

DISTRIBUTION AND MORPHOLOGY OF EELGRASS (*ZOSTERA MARINA* L.) AT THE CALIFORNIA CHANNEL ISLANDS

JOHN M. ENGLE¹ AND KATHY ANN MILLER²

¹Marine Science Institute, University of California, Santa Barbara, CA 93106; j_engle@lifesci.ucsb.edu

²Wrigley Marine Science Center, University of Southern California, 1 Big Fisherman Cove, Avalon, CA 90704

ABSTRACT—Benthic studies at the California Channel Islands have focused on rocky reef kelp forests, leaving nearshore soft-bottom communities relatively unexplored. At the islands, eelgrass (*Zostera marina*) meadows occur in habitats that are deeper and sandier than the muddy bays and estuaries where *Zostera* is typically found along the mainland. Eelgrass meadows are ecologically important for primary production, nutrient cycling, and substrate stabilization. They provide shelter and food for a unique assemblage of organisms, including juvenile fishes. Since 1979, survey cruises by the Channel Islands Research Program have documented *Zostera* beds at 37 sheltered or semi-sheltered locations at six of the eight islands (not San Miguel or Santa Barbara), with the most extensive meadows at Santa Catalina, Santa Cruz, and Santa Rosa islands. Eelgrass occurred at depths ranging from 3–22 m; however, inter-site variability was high, with shallow limits likely determined by swell disturbance and deep limits by light penetration. Beds sampled repeatedly appear to be stable over annual to decadal periods, except at Anacapa Island where nearly all eelgrass disappeared during the 1980's coincident with increased abundance of white urchins (*Lytechinus pictus*). Two locations at Santa Catalina Island were colonized in recent years. *Zostera* leaves at the four cooler-water, northwesterly islands were substantially wider (12–16 mm) than those at the two warmer-water southeasterly islands (2–10 mm). Leaf widths did not vary consistently with depth except at one San Clemente Island site, where two width variants co-occurred. There, the wider variant predominated in deeper water. Leaf lengths, though more variable, showed similar trends to leaf widths. We have yet to determine if a second species (*Z. asiatica* Miki or *Z. pacifica* S. Watson), reported from the mainland, is present at the islands. We have initiated genetic studies.

Keywords: Channel Islands, distribution, eelgrass, morphology, *Zostera marina*

INTRODUCTION

Eelgrass (*Zostera marina* L.) is a marine flowering plant that can form extensive meadows in sheltered soft-bottom habitats along North Atlantic and North Pacific temperate shores (in California, the name “eelgrass” is often mistakenly applied to *Phyllospadix* spp. that grow on rocky reefs). *Zostera* beds are ecologically important for primary production, nutrient cycling, and substrate stabilization (Phillips 1984). They provide habitat complexity, shelter and food for numerous invertebrate and fish species, including juvenile fishes (McConnaughey and McRoy 1979). Some invertebrates, such as the limpet *Tectura depicta* and the opisthobranch *Phyllaplysia taylori*, occur solely on *Zostera*. However, seagrass meadows

have suffered dramatic declines worldwide during the past 25 years through a combination of natural and anthropogenic deterioration (Short and Wyllie-Echeverria 1996, Hemminga and Duarte 2000). The ecological consequences of these declines are largely unknown.

Zostera ranges along the U.S. West Coast from Alaska to Baja California, where it is typically found in bays and estuaries from the low intertidal zone to depths of about 6 m. In southern California, eelgrass also occurs in some protected outer coast locations, where it has been reported to occur as deep as 30 m (Cottam and Munro 1954, Phillips 1984). This deeper form, with wide blades, smooth seed coats and later flowering season, has been variously recognized as *Z. marina* var. *latifolia* Morong (Dawson and Foster 1982, Armstrong and

Thorne 1989), a second native species, *Z. pacifica* S. Watson, (Hickman 1993, Junak et al. 1995), and a Japanese species, *Z. asiatica* Miki (Phillips and Echeverria 1990). Leaf lengths can vary from less than 0.5 m to nearly 4 m (Phillips 1984). Leaf widths for *Z. marina* range from 1.5–12 mm; widths of *Z. asiatica* and *Z. pacifica* range from 12 to over 18 mm (Phillips and Meñez 1988, Phillips and Echeverria 1990, Hickman 1993, Junak et al. 1995). The distribution of eelgrass at the California Channel Islands is not well known because most benthic studies at the islands have focused on rocky reef kelp forests, leaving nearshore soft-bottom communities relatively unexplored. Due to their isolation from the mainland, where shoreline development has impacted most *Zostera* beds, the island *Zostera* populations represent some of the most “natural” in California.

This study is part of a long-term effort to characterize the marine flora and fauna of the California Channel Islands. Our objective in this paper is to describe the distribution and abundance of eelgrass at the eight islands, including depth ranges and leaf morphology. Other work in progress will address genetic differentiation among populations, species identification and biotic assemblages in island *Zostera* beds.

MATERIALS AND METHODS

Hundreds of reconnaissance scuba-diving surveys of subtidal soft-bottom habitats at the eight California Channel Islands were conducted from 1979–2003 during 160 Channel Islands Research Program multi-day cruises aboard the R/V Cormorant. Except for highly exposed coasts, nearly every cove and regional shoreline segment was explored. Additional diving observations were made at Santa Catalina Island at various times since 1972, while conducting ecological studies based at the USC Wrigley Marine Science Center. The reconnaissance surveys characterized representative soft-bottom habitats around each of the islands, emphasizing relatively sheltered stable sand or mud bottoms and sites where eelgrass had been reported by others or where conditions likely were suitable for *Zostera* establishment. Surveys typically consisted of two to four diver pairs (four to eight divers) searching throughout each location,

recording identifiable species and estimating their relative abundances (e.g., rare, present, common, abundant), depth extents, and habitat characteristics (e.g., slope, substrate, heterogeneity, community dominants). Underwater scooters were used occasionally to extend the diver survey area. For the initial distribution analysis, an eelgrass site was defined as a location where eelgrass habitat (patches or beds) was present and essentially continuous (except for interspersed rock reefs), irrespective of areal abundance or shoreline extent.

From 1994–2003, additional qualitative and quantitative surveys targeted known or suspected eelgrass beds to determine areal extents, depth ranges, plant density, and community composition. These surveys were repeated at some sites in subsequent years to assess annual and multi-year changes. Most surveys took place during the months of April–October, with northern island surveys occurring primarily during June–September. For large beds, scouting teams located the boundaries and sent up floats so maps could be constructed with relation to shore features. Some extensive eelgrass meadows were mapped using the ship’s fathometer or by visual sighting from the ship. Areal extent of *Zostera* cover was measured or estimated. Scuba surveys have practical limitations in determining cover of irregular or discontinuous eelgrass beds; therefore, abundance values were pooled by order of magnitude levels. Upper and lower depth limits for the main eelgrass beds (nearly continuous cover) and for patches (including individual plants) were determined. At each site, a minimum of 10 plants were collected haphazardly throughout the bed, or 10 plants each from shallow and deep portions of the bed, for morphometric measurements and preservation (dried pressings) of voucher specimens. Leaf length was measured for the longest intact leaf of each plant, starting from the top of the leaf sheath. Leaf width was measured 10 cm above the top of the leaf sheath.

RESULTS

Geographic Distribution and Abundance

Zostera was documented at 37 separate locations at six of the eight California Channel Islands (Santa Rosa [SRO], Santa Cruz [SCR], Anacapa [ANA], San Nicolas [SNI], Santa

Catalina [SCA] and San Clemente [SCL]) during the 25-year survey period (1979–2003), with additional observations at Santa Catalina Island as early as 1973 (Table 1). *Zostera* was never found at San Miguel (SMI) or Santa Barbara (SBA) islands, despite searches in locations where it would most likely have occurred (e.g., Cuyler Harbor [SMI] and Landing Cove [SBA]).

With few exceptions, *Zostera* beds at Channel Island sites were persistent and generally similar in extent over the time period of repeated surveys. The greatest changes were observed at Anacapa Island (six sites) and at Little Scorpion Anchorage (SCR) where all known eelgrass beds and patches disappeared during the 1980s and 1990s, coincident with a period of high abundances of herbivorous white sea urchins (*Lytechinus pictus*; Engle 1994 and unpubl. data). Recently (2002–2003), an experimental transplant returned eelgrass to one Anacapa site, Frenchys Cove (Altstatt 2005). Natural colonization of *Zostera* was documented at two Santa Catalina Island sites. At Big Fisherman Cove (SCI), location of the USC Wrigley Marine Science Center, *Zostera* was not recorded during general species reconnaissance dives conducted from 1972–1995 and was not found during specific eelgrass surveys in 1988 and 1991; however, patches were discovered in 1996 that have persisted through 2003. From 1985–2001, no *Zostera* was present at West Willow Cove (SCI), which was surveyed annually (or more frequently) during mantis shrimp (*Hemisquilla ensigera*) studies. Several small patches of eelgrass appeared in 2002 that expanded in size slightly in 2003. Two extensive *Zostera* beds, Old Ranch Canyon (SRO) and Coast Guard Beach (SNI) were discovered in 2002 in areas not previously surveyed. The large size of these beds, coupled with prior observations of drift eelgrass and reports from commercial fishermen, indicates that these beds existed for considerable time before our discovery.

Of the 30 sites where eelgrass is currently present (excluding the transplant site at Frenchys Cove), order-of-magnitude areal cover was less than one hectare at 21 (70%) of the sites (Table 1). Each of the five islands with eelgrass currently present had at least one site with beds greater than one hectare and shoreline extent greater than 0.5 km (Table 1).

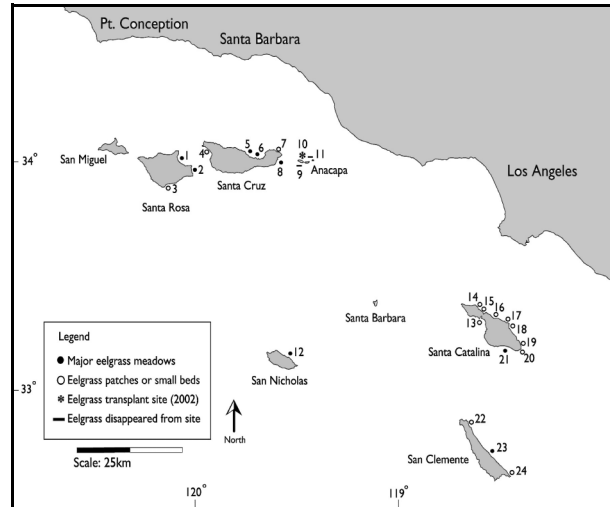


Figure 1. Regional eelgrass locations at the California Channel Islands. Major meadows are those estimated to cover more than two hectares. Site names are listed in Table 1.

Eleven of the island eelgrass sites, though distinct, were relatively close (generally <1 km) to one or two other sites, separated only by expanses of rock reefs. Combining these closely-occurring sites for broad scale comparisons resulted in 24 regional eelgrass locations (Table 1, Fig. 1). With few exceptions, eelgrass was located in the most sheltered areas of the islands, protected from prevailing northwest, west, and south oceanic swells. Two-thirds of the regional eelgrass locations face northerly or easterly toward the mainland. They were typically located in protected coves or in the lee of headlands. The relatively few *Zostera* locations that faced northwesterly, westerly or southerly are protected by local headlands, reefs, or nearby islands, or occur in deeper water (see below). For example, Catalina Harbor (SCA) faces southwest; however, it is the most protected cove at the Channel Islands due to sheltering headlands and reefs. Forneys Cove (SCR) is protected by headlands, reefs, and nearby Santa Rosa Island.

Although eelgrass sites were similar in protection from ocean swells and possessing soft-bottom substrates, we observed that sites varied on a smaller scale in physical features such as relative magnitude of wave exposure, slope of sea floor, sediment composition (from gravelly sand to fine mud), and presence and extent of adjacent rock reefs.

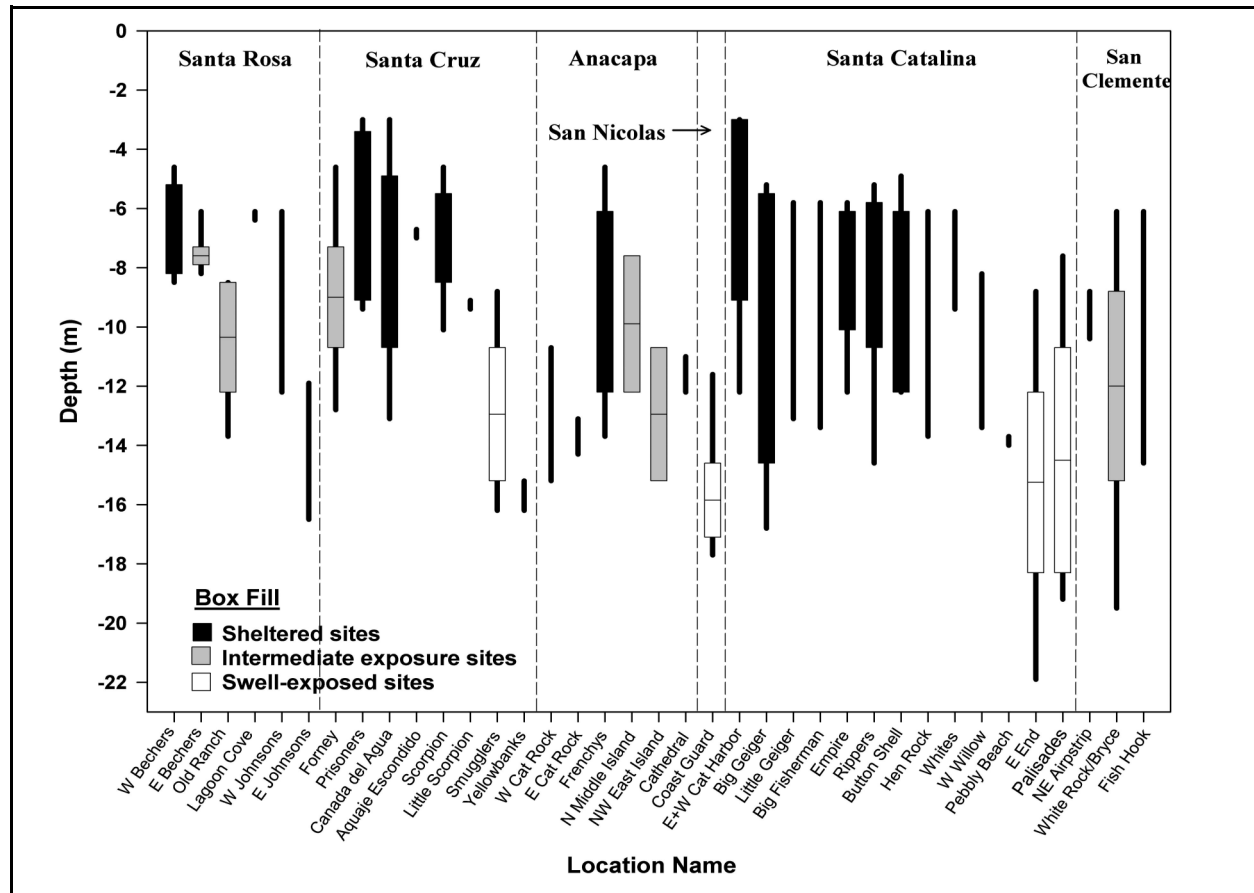


Figure 2. Depth ranges of eelgrass beds and patches at 37 Channel Islands sites. Boxes represent depth ranges for main eelgrass beds (nearly continuous cover). Lines represent depth limits for eelgrass patches (including individual plants). Box fill types represent degree of site exposure to prevailing oceanic swells (powerful waves arriving from the northwest, west, southwest, or south).

Depth Distribution

Twenty of the 37 specific eelgrass sites had obvious beds (nearly continuous cover), with the other 17 sites possessing scattered patches (Fig. 2). The maximum depth range of *Zostera* beds and patches over all sites was 3–22 m; however, individual sites showed considerable variation (Fig. 2). The widest range in eelgrass depth distributions occurred at the southeastern islands (SCA and SCL). Depth records at Anacapa Island are incomplete since most eelgrass habitats had disappeared prior to documenting depth boundaries.

Eelgrass depth ranges varied substantially at each of the five islands with multiple sites (Fig. 2). For example, shallow beds at Bechers Bay on Santa Rosa Island did not overlap in depth range with intermediate-depth meadows at Old Ranch Canyon. Patches at West Johnsons Lee occurred

shallower than those at East Johnsons Lee. *Zostera* habitats on south Santa Cruz Island were found deeper than those on the north side. At Santa Catalina and San Clemente islands, mainland-facing sites had overlapping *Zostera* depth ranges. Eelgrass habitats at the southeast end of Santa Catalina Island were notably deeper.

Inshore and offshore depth limits of *Zostera* beds were positively associated with increasing levels of swell exposure (Fig. 2). Mean inshore bed edge depth for sheltersed beds was 5 m compared to 8 m for intermediate exposure beds and 12 m for the most exposed beds. Mean offshore bed edge depth for sheltersed beds was 11 m compared to 12 m for intermediate exposure beds and 17 m for the most exposed beds. The shallowest inshore and offshore bed edges were found at highly protected island sites. The deepest inshore and offshore bed margins occurred at sites exposed to oceanic swells.

Table 1. Location and abundance of *Zostera* habitats at the Channel Islands. Shoreline extent and north/west or south/east margins are listed for *Zostera* habitats occurring along at least 0.5 km of shore; otherwise, latitude/longitude represents center of habitat.

Island	Location	Site code	<i>Zostera</i> abundance level ^a	<i>Zostera</i> shoreline (km)	Extent of <i>Zostera</i> beds and patches				<i>Zostera</i> survey dates (month/year) (Bold underlined dates indicate <i>Zostera</i> absent)
					North or west edge Latitude	North or west edge Longitude	South or east edge Latitude	South or east edge Longitude	
Santa Rosa	West Bechers Bay	1A	4	1.3	34 01.550	120 02.484	34 00.933	120 02.833	9/84, 8/94, 8/96, 8/97, 9/02, 8/03
	East Bechers Bay	1B	4	0.5	33 59.941	120 02.514	33 59.749	120 02.350	8/97, 8/03
	Old Ranch Canyon	2A	5	0.5	33 57.901	119 58.481	33 57.641	119 58.388	9/02, 8/03
	Lagoon Cove	2B	1		33 57.543	119 58.527			9/02
	West Johnsons Lee	3A	3		33 54.071	120 06.319			8/81, 8/95, 8/96, 8/03
	East Johnsons Lee	3B	3		33 54.203	120 05.952			9/80, 7/87, 8/96, 9/97, 8/03
Santa Cruz	Fornes Cove	4	3		34 03.392	119 55.073			7/80, 8/83, 8/94, 8/95, 8/97, 8/98, 8/03
	Prisoners Harbor	5	5	1.0	34 01.424	119 41.231			7/81, 8/84, 8/94, 8/95, 8/97, 8/98
	Canada del Agua	6A	4		34 01.095	119 40.077	34 01.265	119 40.700	8/97, 8/03
	Aguaje Escondido	6B	1		34 01.002	119 38.894			8/03
	Scorpion Anchorage	7A	3		34 02.981	119 33.273			8/94, 8/95, 8/97, 8/98, 8/99, 7/03
	Little Scorpion Anchorage	7B	1*		34 02.783	119 32.782			9/79, 7/85, 8/95, 7/03
	Smugglers Cove	8A	5	0.8	34 00.991	119 32.328	34 01.324	119 32.039	7/81, 8/88, 8/94, 8/95, 8/97, 6/00, 7/01, 7/02, 7/03
	Yellowbanks Anchorage	8B	1		34 00.666	119 32.434			12/95
Anacapa	West Cat Rock	9A	1*		34 00.198	119 25.484			9/79, 8/95, 8/99
	East Cat Rock	9B	2*		34 00.183	119 25.138			6/81, 8/95, 7/99, 8/99
	Frenchys Cove	10	3**		34 00.502	119 24.658			10/80, 6/81, 6/82, annually 1991-2003
	North Middle Island	11A	3*		34 00.419	119 23.902			10/80, 3/82, 12/95
	Northwest East Island	11B	3*		34 00.899	119 22.596			10/80, 12/95
	Cathedral Cove	11C	2*		34 00.992	119 22.194			6/81, 12/95, 6/96, 8/96, 7/97, 6/98, 7/99, 2/01
	Coast Guard Beach	12	4	0.6	33 15.118	119 26.876	33 14.875	119 26.674	8/02
	Catalina Harbor	13	3		33 25.680	118 30.593	33 25.743	118 30.389	10/73, 10/74, 11/84, 11/91, 5/96, 4/98, 10/03
	Big Geiger Cove	14A	3		33 27.530	118 31.038			4/79, 10/96, 4/97, 4/98, 4/99, 10/01, 9/03
	Little Geiger Cove	14B	2		33 27.490	118 30.914			4/79, 10/96, 4/97
	Big Fisherman Cove	15	2		33 26.654	118 29.138			9/88, 10/91, 5/96, 10/96, 9/97, 4/98, 10/01, 9/03
Empire Landing	16A	3		33 25.758	118 26.480			10/96, 9/03	
Rippers Cove	16B	3		33 25.703	118 26.221			10/96, 4/97, 9/03	
Button Shell Beach	17A	3		33 24.288	118 22.056			3/88, 5/96, 6/01, 9/01, 4/02, 10/02, 5/03	
Hen Rock	17B	2		33 24.045	118 21.928			5/96, 5/00, 5/03	
White Cove	17C	2		33 23.624	118 22.092			5/96, 6/01	
West Willow Cove	18	1		33 22.814	118 21.373			annually 1985-2001, 10/02, 6/03, 9/03	
Pebbly Beach	19	1		33 20.041	118 18.486			8/01	
East End	20	3	1.8	33 18.332	118 18.446	33 17.854	118 19.485	12/79, 9/87, 6/93, 9/98	
Palisades	21	5	6.1	33 18.857	118 25.420	33 18.590	118 21.510	10/93, 5/96	
San Clemente	Northeast Airstrip	22	1		33 01.866	118 34.314			9/98
	White Rock/Bryce Canyon	23	4	3.2	32 53.217	118 25.950	32 52.101	118 24.385	6/82, 9/87, 6/93, 5/96, 6/97, 9/98, 8/00, 6/03
	Fish Hook Cove	24	2		32 49.757	118 21.508			11/83, 9/91, 5/99, 8/01, 5/03

^a Abundance codes: 1 = < 0.01 hectare; 2 = 0.01-0.1 hectare; 3 = 0.1-1 hectare; 4 = 1-10 hectares; 5 = >10 hectares.

* *Zostera* currently absent from site.

** *Zostera* disappeared from site, then recently re-established via experimental transplantation.

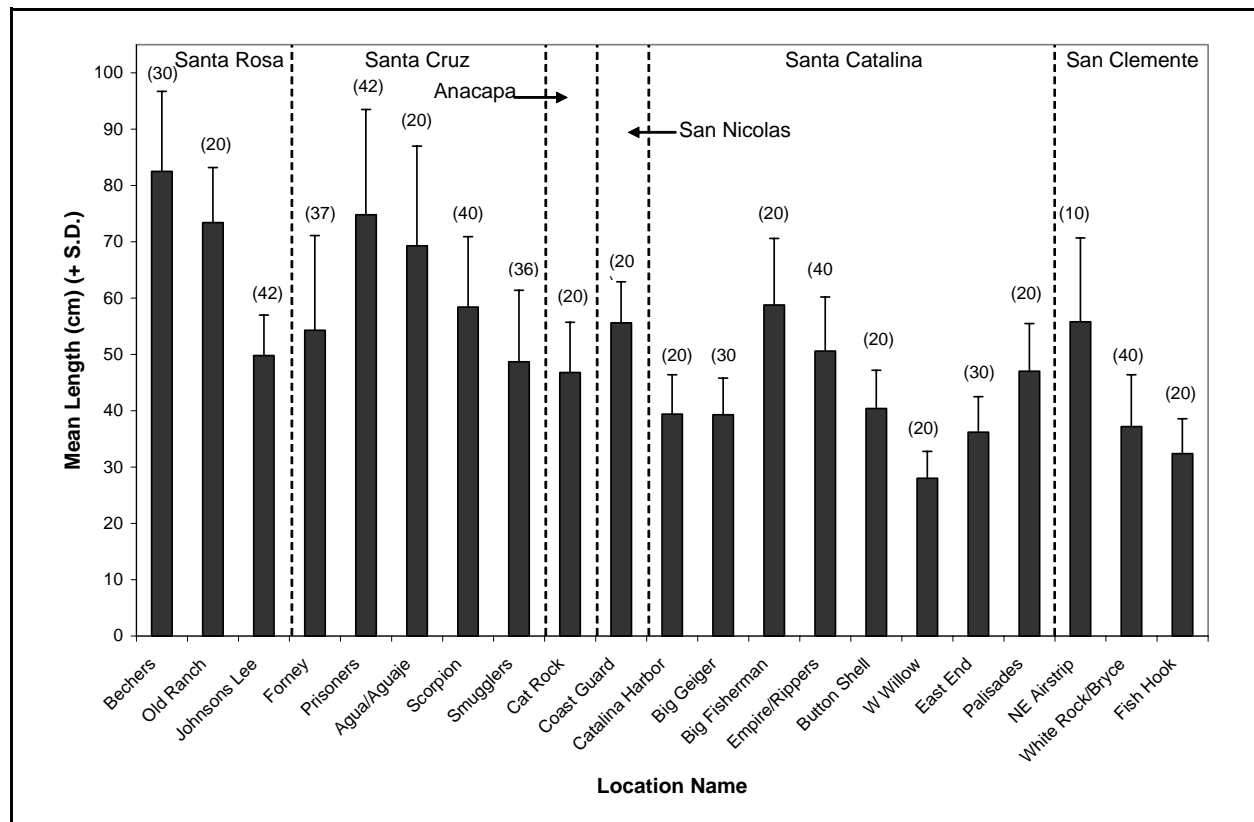


Figure 3. Eelgrass lengths at 21 of the 24 regional locations at the California Channel Islands. Numbers in parentheses indicate sample size for measurements taken at various times from 1994–2003. Measurements at some locations were pooled from two or three different years.

Leaf Morphology

Overall, *Zostera* individual leaf lengths varied from 19–118 cm, with mean sizes per regional site ranging from 28–83 cm (Fig. 3). Long- and short-leaved plants were found at each of the four islands with multiple sites. The four sites with tallest plants (mean 69–83 cm) were found at northwesterly islands, while the four locations with shortest plants (mean 28–37 cm) were found at southeasterly islands. There was a northwest to southeast trend of decreasing leaf lengths at the six islands: mean lengths (cm) = 66 (SRO), 61 (SCR), 49 (ANA), 56 (SNI), 43 (SCA), and 39 (SCL).

At sites with leaf measurements recorded in different years, variations in mean eelgrass leaf length ranged from no change to 25 cm difference between years, with a mean variation of 12 cm. Leaf length measurements taken at shallow and deep margins of beds at five sites where *Zostera* depth varied from 5–11 m showed no depth trends (lengths decreased with depth by 2, 6, and 8 cm at three sites and increased by 7 and 16 cm at two sites).

Overall, *Zostera* leaf widths varied from 1–20 mm, with mean sizes per site ranging from 2–16 mm (Fig. 4). Plants from the three northern islands and San Nicolas Island were clearly wider than those from the two southern islands, except for three sites at the eastern end of Santa Catalina Island where leaves were moderately wide. The widest blades (mean 15–16 mm) were found at the three Santa Rosa Island locations. The narrowest blades (mean 2–4 mm) were found at eight Santa Catalina and San Clemente island locations. There was a northwest to southeast trend of decreasing leaf widths at the six islands: mean widths (mm) = 15 (SRO), 13 (SCR), 12 (ANA), 13 (SNI), 5 (SCA), and 3 (SCL).

Mean eelgrass leaf width differences at sites with repeated samplings ranged from no change to 4 mm variation between years, with a mean variation of 2 mm. Leaf width measurements taken at shallow and deep margins of beds at five sites (where bed depth varied from 5–11 m) showed no depth trends. Differences in width from shallow to

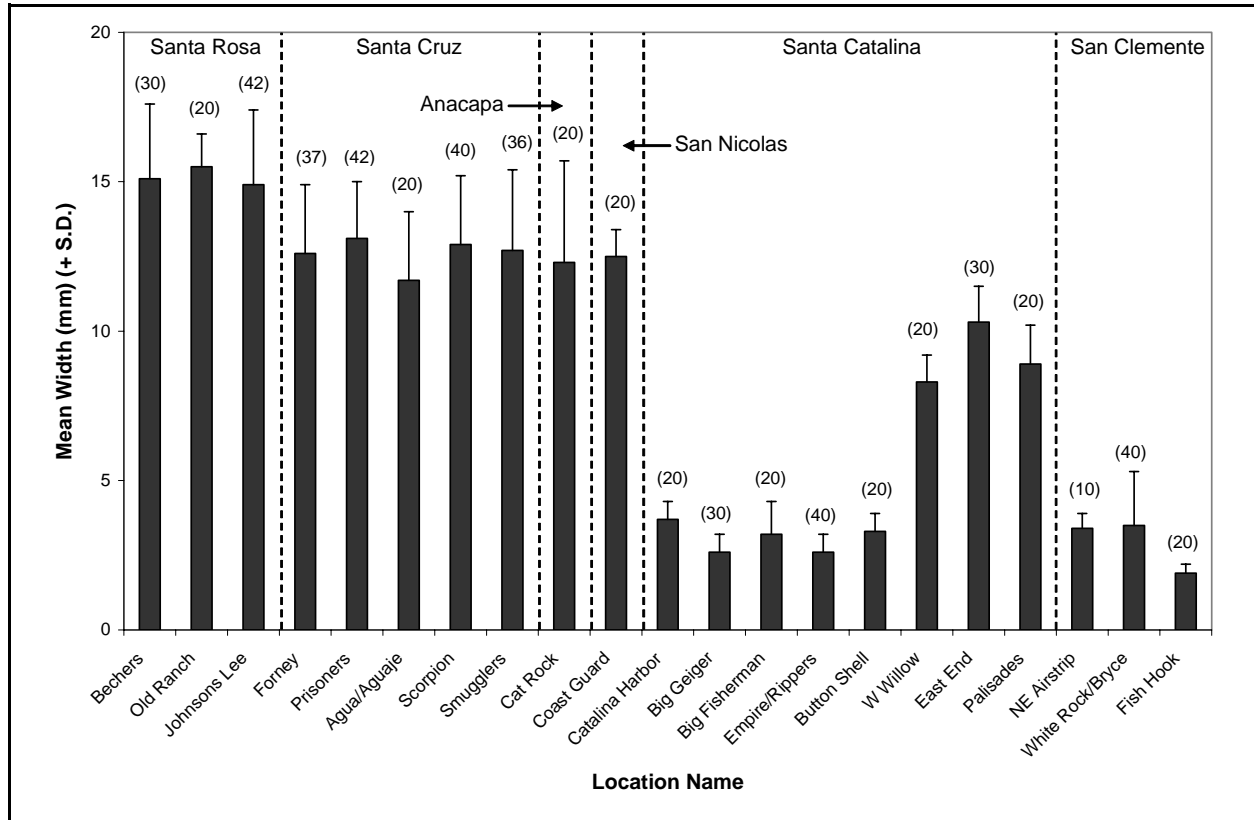


Figure 4. Eelgrass widths at 21 of the 24 regional locations at the California Channel Islands. Numbers in parentheses indicate sample size for measurements taken at various times from 1994–2003. Measurements at some locations were pooled from two or three different years.

deep varied from -1–3 mm, with overall mean difference of 0.1 mm.

DISCUSSION

Geographic Distribution

We found *Zostera* to be more widespread than expected at the California Channel Islands, with patches or meadows occurring in sheltered stable sand/mud habitats at six of eight islands, in some cases spread over kilometers of shoreline. San Miguel and Santa Barbara islands are apparently too wave-swept to support eelgrass beds or patches. Because our surveys have been numerous and comprehensive over the years, we believe that we have located most, if not all, major *Zostera* beds; however, additional small beds or patches may yet be discovered. *Zostera* cover at identified sites varied depending on the extent of suitable sand/mud substrate, bottom slope (e.g., steep slopes had narrow zone of appropriate depths), eelgrass depth range, and eelgrass patchiness.

Our results indicate that most beds around the islands persist over decades. This stability is remarkable since many of the sites are used as small boat harbors, with obvious impacts from anchoring and in some cases possible disturbance from shoreline development. The extinction of beds at Anacapa Island, apparently due to widespread overgrazing by *Lytechinus pictus* in the 1980s, was a highly unusual situation because white sea urchins are not normally abundant in shallow-water island habitats (J. Engle unpubl. data). There has been no sign of recruitment at Frenchys Cove (ANA) since 1991, underlining the limited long-distance dispersal capabilities of this species (Ruckelshaus 1996, 1998, Reusch et al. 2000). Another possible indication of low dispersal was the absence of *Zostera* from many protected coves where the habitat appeared suitable. To date, we documented only two cases of colonization of new sites. These new populations at Santa Catalina Island, which arose within 3 km of existing eelgrass beds, may have been established by

rafting inflorescences bearing fertile seeds (Reusch 2001) or the re-establishment of drifting turions (Phillips and Meñez 1988, J. Engle and K.A. Miller pers. observ.).

Depth Distribution

Depth distributions at some sites appeared limited by lack of suitable substrate. For example, rock reefs at West Bechers (SRO), Old Ranch Canyon (SRO), and Coast Guard (SNI) determine shallow bed limits. Given suitable habitat, exposure to wave shock evidently is important in determining the shallow depth limit for eelgrass; the more sheltered the site, the shallower it can occur (Phillips 1984). The shallowest grass occurred at the two most protected sites – Catalina Harbor (SCA) and Prisoners (SCR). There was also a positive association between wave exposure and lower depth limits, with deeper beds occurring in locations relatively exposed to weather from the north, northwest and southwest, e.g., Coast Guard (SNI). South-facing sites, such as Smugglers (SCR), East End (SRO) and East End (SCA), while protected from prevailing north and northwest storms, can be subject to powerful long-period swells from distant southern storms and hurricanes. Eelgrass beds at these sites extend to deeper depths than those in more protected locations.

A critical component of the offshore depth limit is the extent of light penetration, which is in turn affected by turbidity (Dennison and Alberte 1985, Dennison 1987, Orth and Moore 1988, Duarte 1991, Cabello-Pasini et al. 2002, Abe et al. 2003). Offshore island waters are typically clear compared to most mainland shores that receive suspended sediment plumes from rivers and streams; thus *Zostera* often is able to occur at greater depths around the islands. However, even at the islands, sediments that accumulate in highly sheltered eelgrass habitats tend to be composed of fine, light particulates that can coat eelgrass leaves and are easily suspended in water column, thereby reducing available light. Conversely, exposed island eelgrass sites, with sandier substrates, are subject to clear, oceanic water allowing light penetration to greater depths.

Leaf Morphology

Many variables influence *Zostera* leaf width

and length, including water temperature, wave exposure, nutrients, and genetics (Phillips 1984, Schanz and Asmus 2003). Water temperature patterns at the islands show an obvious trend of increasing temperature from the northwest to the southeast (Engle 1994). We found a trend toward shorter and narrower eelgrass blades from the cool northwestern islands to the warm southeastern islands. There is evidence that environmental stress (high temperature and high light levels) can retard growth, leading to narrower leaves (McMillan 1978, Phillips and Lewis 1983, Abal et al. 1994), which is supported by our findings of narrower leaves in the warmer southeastern locations. Also, we have observed extremely small internodes in the rhizomes of narrow-leaved plants from SCA, indicating slow growth rates.

Although eelgrass exhibits a morphological response to environmental parameters, there also is evidence for genetic control of blade width (McMillan 1978, Phillips and Lewis 1983). We found patches of *Zostera* with distinctly different blade widths side by side in shallow depths at warm-water SCL. The wider form also occurred in deeper water, but not the narrow form. It is possible that the two represent genetically differentiated strains with different morphological and physiological characteristics. Also, the intermediate width blades at the East End, Palisades and Willow Cove are unusual for warm-water Santa Catalina Island. The East End and Palisades are deeper beds on the windward side of the island, with substantial water motion, especially swell and currents. Perhaps the exposure brings cooler, more oceanic water (possibly upwelled from Catalina Canyon) than that typical of sites on the lee side of the island; these deep populations may be less stressed by high light conditions. However, the intermediate width blades at Willow Cove are exposed to warm water similar to that at nearby Button Shell, where the narrow form occurs. Maybe this population has been introduced from a genetically different population, perhaps from the East End, and has maintained its morphology even in the warmer conditions. Molecular studies now underway will reveal the genetic relationships among these populations and allow us to distinguish between morphological plasticity and genetic differentiation (Reusch et al. 1999).

Species Identities

How many species of *Zostera* occur in California and at the California Channel Islands? Is the wide leaf form a different species from the narrow? Our results clearly indicate a break in leaf width between the populations occurring at the northern islands and those at the southern islands – with an intermediate width occurring at three sites at SCA. The ecological setting (deep, more exposed sites) and the greater leaf width in the northern populations are consistent with the description of both *Z. pacifica* and *Z. asiatica*. In fact, some authors consider these to be a single species, recognizing the earliest epithet, *Z. pacifica* as correct (Hickman 1993, Junak et al. 1995). Others consider both forms to be variants of *Z. marina* (den Hartog 1970, Dawson and Foster 1982, Armstrong and Thorne 1989). The species question cannot be resolved until seed coat morphology (a trait less susceptible to plasticity) is examined in more detail and molecular studies using nuclear and chloroplast markers have been conducted. Currently, we take a conservative approach, accepting the null hypothesis that one highly variable species of eelgrass, *Z. marina*, occurs in the California Channel Islands. In any case, the genus is well represented in a variety of sites, providing the architecture for an ecologically important community that warrants further studies and conservation efforts.

ACKNOWLEDGMENTS

We thank the many volunteers of the Channel Islands Research Program who helped in the underwater surveys, particularly J. Altstatt, R. Ambrose, J. Carroll, D. Farrar, C. Gramlich, R. Herrmann, D. Martin, D. Richards, D. Smith, and J. Wible. J. Chomeau, H. Chomeau, C. Bungener, and other crew of the *R/V Cormorant* provided expert topside assistance. Staff of the USC Wrigley Marine Science Center provided valuable shore-side support. We also thank D. Martin, D. Farrar, S. Adams, and J. Klaib for assistance in data analysis. Our perspective benefited greatly from discussions with J. Coyer and D. Richards. We are grateful for information exchange and cooperative arrangements with Channel Islands National Park, facilitated by G. Davis and D. Richards. This work

was supported primarily by The Tatman Foundation. Surveys at the northern Channel Islands from 1994–1997 were supported by a grant to R. Ambrose, P. Raimondi, and J. Engle from the California Coastal Commission. This is contribution # 232 from the University of Southern California's Wrigley Marine Science Center on Santa Catalina Island.

REFERENCES

- Abal, E.G., N. Loneragan, P. Bowen, C.J. Perry, J.W. Udy and W.C. Dennison. 1994. Physiological and morphological responses of the seagrass *Zostera capricorni* Aschers. to light intensity. *Journal of Experimental Marine Biology and Ecology* 178:113–129.
- Abe, M., N. Hashimoto, A. Kurashima and M. Maegawa. 2003. Estimation of light requirement for the growth of *Zostera marina* in central Japan. *Fisheries Science* 69:890–895.
- Altstatt, J. 2005. Restoration of a historic eelgrass (*Zostera marina*) bed at Frenchy's Cove, Anacapa Island. Pages 397–404. *In*: Garcelon, D.K. and C.A. Schwemm (eds.), *Proceedings of the Sixth California Islands Symposium*. National Park Service Technical Publication CHIS-05-01, Institute for Wildlife Studies, Arcata, CA.
- Armstrong, W.P. and R.F. Thorne. 1989. California seagrasses. *Fremontia* 16:15–21.
- Cabello-Pasini, A., C. Lara-Turrent and R.C. Zimmerman. 2002. Effect of storms on photosynthesis, carbohydrate content and survival of eelgrass populations from a coastal lagoon and the adjacent open ocean. *Aquatic Botany* 74:149–164.
- Dawson, E.Y. and M.S. Foster. 1982. *Seashore Plants of California*. University of California Press, Berkeley, CA, 226 pp.
- Cottam, C. and D.A. Munro. 1954. Eelgrass status and environmental relations. *Journal of Wildlife Management* 18:449–460.
- Dennison, W.C. 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquatic Botany* 27:15–26.
- Dennison, W.C. and R.S. Alberte. 1985. Role of daily light period in the depth distribution of

- Zostera marina* (eelgrass). Marine Ecology Progress Series 25:51–61.
- Duarte, C.M. 1991. Seagrass depth limits. Aquatic Botany 40:363–377.
- Engle, J.M. 1994. Perspectives on the structure and dynamics of nearshore marine assemblages of the California Channel Islands. Pages 13–26. In: Halvorson, W.L. and G.J. Maender (eds.), The Fourth California Islands Symposium: Update on the Status of Resources. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- den Hartog, C. 1970. Seagrasses of the World. North-Holland Publishing Company, Amsterdam, The Netherlands, 275 pp.
- Hemminga, M.A. and C.M. Duarte. 2000. Seagrass Ecology. Cambridge University Press, Cambridge, UK, 298 pp.
- Hickman, J.C., editor. 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley, CA, 1,400 pp.
- Junak, S., T. Ayers, R. Scott, D. Wielken and D. Young. 1995. A Flora of Santa Cruz Island. Santa Barbara Botanic Garden, Santa Barbara, CA, 397 pp.
- McConnaughey, T. and C.P. McRoy. 1979. ¹³C label identifies eelgrass (*Zostera marina*) carbon in an Alaskan estuarine food web. Marine Biology 53:263–269.
- McMillan, C. 1978. Morphogeographic variation under controlled conditions in five seagrasses, *Thalassia testudinum*, *Halodule wrightii*, *Syringodium filiforme*, *Halophila engelmannii*, and *Zostera marina*. Aquatic Botany 4:169–189.
- 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, USA. 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., 85 pp.
- Phillips, R.C. and R.R. Lewis. 1983. Influence of environmental gradients in leaf widths and transplant success in North American seagrasses. Marine Technical Society Journal 17:59–68.
- Phillips, R.C. and S.W. Echeverria. 1990. *Zostera asiatica* Miki on the Pacific Coast of North America. Pacific Science 44:130–134.
- Phillips, R.C. and E.G. Meñez. 1988. Seagrasses. Smithsonian Contributions to the Marine Sciences No. 34. Smithsonian Institution Press, Washington, D.C., 65 pp.
- Reusch, T.B.H. 2001. New markers – old questions: population genetics of seagrasses. Marine Ecology Progress Series 211:261–274.
- Reusch, T.B.H., C. Boström, W.T. Stam and J.L. Olsen. 1999. An ancient eelgrass clone in the Baltic Sea. Marine Ecology Progress Series 183:301–4.
- Reusch, T.B.H., W.T. Stam and J.L. Olsen. 2000. A microsatellite-based estimation of clonal diversity and population subdivision in *Zostera marina*, a marine flowering plant. Molecular Ecology 9:127–40.
- Ruckelshaus, M.H. 1996. Estimation of genetic neighborhood parameters from pollen and seed dispersal in the marine angiosperm *Zostera marina* L. Evolution 50:856–864.
- Ruckelshaus, M.H. 1998. Spatial scale of genetic structure and an indirect estimate of gene flow in eelgrass, *Zostera marina*. Evolution 52:330–343.
- Schanz, A. and H. Asmus. 2003. Impact of hydrodynamics on development and morphology of intertidal seagrasses in the Wadden Sea. Marine Ecology Progressive Series 261:123–134.
- Short, F.T. and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. Environmental Conservation 23:17–27.