

Long-term Change in Eelgrass Distribution at Bahía San Quintín, Baja California, Mexico, using Satellite Imagery

DAVID H. WARD^{1,*}, ALEXANDRA MORTON², T. LEE TIBBITTS¹, DAVID C. DOUGLAS³, and EDUARDO CARRERA-GONZÁLEZ⁴

¹ Alaska Science Center, Biological Science Office, U.S. Geological Survey, 1011 E. Tudor Rd., Anchorage, Alaska 99503

² Wetlands and Waterfowl Research Center, Ducks Unlimited Inc., One Waterfowl Way, Memphis, Tennessee 38120-2351

³ Alaska Science Center, Biological Science Office, U.S. Geological Survey, Glacier Bay Field Station, Juneau Office, P. O. Box 240009, Douglas, Alaska 99824-0009

⁴ Ducks Unlimited de Mexico, Ave. Vasconcelos 209 Ote., Residencial San Agustín, Garza García, Nuevo León, Mexico

ABSTRACT: Seagrasses are critically important components of many marine coastal and estuarine ecosystems, but are declining worldwide. Spatial change in distribution of eelgrass, *Zostera marina* L., was assessed at Bahía San Quintín, Baja California, Mexico, using a map to map comparison of data interpreted from a 1987 Satellite Pour l'Observation de la Terre multispectral satellite image and a 2000 Landsat Enhanced Thematic Mapping image. Eelgrass comprised 49% and 43% of the areal extent of the bay in 1987 and 2000, respectively. Spatial extent of eelgrass was 13% less (–321 ha) in 2000 than in 1987 with most losses occurring in subtidal areas. Over the 13-yr study period, there was a 34% loss of submerged eelgrass (–457 ha) and a 13% (+136 ha) gain of intertidal eelgrass. Within the two types of intertidal eelgrass, the patchy cover class (<85% cover) expanded (+250 ha) and continuous cover class (≥85% cover) declined (–114 ha). Most eelgrass losses were likely the result of sediment loading and turbidity caused by a single flooding event in winter of 1992–1993. Recent large-scale agricultural development of adjacent uplands may have exacerbated the effects of the flood. Oyster farming was not associated with any detectable losses in eelgrass spatial extent, despite the increase in number of oyster racks from 57 to 484 over the study period.

Introduction

Seagrasses are important components of many marine coastal and estuarine ecosystems. They are highly productive habitats that stabilize and enrich sediments and support a complex trophic web and a detritus-based food chain (Zieman 1982; Phillips 1984; Thayer and Fonseca 1984). Seagrasses occur in shallow water areas and their growth is controlled by abiotic and biotic factors including disease (Short et al. 1988), light availability (Dennison 1987), nutrient availability (Short 1987), grazing (Heck and Valentine 1995), and wave and current patterns (Fonseca and Fisher 1986; Fonseca and Kenworthy 1987). Light availability is considered to have the greatest influence on seagrass survival (Backman and Barilotti 1976; Dennison 1987; Zimmerman et al. 1995) and even small declines in irradiance levels can dramatically slow growth and limit distribution of seagrass meadows (Lee and Dunton 1997; Longstaff and Dennison 1999).

In the last 25 yr, seagrass habitats have been re-

duced worldwide due to natural and anthropogenic perturbations (Short and Wyllie-Echeverria 1996). Much of the loss has been linked to declines in water quality from eutrophication (Lee and Olsen 1985; Short and Burdick 1996) and sediment loading and resuspension (Orth and Moore 1983; Dennison et al. 1993; Preen et al. 1995). As human communities and developments expand in coastal areas, it is crucial that scientists and resource managers monitor changes in extent, abundance, and health of seagrass habitats. If a downward trend is detected in any of these parameters, then mitigation and/or conservation efforts can be implemented using the change data. In recent years, remote sensing techniques, such as, satellite imagery (e.g., Ward et al. 1997a), aerial photography (e.g., Ferguson et al. 1993), and airborne digital sensors (e.g., Mumby et al. 1997), have been used to map the distribution of seagrasses. Although photogrammetric interpretation of vertical aerial photography is the standard method for monitoring seagrasses (Dobson et al. 1995), satellite imagery in combination with field sampling is an effective approach to retrospective spatial inventories and

* Corresponding author: tele: 907/786-3525; fax: 907/786-3636; e-mail: david_ward@usgs.gov

change detection analysis of seagrass habitats (Ferguson and Korfmacher 1997; Ward et al. 1997a).

Eelgrass, *Zostera marina* L., is the predominant seagrass species in embayments and protected coastal areas along the Pacific coast of Baja California (Dawson 1962; Wiggins 1980; Carrera-González unpublished data). Preserving and maintaining healthy eelgrass habitats is important to both the economy and ecology of the region as they provide food and substrate for a variety of fish and shellfish species (Barnard 1962; Rosales-Casian 1996, 1997), some of which are the basis for local subsistence and commercial fisheries (e.g., shellfish mariculture, lobstering, sportfishing) (Aguirre-Muñoz et al. 2001; Ibarra-Obando et al. 2001). Large numbers of a variety of migratory waterbirds (Massey and Palacios 1994; Page et al. 1997), including >50% of the entire Pacific flyway population of black brant (*Branta bernicla nigricans*) (Reed et al. 1998; Perez-Arteaga et al. 2002), spend several months each year in coastal Baja California where they rely on food found in eelgrass communities or on the plants themselves.

In contrast to nearby coastal areas in southern California and the west coast of Mexico, embayments along the Pacific coast of Baja California are relatively undisturbed (Palacios 2000; Ibarra-Obando et al. 2001). There is increasing pressure to develop these areas for commercial, recreational, and residential purposes (Ibarra-Obando and Escofet 1987; Aguirre-Muñoz et al. 2001). In spite of the potential for substantial alterations to bays in upcoming years, there have been no comprehensive assessments of seagrass extent in Baja California.

During a period (1990–2000) of intensive research on seagrass population dynamics (Meling-López and Ibarra-Obando 1999; Poumian-Tapia and Ibarra-Obando 1999; Cabello-Pasini et al. 2003; Cabello-Pasini et al. 2004) and herbivory by black brant (Ward 1997) in Pacific embayments of Mexico, we developed habitat maps and conducted a retrospective change detection analysis of eelgrass distribution in Bahía San Quintín, the northernmost embayment in Baja California and one of the most important wintering areas for black brant (Ward 1997; Reed et al. 1998). Distribution of habitats was estimated from satellite images collected in 1987 and 2000. These images represented periods both before and after considerable aquaculture and agriculture development occurred in and around Bahía San Quintín (Aguirre-Muñoz et al. 2001). We then compared eelgrass cover between these years and evaluated the observed changes in spatial distribution of eelgrass with respect to development (e.g., oyster farming and agricultural

development) and stochastic events (e.g., flooding).

Study Area

Bahía San Quintín is a 4,800 ha, shallow water embayment situated on the northwestern coast of the Baja California Peninsula (Fig. 1). It is characterized by expansive intertidal flats, narrow tidal channels, and a permanent entrance protected on the west and south by sand spits (Dawson 1962). Bottom sediment is a mixture of sand, silt, and clay with soft mud comprising a significant portion of the substrate (Cabello-Pasini et al. 2003). Bahía San Quintín receives little annual precipitation (mean = 15 cm), except during infrequent storms that usually occur between October and March (Ibarra-Obando et al. 2001). If rainfall accumulation is high, runoff from the 2,000 km² San Simón River watershed empties into the bay. Strong coastal winds generate a nearshore upwelling system that is an important source of nutrients for the bay and surrounding ocean areas (Camacho-Ibar et al. 2003). Generally, winds and upwelling events are persistent throughout the year but strongest in spring and early summer (Bakun and Nelson 1977). Tides are mixed semidiurnal with a maximum range of 2.0 m. Eelgrass is the dominant submerged aquatic vegetation in the bay. Widgeongrass (*Ruppia maritima*) and some seaweeds (e.g., *Ulva* spp., *Enteromorpha* spp.) occur in low abundance (Dawson 1962; Kramer 1976).

The bay shoreline is largely undeveloped, while the adjacent uplands are sparsely settled and covered either by coastal chaparral vegetation (Wiggins 1980) or agricultural fields. A large and rapidly growing, agriculturally-based community of approximately 60,000 inhabitants is located 15 km north and east of Bahía San Quintín (Aguirre-Muñoz et al. 2001). Farming occurs year-round (with and without irrigation) and in years of little rain, non-irrigated fields remain unplanted and mostly unvegetated for long periods. Mariculture of oysters (primarily *Crassostrea gigas*) is the most significant economic resource in the bay (Aguirre-Muñoz et al. 2001) and generates the most human activity. Oyster farming was introduced in the early 1970s (Kramer 1976) and became a large scale commercial activity in the mid-1990s (Aguirre-Muñoz et al. 2001). Oysters are grown from 1–2 m high by 1–2 m wide plastic or wooden racks that are fixed to the bottom in low intertidal to shallow subtidal areas. Each rack consists of a series of evenly spaced poles upon which bundles of oysters are suspended on lines. Racks vary in length (10–500 m long) and spacing (1–70 m apart), and are generally located close to main channels to maximize tidal flow through the oysters.

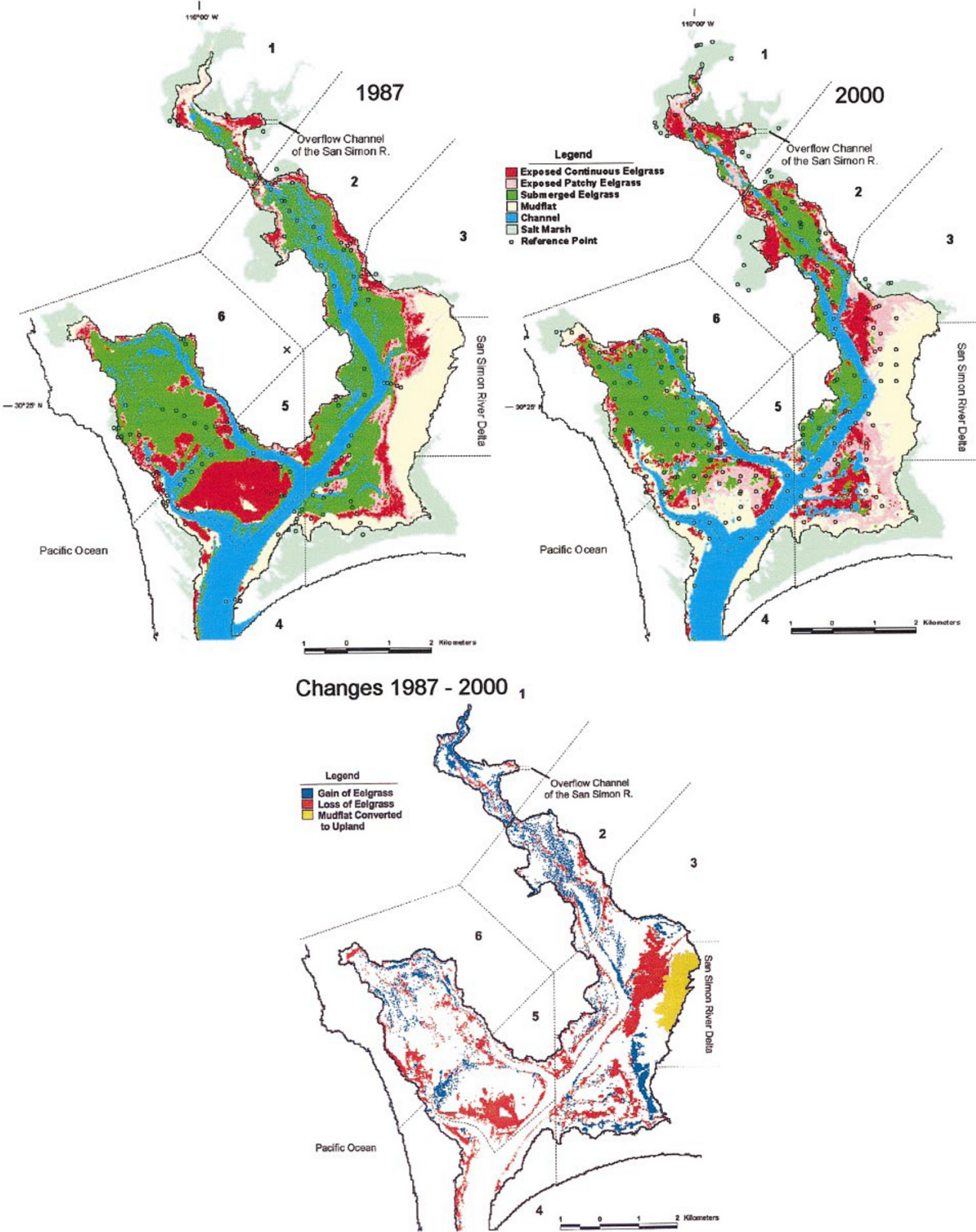


Fig. 1. Distribution of eelgrass and other habitats in 1987 and 2000 within six zones of Bahía San Quintín, Baja California. X denotes the top of cinder cone where color photographs were taken of oyster racks in 1991. Also shows change in eelgrass distribution within six zones of Bahía San Quintín, Baja California, between 1987 and 2000.

TABLE 1. Satellite imagery used to assess eelgrass extent in Bahía San Quintín, Baja California. ^a Pacific standard time. ^b Mean lower low water.

Satellite Scene	Acquisition Date	Time of Acquisition ^a	Tide Height ^b (m)	Tide Stage
SPOT	January 8, 1987	1140	+0.2	Slack
Landsat-5 TM	December 29, 1991	1155	+0.3	Slack
Landsat-5 TM	January 19, 1994	1153	+0.7	Ebb
IRS	September 3, 1999	1155	+0.9	Flood
Landsat-7 ETM+	May 11, 2000	1150	+0.0	Slack

Methods

DATA PROCESSING

Two multispectral satellite images were obtained for the change detection analysis: a January 8, 1987, Satellite Pour l'Observation de la Terre (SPOT) image and a May 11, 2000, Landsat-7 Enhanced Thematic Mapper Plus (ETM+) image. These images were selected because they were captured at low tide to optimize estimation of eelgrass cover and under similar conditions: calculated tide heights differed by 20 cm and time of day differed by <10 min (Table 1). Two other Landsat images, December 29, 1991, and January 19, 1994, Landsat-5 TM, were selected to evaluate impacts of a series of severe storms during the winter of 1992–1993 on high intertidal habitats. A higher resolution Indian Remote Satellite (IRS) image was acquired to create a geo-rectified base map of the bay because an accurate reference map was lacking. The base map was produced by importing the IRS scene into a Universal Transverse Mercator (UTM) zone 11 projection and a 1984 World Geodetic System datum (WGS-84), and rectifying the scene with 86 differentially-corrected global positioning satellite (GPS) ground control points. The base map was refined further using a high resolution (2-m pixel resolution) photomosaic of the bay (1:22,000 scale) and additional ground control points.

Subsets of the 1987 SPOT and 2000 Landsat ETM+ scenes that encompassed the entire bay were registered to the base map using an array of control points that were positioned around the bay. A second order, least-squares transformation equation was derived for each image that resampled the scenes to the UTM projection with 20-m pixel resolution for the SPOT scene and a 25 m pixel size for the Landsat ETM+ scene.

Unsupervised image classifications techniques (Swain and Davis 1978) and an isodata clustering algorithm were used to identify statistically separable spectral classes in each of the SPOT and Landsat ETM+ scenes. Each pixel within a registered scene was assigned to a spectral class using a maximum likelihood classifier and labeled as channel (i.e., submerged unvegetated), eelgrass, intertidal mudflats (i.e., exposed unvegetated), or salt

marsh. The eelgrass class was divided further into three subclasses: exposed-continuous, exposed-patchy, and submerged. Subclass determinations were made using a two-step process. The eelgrass class was labeled as either exposed or submerged based on its near-infrared reflectance (Band 3 in SPOT and Band 4 in Landsat ETM+). Near-infrared light is absorbed within a few cms of the water surface (Lillesand and Kieffer 2000), and can be used to differentiate between exposed (i.e., above and at the water surface) and submerged (i.e., in the water column) vegetation. The boundary between exposed and submerged subclasses was determined by the approximate tide height at the time of image acquisition, which in both cases was close to mean lower low water (0.0 m MLLW). The signature of eelgrass across all spectral bands and the reference data (see below) were then used to assign all exposed eelgrass grid cells to either continuous ($\geq 85\%$ cover) or patchy ($< 85\%$ cover) subclasses. These percent cover classes were chosen because they represented natural breaks in the reference data. Percent cover refers to area of a grid cell.

Good spectral distinction between habitat classes and the monospecific nature of the aquatic vegetation in Bahía San Quintín assured robust spectral classification of eelgrass and all other habitats in the satellite images. To evaluate and verify spectral class labeling for the 1987 SPOT map, we relied on reference data collected at 129 points in January–March 1991 and 1992, and our first hand knowledge of the bay in the late 1980s and early 1990s. Development of the 2000 Landsat ETM+ map was verified by reference data collected at 271 points in November–December 1999 and 2000 and July 2000. Percent cover of each habitat type was estimated within an approximate 20-m diameter circle around the point. In 2000, presence or absence of widgeongrass, *Ulva* spp., and water depth (± 0.01 m) was recorded at each point. Points were spaced over the entire bay (50–500 m apart) and spread across the full spectrum of vegetation and physiographic conditions that existed in the bay. Eelgrass cover was estimated at reference points during low tides or by skin diving during high tides. Using an independent set of random points

collected in 2000, the overall accuracy of the four classes and three eelgrass subclasses in the 2000 Landsat ETM+ classified map was 81% (overall accuracy of the four classes was 94%). The Kappa statistic, which is a measure of accuracy incorporating random chance agreements, was 75% (with 100% representing perfect agreement [Congalton 1991]). No independent reference data were available to assess the accuracy of the SPOT classified image.

To obtain a measure of the rate of aquaculture development in Bahía San Quintín, the distribution of oyster racks was compared between 1991 and 2000. Because oyster racks were not visible at the tide height (i.e., below the water surface) of the satellite images, it was necessary to use color photographs taken at a lower tide (< -0.5 m MLLW) to map their distribution. Location of oyster racks in 1991 were documented using oblique color photographs taken in that year from the top of an adjacent cinder cone (250 m elevation) (Fig. 1) that had an unobstructed view of the entire bay. Distribution of oyster racks in 2000 was mapped from the georectified aerial photographs and validated by visiting sites. All oyster racks present in 1991 were still present in 2000; positions of the oyster racks in 1991 were located using a combination of the oblique photographs and the digitized map of oyster racks in 2000.

To gain perspective on effects of spatial change of upland habitats, particularly agricultural development, on the ecology of eelgrass in the bay, estimates of areal extent of upland habitats were obtained using the satellite imagery. For this analysis, we used larger subsets of the 1987 SPOT and 2000 Landsat ETM+ scenes encompassing roughly a 4–9 km-wide area around the bay. The scenes were registered to the base map and a UTM projection using an additional array of control points positioned adjacent to the bay. After masking the bay from the analysis, we followed the same image classification procedures as mentioned above and assigned each pixel to one of three habitat classes: coastal chaparral, agricultural fields, or other (i.e., developed land, salt pans, beach).

DATA ANALYSIS

A parsimonious comparison of areal extent of bay classes and upland classes was made between the 1987 and 2000 satellite images by constructing a difference map using GIS software ARC/INFO (i.e., grid cell values of the 1987 image were subtracted from the same grid cells of the 2000 image to determine if that grid cell had changed). Class comparisons were calculated based on a sampling grid cell size of 20 m². Differences in total extent of bay classes were compared across 6 zones in Ba-

hía San Quintín (Fig. 1). Zones varied in size from 490 to 1,741 ha and were delineated based on natural boundaries, such as channels, points of land, and our a priori knowledge of human activities and natural events that may have affected eelgrass distribution within different areas of the bay (e.g., oyster farming in zones 5 and 6, river delta in zone 3).

We assessed the effect of oyster racks on eelgrass beds by correlating location of racks in 2000 with gain and loss of eelgrass between 1987 and 2000. We hypothesized that oyster racks would have a negative impact on eelgrass cover (Waddell 1964; Everett et al. 1995) and loss of eelgrass would be greater inside than outside the impact areas of the racks. The analysis was restricted to zones 5 and 6, where 97% of all oyster racks present in 2000 were situated. We calculated loss and gain of eelgrass inside and outside of potential impact areas of 2, 5, and 10 m drawn from the center of racks and standardized these estimates by their respective unit area. We chose 3 different potential impact areas because effects of oyster racks may vary with distance from a rack depending on the hydrodynamics, sedimentation rates, and density of racks at a location (Everett et al. 1995; Rumrill personal communication). Mean estimates of change in eelgrass were compared inside and outside potential impact areas using a 1-sample *t*-test.

Results

Eelgrass meadows were the dominant structural habitat throughout Bahía San Quintín, comprising 49% and 43% of the areal extent of the bay in 1987 and 2000, respectively (Table 2; Fig. 1). Eelgrass extended subtidally to approximately -3.0 m MLLW and intertidally to about $+1.0$ m MLLW. Exposed eelgrass beds (>0.0 m MLLW) comprised a significant portion of the overall extent of eelgrass in the bay in 1987 (44%) and 2000 (57%). Large contiguous beds of eelgrass (>100 ha) were found in zones 2, 3, and 6 and together these zones accounted for 75% and 77% of all eelgrass in the bay in 1987 and 2000, respectively (Fig. 1). Based on reference data in 2000, widgeongrass was present in low abundance in 4 of the 6 zones (1, 3, 5, and 6), the most extensive patches of widgeongrass were associated with the San Simón River delta in zone 3 and the large intertidal mudflat in zone 5. Widgeongrass occurred primarily in high intertidal areas ($>+0.4$ m MLLW), beyond most eelgrass, and less frequently lower in the intertidal, intermixed with eelgrass. Salt marshes (20%) and intertidal mudflats (19%) were the next most abundant habitats in the bay. Greatest areal extent of salt marsh occurred in zones 1 and 3 while largest contiguous intertidal mudflats were

TABLE 2. Hectares of each class within different zones^a of Bahía San Quintín, Baja California, in 1987 and 2000. ^a See Fig. 1. ^b Eelgrass included exposed (≥ 0.0 m mean lower low water [MLLW]) and submerged (< 0.0 m MLLW) beds. ^c $\geq 85\%$ cover of eelgrass. ^d $< 85\%$ cover of eelgrass.

Habitat	Zone 1		Zone 2		Zone 3		Zone 4		Zone 5		Zone 6		Total	
	1987	2000	1987	2000	1987	2000	1987	2000	1987	2000	1987	2000	1987	2000
Eelgrass ^b	126	163	314	349	819	655	70	20	399	286	662	596	2,390	2,069
Exposed	78	138	101	174	361	518	44	17	293	202	169	133	1,046	1,182
Continuous ^c	38	67	46	123	152	176	31	15	269	73	105	73	641	527
Patchy ^d	40	71	55	51	209	342	13	2	24	129	64	60	405	655
Submerged	48	25	212	175	459	137	26	3	106	84	493	463	1,344	887
Mudflat	52	19	26	37	437	452	91	154	17	121	35	102	658	885
Channel	20	17	105	58	201	237	299	287	153	161	93	93	871	853
Salt marsh	292	281	128	127	283	307	177	159	0	0	68	83	948	957
Total	490	480	573	571	1,740	1,651	637	620	569	568	858	874	4,867	4,764

associated with the river delta in zone 3 and entrance of the bay in zone 4.

Overall size of Bahía San Quintín and net spatial extent of eelgrass throughout the entire bay declined 2% (-103 ha) and 13% (-321 ha), respectively, between 1987 and 2000 (Table 2; Fig. 1). Nearly all (98%) of the loss in bay size was associated with the conversion of a large expanse of intertidal mudflat (101 ha) to upland vegetation at the river delta in zone 3 (Fig. 1). This conversion

occurred in winter 1992–1993 based on our direct observations and examination of the December 1991 and January 1994 Landsat TM satellite images. Net losses in eelgrass extent between 1987 and 2000 were detected in zones 3–6 (Table 2) and primarily involved eelgrass changing to mudflat (Fig. 1). Small (< 40 ha) net gains in eelgrass extent were detected in zones 1–2 (Table 2) and were the result of mudflat and channel converting to exposed eelgrass. Greatest reductions in areal extent of eelgrass occurred in the relatively large zone 3 (-164 ha) near the San Simón River delta and in zone 5 (-113 ha) at the bay entrance. Throughout the bay, submerged eelgrass declined 34% (-457 ha) whereas exposed eelgrass increased 13% (+136 ha) (Table 2). Within the exposed eelgrass subclasses, there was a net gain in the patchy cover class (+250 ha) and net loss in the continuous cover class (-114 ha).

Total extent of mudflat areas increased 34% (+227 ha) between 1987 and 2000 (Table 2) and gains in this class accounted for 64% of the loss in eelgrass. Net increases in mudflat areas were evident in 5 of the 6 zones with greatest gains occurring in the western portion of the bay in zones 6 (+67 ha), 5 (+104 ha), and 4 (+63 ha). Net changes in extent of channels and salt marshes were minimal ($< 2\%$) between 1987 and 2000.

There was a substantial increase in the number of oyster racks from 1991 ($n = 57$) to 2000 ($n = 484$) with virtually all (99%) of the increase occurring in zones 5 and 6 (Fig. 2). Oyster racks covered 33, 81, and 137 ha of zones 5 and 6 when the potential impact area around a rack was designated as 2, 5, or 10 m from the center, respectively. In all scenarios, there was an apparent gain in eelgrass inside the potential impact areas and a small loss estimated outside the potential impact areas (Table 3), indicating no significant negative impact on eelgrass distribution from oyster racks (one-tailed $p > 0.10$).

Coastal chaparral and agricultural lands were

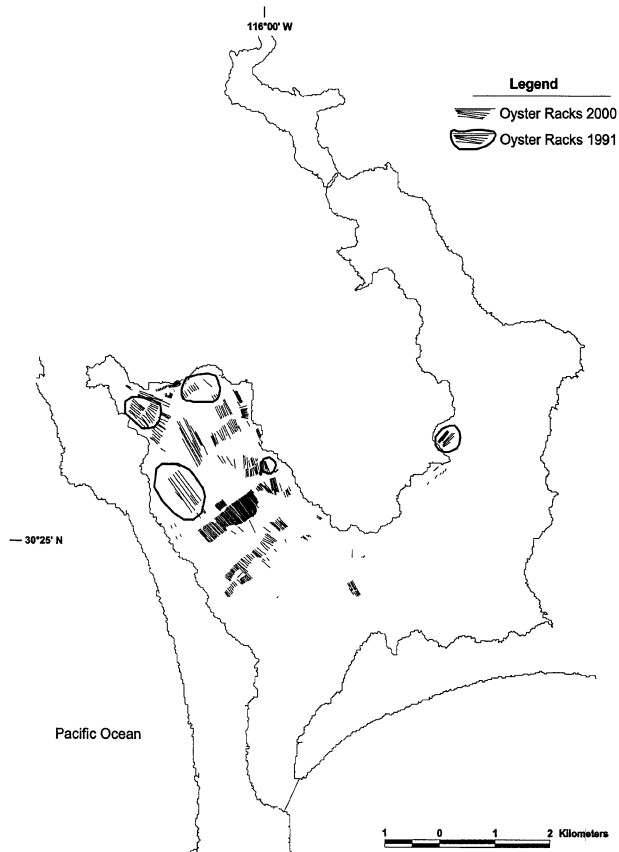


Fig. 2. Change in oyster racks in Bahía San Quintín, Baja California, between 1991 and 2000.

TABLE 3. Mean \pm SD loss or gain (ha) of eelgrass inside and outside of potential oyster rack impact areas in zones 5 and 6 of Bahía San Quintín, Baja California.

Potential Impact Area of Oyster Rack (m)	Oyster Racks		Mean Difference	95% CI		Significance (1-tailed)
	Inside	Outside		Lower	Upper	
2	0.007 \pm 0.308	-0.0001 \pm 0.0032	0.007	-0.023	0.036	0.672
5	0.022 \pm 0.282	-0.0001 \pm 0.0018	0.022	-0.006	0.051	0.941
10	0.055 \pm 0.269	-0.0001 \pm 0.0020	0.054	0.018	0.089	0.999

the most abundant upland habitat adjacent to Bahía San Quintín in 1987 and 2000, respectively (Table 4). Agricultural lands increased by 35% to nearly 10,000 ha between 1987 and 2000 with most (59%) gain occurring northwest of the bay and in the San Simón River valley (Fig. 3).

Discussion

Bahía San Quintín stands out as an important seagrass area in North America and is especially significant in the southern portion of eelgrass range along the Pacific coast. Estimates of total extent of eelgrass were greater for Bahía San Quintín (2,069 ha and 2,390 ha) than for nearby embayments in California (San Diego Bay: 1,600 ha, Hoffman unpublished data; Morro Bay: 400–800 ha, Chestnut unpublished data, and Humboldt Bay: 1,250–1,950 ha, Harding and Butler 1979; McBride et al. unpublished report). Quantitative assessments of seagrass distribution have only recently been initiated in Baja California, and preliminary analyses indicate that eelgrass extent was greater in Bahía San Quintín than in most, but not all, Pacific embayments (i.e., Estero Punta Banda: <1,000 ha; Laguna Manuela: 300–400 ha; Estero Coyote: 100 ha; Laguna Ojo de Liebre: 10,000–15,000 ha, Laguna San Ignacio: 5,000–6,000 ha, Ward and Carrera-González unpublished data). Only those embayments that were much larger in size (3–5 times larger) contained more eelgrass, but the eelgrass meadows at these sites had lower biomass (approximately 3–4 times less) and grew more subtidally than in Bahía San Quintín (Cabello-Pasini et al. 2003).

The extensive intertidal eelgrass meadows at Bahía San Quintín are a unique feature of this bay

relative to other embayments in southern California and Mexico. Intertidal meadows appear to be a significant factor contributing to use of this bay by >100 species of birds, many of which forage in eelgrass (Massey and Palacios 1994; Tibbitts unpublished data). A good example of bird use of intertidal eelgrass is the black brant. This arctic-breeding goose feeds almost exclusively on eelgrass during its 6-mo-long wintering season along the Pacific coast of North America. Black brant stay primarily in bays that contain accessible (i.e., intertidal) seagrasses (Wilson and Atkinson 1995; Reed et al. 1998) and each year, Bahía San Quintín provides food for up to 55% of the entire Pacific flyway population of this species (Conant and Voelzer 2002; Trost and Drut 2001). Such a strong reliance by black brant on Bahía San Quintín has prompted international entities involved with wildlife management to state that loss or degradation of eelgrass habitats in this bay could have a detrimental effect on the ability, of at least this one species, to survive and reproduce (Ward 1997; Ward et al. 1997b; Schamber 2001; Perez-Arteaga et al. 2002). There is little detailed information on use of eelgrass at Bahía San Quintín by other avian species and other taxa (e.g., fish, invertebrates), but several anecdotal accounts and qualitative studies report eelgrass-taxon dependencies (Palacios 2000).

Although the expanse of eelgrass at Bahía San Quintín has been noted for some time (e.g., Dawson 1962; Kramer 1976), the status and trends of this valuable resource has never been investigated. The 1987 and 2000 habitat maps presented here along with a recent habitat map developed using digital multispectral videography (Ward et al. 2004) offer the most quantitative and spatially ex-

TABLE 4. Landcover change (ha) adjacent^a to Bahía San Quintín, Baja California, between 1987 and 2000. ^a See Fig. 3. ^b Includes developed land, beach, and salt pan.

Habitat	North and West of Bay	East of Bay	Total
Coastal sage shrub no change	4,035	2,169	6,204
Coastal sage shrub to agricultural	1,646	1,157	2,803
Coastal sage shrub to other ^b	40	24	64
Agricultural no change	987	6,139	7,126
Agricultural to other	12	107	119
Agricultural to coastal sage shrub	0	0	0
Other no change	31	52	83

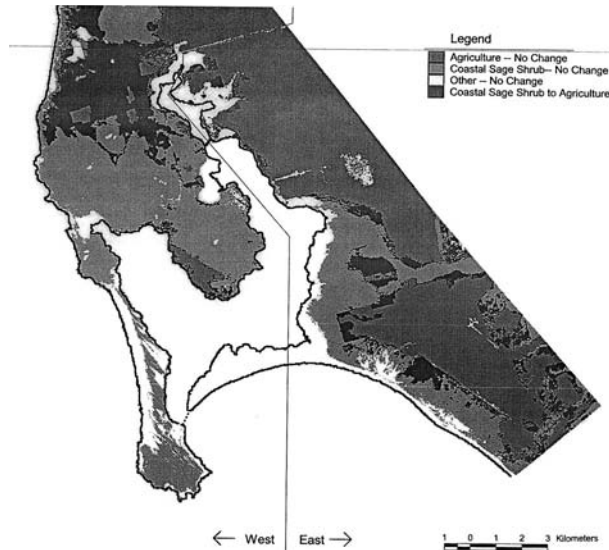


Fig. 3. Landcover change within two zones of Bahía San Quintín, Baja California, between 1987 and 2000. Other habitats include developed lands, beach, and salt pans.

licit estimates of eelgrass extent in this bay and in the region. The maps presented here were derived using satellite images that allowed us to conduct a retrospective analysis of habitat change, information that could not be estimated by other means. Satellite images that were suitable for the change detection analysis only existed for the years 1987 and 2000. Other habitat maps of the bay have been produced, but because they are less detailed, it is only possible to qualitatively compare our maps with them. Eelgrass distribution in our maps is consistent with less detailed maps of Bahía San Quintín made in 1974 (boat survey, Kramer 1976) and 1994 (satellite imagery, Carrera-González unpublished data), but different from a map created in 1960 (boat survey, Dawson 1962). This latter map indicated considerably less eelgrass cover throughout the bay, about half of the area detected in 1987 and 2000, and virtually no eelgrass in zone 1. It is unclear if differences in distribution between 1960 and other years represent an actual increase in eelgrass cover, or are an artifact of different mapping techniques.

Observed changes in the spatial distributions of eelgrass between 1987 and 2000 could have been influenced by the differences in tides (0.2 versus 0.0 m) or season (winter versus spring) of the respective satellite images (Table 1). There is usually some uncertainty associated with change detection analyses because spatial data is not often collected using the same techniques and under the same conditions (e.g., Ferguson and Korfmacher 1997). One would expect more eelgrass to be detected in 2000 because this image was obtained at a slightly

lower tide when more subtidal eelgrass would be visible, and during spring when eelgrass productivity, biomass, and cover would be greater (Poumian-Tapia and Ibarra-Obando 1999; Cabello-Pasini et al. 2003). In 1987, Bahía San Quintín was under the influence of an El Niño event, when warmer sea surface temperatures were associated with reduced eelgrass biomass and cover (Short and Neckles 1999; Ibarra-Obando et al. 2002; Ward unpublished data). We consider our overall assessment of diminished eelgrass cover at Bahía San Quintín in 2000 to be conservative, and are concerned that eelgrass loss may have been greater than our results indicate.

A significant portion of the loss of eelgrass cover at Bahía San Quintín was associated with a series of storms and flooding in the winter of 1992–1993. San Quintín Valley received approximately 45 cm of rain (3 times the yearly average) between December 1992 and March 1993, which was the highest rain accumulation since the El Niño winter of 1978–1979 (Aguirre-Muñoz et al. 2001). The majority of rainfall was concentrated during 1 wk in early January (>30 cm; Smith unpublished data) and was followed by about 4 mo of extensive flooding. Episodic storm events that coincide with extensive flooding, strong currents, or waves have dramatically altered seagrass distribution in other bays (e.g., Larkum and West 1990; Preen et al. 1995). Although data on discharge rates are lacking for the San Simón River, the 1992–1993 flooding was extensive enough to collapse a major bridge, inundate most neighborhoods, roads, and fields within the floodplain, and transport huge amounts of sediment into the bay (Ward personal observation). High erosion rates during flooding are typical for cleared and cultivated lands in arid environments (Schumm and Hadley 1963) and the level of sediment loading observed at Bahía San Quintín in 1992–1993 may have been greater than in previous flooding events due to the recent large-scale clearing of land for agriculture, particularly in the San Simón River valley (Table 4, Fig. 3).

Sediment loading decreases seagrass cover directly by burying plants and indirectly by increasing turbidity levels in the water column (Fortes 1988; Preen et al. 1995). Sediment loads deposited by the San Simón River in 1992–1993 buried entire beds of intertidal and subtidal eelgrass that were adjacent to the river delta in zone 3 and portions of beds that were in the path of sediments carried by tidal and river currents between the river delta and bay mouth in zones 4 and 5 (Ward personal observation). Significant amounts of sediments were also discharged for about a month into the northern portion of the bay by an overflow channel of the river. As of winter 2000, most of the beds

adjacent to the river delta had not reverted back to eelgrass, possibly because the affected area had become too shallow for eelgrass to grow. Depth measurements taken in 2000 in the affected area (mean = 1.1 ± 0.24 m MLLW; $n = 7$) revealed that this area was above the tidal range of eelgrass growth in Bahía San Quintín. Sediment loading from this flooding event may have also altered bathymetry in other portions of the bay. Local fishermen and waterfowl guides consistently reported that side channels in zones 1, 2, and 3 were no longer navigable during low tide since the 1992–1993 floods. A decrease in water depth in the bay may account for the increase in intertidal eelgrass in zones 1–3.

Reasons for the loss of subtidal eelgrass away from the river delta are difficult to assess because of the lack of historical data on water quality, nutrient dynamics, and macroalgae abundance, but recent studies of the photosynthetic characteristics of eelgrass in Bahía San Quintín point to turbidity as a factor limiting depth distribution of eelgrass plants (Cabello-Pasini et al. 2003, 2004). Cabello-Pasini et al. (2003) found that attenuation coefficient values were about three-fold greater in this bay than at other nearby Pacific lagoons in Baja California (i.e., Lagunas San Ignacio and Ojo de Liebre) and that subtidal plants in Bahía San Quintín were light limited for at least 15% of the year. Such patterns make it reasonable to speculate that the loss in subtidal beds not directly buried during the flood may be in response to recent increases in turbidity levels.

Reasons for the net loss of continuous cover of intertidal eelgrass are also unclear, but may be influenced by competition from macroalgae for available space (Short and Burdick 1996). Large mats of *Ulva* spp. and *Enteromorpha* spp. were observed covering portions of mudflats and eelgrass beds. In 2000, macroalgae (primarily *Ulva* spp.) was found four times more often in exposed-patchy than exposed-continuous eelgrass beds suggesting that there is an inverse relationship between macroalgae abundance and eelgrass cover.

Oyster farming has caused direct loss of eelgrass and degraded eelgrass beds in other systems (Waddell 1964; Everett et al. 1995). In an experimental study of the effects of oyster racks on eelgrass beds in Coos Bay, Oregon, Everett et al. (1995) found that oyster racks caused total loss of shoots directly under racks and reduced shoot densities up to 4 m away from racks within 14 mo of placement. We found that location of oyster racks in 2000 was not associated with eelgrass loss between 1987 and 2000 (Table 3), despite the considerable increase in the number oyster racks (57 to 484) over the 13-yr period. Effects may have been too subtle to

detect at our map resolution (0.04 ha pixels versus a mean of 0.03 ha; range = 0.002 to 0.175 ha for a typical 1 m-wide oyster rack), especially since we only measured presence-absence, not degradation (i.e., change from continuous to patchy beds), of eelgrass in submerged areas. The potential deleterious effects of oysters on eelgrass (e.g., shading) may also have been diminished in Bahía San Quintín by the ability of oysters to improve water clarity by filtering sediments from the water column (Osorno-Velazquez 2000), so we remain uncertain of the impacts of oyster farming on eelgrass in the bay.

Although much of the decline in eelgrass detected over the 13-yr period could be attributed to sediment loading during one flooding event, the bay-wide decrease in seagrass extent and density (i.e., continuous beds converting to patchy beds) suggests that other factors are contributing to the observed reductions in eelgrass cover. To understand the relative importance of the factors that influence eelgrass distribution, we suggest using higher resolution mapping techniques and ground-based studies to assess eelgrass abundance, productivity, and survival with respect to various interacting levels of water quality criteria (e.g., light attenuation coefficients, chlorophyll, dissolved nitrogen and phosphorus) and interactions with macroalgae. Numerical models could then be used to explore interactions between environmental factors and eelgrass communities in Bahía San Quintín to provide a better understanding of the dynamics of spatial distribution and health of eelgrass meadows in this system.

ACKNOWLEDGMENTS

This study was funded by Ducks Unlimited de Mexico, Institute of Wetland and Waterfowl Research of Duck Unlimited Inc., Alaska Science Center of U. S. Geological Survey, and the U. S. Fish and Wildlife Service through the North American Wetlands Conservation Act. We are grateful to Bruce Batt, Douglas Ryan, and Dirk Derksen for their support of the project. Matthew Anderson, Adrian Gall, Tyler Lewis, Danielle Mather, Ryan Mathis, Dina Roberts, and Marnie Shepherd assisted with collection of reference data. Roxie Anderson and Carl Markon assisted with image processing, and Alan Brelsford and John Terenzi helped produce the figures. Aerial photographs were acquired by Jim Bredy and Al Cilurso of U. S. Fish and Wildlife Service-Region 2. We thank Alejandro Cabello-Pasini, staff of San Diego National Wildlife Refuge, Richard and Dorothy Wheeler, and James White for providing logistical support and assistance. The manuscript was improved by comments from Victor Camacho-Ibar, Alejandro Cabello-Pasini, Dirk Derksen, Jason Hale, and an anonymous reviewer.

LITERATURE CITED

- AGUIRRE-MUÑOZ, A., R. W. BUDDEMEIER, V. CAMACHO-IBAR, J. D. CARRIQUIRY, S. E. IBARRA-OBANDO, B. W. MASSEY, S. V. SMITH, AND F. WUFF. 2001. Sustainability of coastal resource use in San Quintin Bay, Mexico. *Ambio* 30:42–149.
- BACKMAN, T. W. AND D. C. BARILOTTI. 1976. Irradiance reduc-

- tion: Effects on standing crops of the eelgrass *Zostera marina* in a coastal lagoon. *Marine Biology* 34:33–40.
- BAKUN, A. AND C. S. NELSON. 1977. Climatology of upwelling related processes off Baja California. *California Cooperative Fisheries Report* 19:107–127.
- BARNARD, J. L. 1962. Benthic marine exploration of Bahía San Quintín, Baja California. *Pacific Naturalist* 3:251–274.
- CABELLO-PASINI, A., R. MUÑOZ-SALAZAR, AND D. H. WARD. 2003. Annual variations of biomass and photosynthesis in *Zostera marina* at its southern end of distribution in the north Pacific. *Aquatic Botany* 1633:1–17.
- CABELLO-PASINI, A., R. MUÑOZ-SALAZAR, AND D. H. WARD. 2004. Biochemical characterization of *Zostera marina* at its southern end of distribution in the north Pacific. *Ciencias Marinas* in press.
- CAMACHO-IBAR, V. F., J. D. CARRIQUIRY, AND S. V. SMITH. 2003. Non-conservative P and N fluxes and net ecosystem production in San Quintín Bay, México. *Estuaries* 26:1220–1237.
- CONANT, B. AND J. F. VOELZER. 2002. Winter waterfowl survey: Mexico west coast and Baja California. Annual Report. U.S. Fish and Wildlife Service, Anchorage, Alaska.
- CONGALTON, R. G. 1991. A review of assessing the accuracy of classifications of remotely sensed data. *Remote Sensing Environment* 37:35–46.
- DAWSON, E. Y. 1962. Marine and marsh vegetation of Bahía San Quintín, Baja California. *Pacific Naturalist* 3:275–280.
- DENNISON, W. C. 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquatic Botany* 27:15–26.
- 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: Habitat requirements as barometers of Chesapeake Bay health. *Bio Science* 43:86–94.
- DOBSON, J. E., E. A. BRIGHT, R. L. FERGUSON, D. W. FIELD, L. L. WOOD, K. D. HADDAD, H. IREDALE, J. R. JENSEN, V. V. KLEMAS, R. J. ORTH, AND J. P. THOMAS. 1995. NOAA coastal change analysis program (C-CAP): Guidance for regional implementation. National Oceanic and Atmospheric Administration Technical Report 123. U.S. Department of Commerce, Seattle, Washington.
- EVERETT, R. A., G. M. RUIZ, AND J. T. CARLETON. 1995. Effect of oyster mariculture on submerged aquatic vegetation: An experimental test in a Pacific northwest estuary. *Marine Ecology Progress Series* 125:205–221.
- FERGUSON, R. L. AND K. KORFMACHER. 1997. Remote sensing and GIS analysis of seagrass meadows in North Carolina, USA. *Aquatic Botany* 58:241–258.
- FERGUSON, R. L., L. L. WOOD, AND D. B. GRAHAM. 1993. Monitoring spatial change in seagrass habitat with aerial photography. *Photogrammetric Engineering and Remote Sensing* 59:1033–1036.
- FONSECA, M. S. AND J. S. FISHER. 1986. A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. *Marine Ecology Progress Series* 29:15–22.
- FONSECA, M. S. AND W. J. KENWORTHY. 1987. Effects of current on photosynthesis and distribution of seagrasses. *Aquatic Botany* 27:59–78.
- FORTES, M. D. 1988. Mangrove and seagrass beds of East Asia: Habitats under stress. *Ambio* 17:207–213.
- HARDING, L. W. AND J. H. BUTLER. 1979. The standing stock and production of eelgrass, *Zostera marina*, in Humboldt Bay, California. *California Fish and Game* 65:151–158.
- HECK, K. L. AND J. F. VALENTINE. 1995. Sea urchin herbivory: Evidence for long-lasting effects in subtropical seagrass meadows. *Journal of Experimental Marine Biology* 189:205–217.
- IBARRA-OBANDO, S. E., V. F. CAMACHO-IBAR, J. D. CARRIQUIRY, AND S. V. SMITH. 2001. Upwelling and lagoonal ecosystems of the dry Pacific coast of Baja California, p. 315–329. In U. Seeliger and B. Kjerfve (eds.), Coastal Marine Ecosystems of Latin America. Springer-Verlag, Berlin, Germany.
- IBARRA-OBANDO, S. E. AND A. ESCOFET. 1987. Industrial development effects on the ecology of a Pacific Mexican estuary. *Environmental Conservation* 14:135–141.
- IBARRA-OBANDO, S. E., M. POUMIAN-TAPIA, A. E. MELING-LÓPEZ, AND J. GÓMEZ-VALDÉZ. 2002. Climatic variables and their effects on the aboveground structure of *Zostera marina* in Bahía San Quintín, p. 11. In A. Cabello-Pasini and Z. García-Esquivel (eds.), Proceedings of the 2002 Meeting on Bahía San Quintín. University of Baja California, Ensenada, Baja California, Mexico.
- KRAMER, G. W. 1976. Winter ecology of black brant at San Quintín Bay, Baja California, Mexico. M.S. Thesis, Humboldt State University, Arcata, California.
- LARKUM, A. W. D. AND R. J. WEST. 1990. Long-term changes of seagrass meadows in Botany Bay, Australia. *Aquatic Botany* 37:55–70.
- LEE, K. AND K. H. DUNTON. 1997. Effects of in situ light reduction on the maintenance, growth and partitioning of carbon resources in *Thalassia testudinum* Banks ex König. *Journal of Experimental Marine Biology and Ecology* 210:53–73.
- LEE, V. AND S. OLSEN. 1985. Eutrophication and management initiatives for the control of nutrient inputs to Rhode Island coastal lagoons. *Estuaries* 8:191–202.
- LILLESAND, T. AND R. KIEFFER. 2000. Remote Sensing and Image Interpretation, 4th edition. John Wiley and Sons, New York.
- LONGSTAFF, B. J. AND W. C. DENNISON. 1999. Seagrass survival during pulsed turbidity events: The effects of light deprivation on the seagrasses *Halodule pinifolia* and *Halophila ovalis*. *Aquatic Botany* 65:105–121.
- MASSEY, B. W. AND E. PALACIOS. 1994. Avifauna of the wetlands of Baja California, Mexico: Current status. *Studies Avian Biology* 15:45–57.
- MELING-LÓPEZ, A. E. AND S. E. IBARRA-OBANDO. 1999. Annual life cycles of two *Zostera marina* L. populations in the Gulf of California: Contrasts in seasonality and reproductive effort. *Aquatic Botany* 65:59–69.
- MUMBY, P. J., E. P. GREEN, A. J. EDWARDS, AND C. D. CLARK. 1997. Measurement of seagrass standing crop using satellite and digital airborne remote sensing. *Marine Ecology Progress Series* 159:51–60.
- ORTH, R. J. AND K. A. MOORE. 1983. Chesapeake Bay: An unprecedented decline in submerged aquatic vegetation. *Science* 22:51–52.
- OSORNO-VELAZQUEZ, A. 2000. Impacts of cultivated filter feeding molluscs in phytoplankton and quality of water in Bahía San Quintín. M.S. Thesis, Center for Scientific Investigation and Higher Education-Ensenada, Baja California, Mexico.
- PAGE, G. W., E. PALACIOS, L. ALFARO, S. GONZALÉZ, L. STENZEL, AND M. JUNGERS. 1997. Numbers of wintering shorebirds in coastal wetlands of Baja California, Mexico. *Journal of Field Ornithology* 68:562–574.
- PALACIOS, C. M. C. E. 2000. Inventory of coastal wetlands of Baja California. Technical report. Pro Esteros, Inc., Ensenada, Mexico.
- PEREZ-ARTEAGA, A., K. J. GASTON, AND M. KERSHAW. 2002. Undesignated sites in Mexico qualifying as wetlands of international importance. *Biological Conservation* 107:47–57.
- 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.
- PREN, A. R., W. J. LEE LONG, AND R. G. COLES. 1995. Flood and cyclone related loss, and partial recovery of more than 1000 km² of seagrass in Hervey Bay, Queensland, Australia. *Aquatic Botany* 52:3–17.
- POUMIAN-TAPIA, M. AND S. E. IBARRA-OBANDO. 1999. Demography and biomass of the seagrass *Zostera marina* in a Mexican coastal lagoon. *Estuaries* 22:879–889.

- REED, A., D. H. WARD, D. V. DERKSEN, AND J. S. SEDINGER. 1998. Brant (*Branta bernicla*). In A. Poole and F. Gill (eds.), *The Birds of North America*, No. 337. The Birds of North America, Inc., Philadelphia, Pennsylvania.
- ROSALES-CASIAN, J. A. 1996. Fish of Bahía de San Quintín, Baja California, México, and adjacent coastal areas. *Ciencias Marinas* 22:443–458.
- ROSALES-CASIAN, J. A. 1997. Inshore fishes of two coastal lagoons from the northern Pacific coast of Baja California. *CalCOFI Report* 38:180–192.
- SCHAMBER, J. L. 2001. Cross-seasonal effects on reproductive performance of Pacific black brant. Master's Thesis, University of Alaska-Fairbanks, Fairbanks, Alaska.
- SCHUMM, S. A. AND R. F. HADLEY. 1963. Progress in the application of landform analysis in studies of semi-arid erosion. U.S. Geological Survey Circular 437. U.S. Geological Survey, Anchorage Alaska.
- SHORT, F. T. 1987. Effects of sediment nutrients on seagrasses: Literature review and mesocosm experiment. *Aquatic Botany* 27:41–57.
- SHORT, F. T. AND D. M. BURDICK. 1996. Quantifying eelgrass habitat loss in relation to housing development and nitrogen loading in Waquoit Bay, Massachusetts. *Estuaries* 19:730–739.
- SHORT, F. T., B. W. IBEINGS, AND C. DEN HARTOG. 1988. Comparison of a current eelgrass disease to the wasting disease in the 1930s. *Aquatic Botany* 30:295–304.
- 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. A review of natural and human-induced disturbance of seagrasses worldwide. *Environmental Conservation* 23:17–27.
- SWAIN, P. H. AND S. M. DAVIS. 1978. Remote Sensing: The Quantitative Approach. McGraw-Hill, Inc., New York.
- THAYER, G. W. 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.
- TROST, R. E. AND M. S. DRUT. 2001. 2001 Pacific flyway data book: Waterfowl harvests and status. Annual Report. U.S. Fish and Wildlife Service, Portland, Oregon.
- WADDELL, J. E. 1964. The effect of oyster culture on eelgrass (*Zostera marina* L.) growth. M.S. Thesis, Humboldt State College, Arcata, California.
- WARD, D. H. 1997. International cooperative research to improve management of Pacific black brant. *Arctic Research of the United States* 12:25–27.
- WARD, D. H., C. J. MARKON, AND D. C. DOUGLAS. 1997a. Distribution and stability of eelgrass beds at Izembek Lagoon, Alaska. *Aquatic Botany* 58:229–240.
- WARD, D. H., E. A. REXSTAD, J. S. SEDINGER, M. S. LINDBERG, AND N. K. DAWE. 1997b. Seasonal and annual survival of adult Pacific brant. *Journal of Wildlife Management* 61:773–781.
- WARD, D. H., T. L. TIBBITTS, A. MORTON, E. CARRERA-GONZÁLES, AND R. KEMPKA. 2004. Use of digital multispectral videography to assess seagrass distribution in Bahía San Quintín, Baja California, Mexico. *Ciencias Marinas* in press.
- WIGGINS, I. L. 1980. Flora of Baja California. Stanford University Press, Stanford, California.
- WILSON, U. W. AND J. B. ATKINSON. 1995. Black Brant winter and spring-staging use at two Washington coastal areas in relation to eelgrass abundance. *Condor* 97:91–98.
- ZIEMAN, J. C. 1982. The ecology of the seagrasses of south Florida: A community profile. FWS/OBS-82. U.S. Fish and Wildlife Service, Washington, D.C.
- ZIMMERMAN, R. C., J. L. REGUZZONI, AND R. S. ALBERTE. 1995. Eelgrass (*Zostera marina* L.) transplants in San Francisco Bay: Role of light availability on metabolism, growth, and survival. *Aquatic Botany* 52:67–86.

SOURCES OF UNPUBLISHED MATERIALS

- CHESTNUT, J. Unpublished Data. 531 Highland Drive, Los Osos, California 93402
- HOFFMAN, R. Unpublished Data. National Marine Fisheries Service-Southwest Office, 501 West Ocean Boulevard, Long Beach, California 90802-4213
- MCBRIDE, S., J. MELLO, N. KALSON, V. FREY, J. ROBINSON, AND G. TENNANT. Unpublished Report. Humboldt Bay eelgrass survey: Seasonal plant metrics and aboveground biomass of *Zostera marina*, California Department of Fish and Game, Eureka, California.
- RUMRIL, S. Personal Communication. South Slough National Estuarine Reserve, P. O. Box 5417, Charleston, Oregon 97420
- SMITH, B. Unpublished Data. P. O. Box 54, Valle de San Quintin, San Quintin, Baja California, Mexico.

Received for consideration, September 24, 2002

Revised, April 3, 2003

Accepted for publication, May 13, 2003