations of *Ruppia maritima* L. germinated from seeds and cultured under algae-free laboratory conditions. *Journal of Experimental Marine Biology and Ecology* 152:145–159.

KOCH, E. W. AND U. SEELIGER. 1988. Germination ecology of two *Ruppia maritima* L. populations in southern Brazil. *Aquatic Botany* 31:321–327.

LAZAR, A. C. AND C. J. DAWES. 1991. A seasonal study of the seagrass *Ruppia maritima* L. in Tampa Bay, Florida. Organic constituents and tolerances to salinity and temperature. *Botanica Marina* 34:265–269.

LIEBERMAN, C. H. 2002. Relative contribution of abiotic and biotic factors to changes in distribution of the seagrasses *Zostera marina* and *Ruppia maritima*. M.S. Thesis, San Diego State University, San Diego, California.

LUKATELICH, R. J., N. J. SCHOFIELD, AND A. J. MCCOMB. 1987. Nutrient loading and macrophyte growth in Wilson Inlet, an bar-built southwestern Australian estuary. *Estuarine and Coastal Shelf Science* 24:141–165.

MARTIN, A. C., H. S. ZIM, AND A. L. NELSON. 1961. American Wildlife and Plants. Dover Publications, Inc., New York.

MCROY, C. P. AND C. MCMILLAN. 1977. Productivity and physiological ecology of seagrasses, p. p. 53–88. *In* C. P. McRoy and C. Helfferich (eds.), Seagrass Ecosystems: A Scientific Perspective. M. Dekker, New York.

MICHENER, W. K., E. R. BLOOD, K. L. BILDSTEIN, M. M. BRINSON, AND L. R GARDNER. 1997. Climate change, hurricanes and tropical storms, and rising sea level in coastal wetlands. *Ecological Applications* 7:770–801.

MIDDLETON, M. J., J. D. BELL, J. J. BURCHMORE, D. A. POLLARD, AND B. C. PEASE. 1984. Structural differences in the fish communities of *Zostera capricorni* and *Posidonia australis* seagrass meadows in Botany Bay, New South Wales. *Aquatic Botany* 18:89–109.

NIXON, S. W. AND C. A. OVIATT. 1973. Ecology of a New England salt marsh. *Ecological Monographs* 43:463–498.

ORTH, R. J. 1977. Effect of nutrient enrichment on growth of eelgrass *Zostera marina* in the Chesapeake Bay, Virginia, USA. *Marine Biology* 44:187–194.

ORTH, R. J. AND K. A. MOORE. 1988. Distribution of *Zostera marina* L. and *Ruppia maritima* L. Sensu lato along depth gradients in the lower Chesapeake Bay, U.S.A. *Aquatic Botany* 32:291–305.

PHILLIPS, R. C. 1984. The ecology of eelgrass meadows in the Pacific Northwest: A community profile. FWS/OBS-84/24. U.S. Fish and Wildlife Service, Washington, D.C.

PULICH, JR., W. M. 1985. Seasonal growth dynamics of *Ruppia maritima* L. s.l. and *Halodule wrightä* Aschers. in southern Texas and evaluation of sediment fertility status. *Aquatic Botany* 23:53–66.

PULICH, JR., W. M. AND W. A. WHITE. 1981. Decline of submerged vegetation in the Galveston Bay system: Chronology and relationships to physical processes. *Journal of Coastal Research* 7:1125–1138.

POWELL, G. V. N., J. W. FOURQUREAN, W. J. KENWORTHY, AND J. C. ZIEMAN. 1991. Bird colonies cause seagrass enrichment in a subtropical estuary: Observational and experimental evidence. *Estuarine and Coastal Shelf Science* 32:567–579.

RICHARDSON, F. D. 1980. Ecology of *Ruppia maritima* L. in New Hampshire (U.S.A.) tidal marshes. *Rhodora* 82:403–439.

ROBBLEE, M. B., T. R. BARBER, P. R. CARLSON, M. J. DURAKO, J. W. FOURQUREAN, L. K. MUEHLSTEIN, D. PORTER, L. A. YARBRO, R. T. ZIEMAN, AND J. C. ZIEMAN. 1991. Mass mortality of the tropical seagrass *Thalassia testudinum* in Florida Bay, (USA). *Marine Ecology Progress Series* 71:297–299.

SCHNEIDER, S. H. 1993. Scenarios of global warming, p. 9–23. *In* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey (eds.), Biotic Interactions and Global Change. Sinauer, Sunderland, Massachusetts.

SEELIGER, U., C. CORDAZZO, AND E. W. KOCH. 1984. Germination and algal-free laboratory culture of widgeon grass, *Ruppia maritima*. *Estuaries* 7:176–178.

SETCHELL, W. A. 1924. *Ruppia* and it environmental factors. *Proceedings of the National Academy of Science* 10:286–288.

SEWELL, A. T. 1996. Eelgrass growth and abundance in an urban estuary: The negative effects of anemone coverage. M.S. Thesis, San Diego State University, San Diego, California.

SHORT, F. T. AND H. A. NECKLES. 1999. The effects of global climate change on seagrasses. *Aquatic Botany* 63:169–196.

SHORT, F. T. AND S. WYLLIE-ECHEVERRIA. 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conservation* 23:17–27.

STONER, A. W. 1980. Perception and choice of substratum by epifaunal amphipods associated with seagrasses. *Marine Ecology Progress Series* 3:105–111.

TEGNER, M. J. AND P. K. DAYTON. 1987. El Niño effects on Southern California kelp forest communities. *Advances in Ecological Research* 17:243–279.

THAYER, G. W., W. J. KENWORTHY, AND M. S. FONSECA. 1984. The ecology of eelgrass meadows of the Atlantic coast: A community profile. FWS/OBS-84/02. U.S. Fish and Wildlife Service, Washington, D.C.

THOM, R. M. 1990. Spatial and temporal patterns in plant standing stock and primary production in a temperate seagrass system. *Botanica Marina* 33:497–510.

THORNE-MILLER, B. AND M. M. HARLIN. 1984. The production of *Zostera marina* L. and other submerged macrophytes in a coastal lagoon in Rhode Island, U.S.A. *Botanica Marina* 27:539–546.

THORNE-MILLER, B., M. M. HARLIN, G. B. THURSBY, M. M. BRADY-CAMPBELL, AND B. A. DWORETZKY. 1983. Variations in the distribution and biomass of submerged macrophytes in five coastal lagoons in Rhode Island, U.S.A. *Botanica Marina* 26:231–242.

VAN VIERSSEN, W., C. M. VAN KESSEL, AND J. R. VAN DE ZEE. 1984. On the germination of *Ruppia* taxa in western Europe. *Aquatic Botany* 19:381–393.

VERHOEVEN, J. T. A. 1979. The ecology of *Ruppia*-dominated communities in western Europe. I. Distribution of *Ruppia* representatives in relation to the autecology. *Aquatic Botany* 6:197–268.

WALKER, D. I. AND A. J. MCCOMB. 1992. Seagrass degradation in Australian coastal waters. *Marine Pollution Bulletin* 25:191–195.

WETZEL, R. L. AND P. A. PENHALE. 1983. Production ecology of seagrass communities in the lower Chesapeake Bay. *Marine Technology Society Journal* 17:22–31.

WILLIAMS, S. L. 2001. Reduced genetic diversity in eelgrass transplantations affects both population growth and individual fitness. *Ecological Applications* 11:1472–1488.

WILLIAMS, S. L. AND C. A. DAVIS. 1996. Population genetic analyses of transplanted eelgrass (*Zostera marina*) beds reveal reduced genetic diversity in southern California. *Restoration Ecology* 4:163–180.

WILLIAMS, S. L. AND K. L. HECK, JR. 2001. Seagrass community ecology, p. 317–337. *In* M. Bertness, S. Gaines, and M. Hay

(eds.), Marine Community Ecology. Sinauer Association, Inc., Sunderland, Massachusetts.

WILLIAMS, S. L. AND C. P. McROY. 1982. Seagrass productivity: The effect of light on carbon uptake. *Aquatic Botany* 12:321–344.

ZIEMAN, J. C. AND R. G. WETZEL. 1980. Productivity in seagrasses: Methods and rates, p. 87–116. *In* R. C. Phillips and C. P. McRoy (eds.), A Handbook of Seagrass Biology: An Ecosystem Perspective. Garland STPM, New York.

ZIMMERMAN, R. C., R. D. SMITH, AND R. S. ALBERTE. 1989. Thermal acclimation and whole-plant carbon balance in *Zostera marina* L. (eelgrass). *Journal of Experimental Marine Biology and Ecology* 130:93–109.

SOURCES OF UNPUBLISHED MATERIALS

MERKEL, K. Unpublished Data. Merkel and Associates, Inc., 5434 Ruffin Road, San Diego, Califonia 92123.

TALLEY, T. Personal Communication. Scripps Institution of Oceanography, University of California, San Diego, 9500 Gilman Drive, La Jolla, California 92093-0218.