



## **Eelgrass Meadows Return to Frenchy's Cove, Anacapa Island: Recovery Ten Years after Successful Transplantation**

Authors: Altstatt, Jessica, Ambrose, Richard, Carroll, Jay, Coyer, James, Wible, Joseph, et al.

Source: Monographs of the Western North American Naturalist, 7(1) : 500-517

Published By: Monte L. Bean Life Science Museum, Brigham Young University

URL: <https://doi.org/10.3398/042.007.0139>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

## EELGRASS MEADOWS RETURN TO FRENCHY'S COVE, ANACAPA ISLAND: RECOVERY TEN YEARS AFTER SUCCESSFUL TRANSPLANTATION

Jessica Altstatt<sup>1</sup>, Richard Ambrose<sup>2</sup>, Jay Carroll<sup>3</sup>,  
James Coyer<sup>4</sup>, Joseph Wible<sup>5</sup>, and John Engle<sup>6</sup>

**ABSTRACT.**—A large eelgrass (*Zostera pacifica*) meadow was present at Frenchy's Cove, Anacapa Island, prior to the late 1980s. Extensive grazing by white sea urchins (*Lytechinus anamesus*) in the late 1980s eliminated the meadow by 1991, when a 60-m transect (10-m depth) was established; no natural recovery was observed from 1991 to 2002. In 2002, approximately 450 eelgrass shoots were transplanted to Frenchy's Cove from 2 large meadows at Santa Cruz Island (Smugglers Cove, Prisoners Harbor), and a second transect (7-m depth) was established in 2004. Shoot planting densities ranged from 0.11 m<sup>-2</sup> to 11 m<sup>-2</sup>. Meadow dimensions, shoot density and reproductive status, along with density and species abundance of associated benthic invertebrates and fishes were surveyed annually along each transect from 2003 to 2012. Densities of white urchins remained low, thereby facilitating expansion of the meadow via vegetative growth and seedling recruitment. Individual patches eventually coalesced into an overall meadow at Frenchy's Cove of 0.87 ha in 2009, retracting slightly to 0.62 ha in 2012. Shoot density reached a mean of 108 m<sup>-2</sup> in 2009 and ranged from 23 m<sup>-2</sup> to 90 m<sup>-2</sup> in 2012, comparable to natural meadows at nearby Santa Cruz Island. Increased diversity and abundance of invertebrates and fishes were evident, with an average of 5 (2001), 9 (2005), and 14 (2011) fish species recorded during 30-minute surveys and a dramatic shift in fish guilds, with black perch, pile perch, and half-moon only associated with the new meadow. As a result of the initial 2002 eelgrass transplantation, eelgrass meadows returned to northern Anacapa Island; and by 2012, they expanded along nearly 3 km of nearshore sandy habitat. A diverse biotic assemblage is becoming reestablished at Frenchy's Cove and adjacent shallow sandy substrates along the north side of Middle Anacapa Island.

**RESUMEN.**—Antes de finales de la década de 1980, existía un extenso campo de zosteras marinas (*Zostera pacifica*) en Frenchy's Cove (Cala Frenchy en Isla Anacapa). Hacia finales de los ochentas, comenzó una explotación extensiva del erizo de mar blanco (*Lytechinus anamesus*) que ya en 1991 había eliminado ese campo de zosteras, a la vez que se consolidó un transecto de 60 metros (10 metros de profundidad); sin observar recuperación natural desde 1991 hasta el año 2002. En el año 2002, se trasplantaron ~450 brotes de zosteras en Frenchy's Cove procedentes de dos prados extensos de la Isla de Santa Cruz (Smugglers Cove, Prisoners Harbor) y en el año 2004 se consolidó un segundo transecto (de 7 metros de profundidad). La densidad de los brotes plantados variaba desde 0.11 a 11 m<sup>-2</sup>. Desde el año 2003 hasta el 2012, las dimensiones de la superficie del campo, la densidad de los brotes y el estado reproductivo, así como la densidad y abundancia de especies de invertebrados y peces bentónicos asociados se midieron anualmente a lo largo de cada transecto. Las densidades de los erizos de mar blancos continuaron siendo bajas y, por lo tanto, facilitaron la expansión del campo de zosteras a través de crecimiento vegetativo y recolección de semillas. Algunos parches sueltos se fusionaron en un campo globalizado en Frenchy's Cove llegando a 0.87 hectáreas en el 2009, retrayéndose ligeramente hasta 0.62 hectáreas en 2012. La densidad de los brotes alcanzó un promedio de 108 m<sup>-2</sup> en 2009, y varió entre 23 y 90 m<sup>-2</sup> en 2012, medidas comparables a las de los campos naturales de zosteras en la cercana isla de Santa Cruz. Fue evidente el aumento de la diversidad y abundancia de invertebrados y peces, registrándose promedio de especies de peces de 5 (2001), 9 (2005) y 14 (2011) cada 30 minutos de medición; y un cambio radical en los agrupamientos de percas negras, percas piles y percas de medialuna californianas sólo asociadas a las nuevas plantaciones. Como resultado del trasplante inicial de zosteras en el 2002, los campos de zosteras habían regresado al norte de Isla Anacapa, y para el año 2012, se habían extendido a lo largo de casi 3 kilómetros del hábitat arenoso cercano. Un ensamble biótico diverso se está re-estableciendo en Frenchy's Cove, así como substratos arenosos superficiales adyacentes a lo largo del lado norte de la Isla Media Anacapa.

<sup>1</sup>102 Orange Ave, Goleta, CA 93117. E-mail: jessie.altstatt@gmail.com

<sup>2</sup>Department of Environmental Health Sciences, Box 951772, Rm 46-078 CHS, University of California, Los Angeles, CA 90095-1772.

<sup>3</sup>Tenera Environmental, 141 Suburban Rd., Suite A2, San Luis Obispo, CA 93401.

<sup>4</sup>Shoals Marine Laboratory, Cornell University, 400 Little Harbor Rd., Portsmouth, NH 03801.

<sup>5</sup>Hopkins Marine Station of Stanford University, Pacific Grove, CA 93950-3094.

<sup>6</sup>Marine Science Institute, University of California, Santa Barbara, CA 93106-6150.

Seagrass meadows form important coastal habitats by supporting complex food webs (Hemminga et al. 1994, Valentine and Heck 2005, Heck et al. 2008), filtering nutrients (McGlathery et al. 2012), fixing carbon (Fourqurean et al. 2012) and nitrogen (Cole and McGlathery 2012, McGlathery et al. 2012), transporting metals (Kaldy 2006), and stabilizing sediments (den Hartog 1970, Fonseca et al. 1990, but see Lawson et al. 2012). Furthermore, diversity of invertebrates and fishes in eelgrass (*Zostera* spp.) meadows can be much higher than in nearby sandy intertidal and subtidal habitats (Orth et al. 1984, Engle et al. 1995, Duffy 2006, Reed and Hovel 2006, Fredriksen et al. 2010). In California, for example, eelgrass meadows function as nurseries for many fish species with recreational and commercial importance, including rockfishes (*Sebastes* spp.), surfperches (Embiotocidae), and kelp bass (*Paralabrax clathratus*; Hoffman 1986, Engle et al. 1998).

Seagrass populations have declined worldwide, primarily because of human activities that alter the habitat (eutrophication and land use affecting water quality; Orth and McGlathery 2012, Schmidt et al. 2012), as well as from natural causes such as urchin grazing (Keller 1983, Valentine and Heck 1991, Short and Wyllie-Echeverria 1996). The rate of decline has increased over the past 8 decades (Orth et al. 2006, Waycott et al. 2009).

The dramatic loss of seagrass along the east coast of North America sparked enough concern that large-scale programs have been developed to evaluate and refine protocols for restoration within the Chesapeake Bay region, one of the world's largest estuaries (Shafer and Bergstrom 2010), and the coastal bays of Virginia (Orth and McGlathery 2012), among others. In southern California, eelgrass has been severely impacted by increased turbidity, dredging, construction, and pollution of shallow bays and coastal lagoons (Merkel 1991, Williams 2001). Environmental legislation (e.g., the 1972 Clean Water Act) requires mitigation for any construction project that might impair eelgrass meadows and wetland habitat, and eelgrass mitigation policies have required enhancement or restoration of meadows at ratios of 1.2 to 1 or greater (National Marine Fisheries Service 2011).

Since 1989, there have been 43 eelgrass transplant projects in southern California

(National Marine Fisheries Service 2011), virtually all as mitigation for coastal development. Unfortunately, human activities negatively impacting the original eelgrass meadow/habitat also negatively impact the transplanted or restored meadows; consequently, only 10%–60% of transplantation efforts are successful (Goforth and Peeling 1978, National Marine Fisheries Service 1997, Orth and McGlathery 2012). Moreover, there have been no restoration efforts conducted in relatively pristine waters; all work has been associated with human-impacted coastal areas (Short and Wyllie-Echeverria 1996). However, in situations where eelgrass was eliminated and the mechanism of loss is known and abated, eelgrass recovery can occur with a higher probability of success (Thom et al. 2005).

In addition to large populations in tidal estuaries such as Humboldt, San Francisco, and San Diego Bays, there are also subtidal eelgrass meadows along the California coast and offshore California Channel Islands (Engle et al. 1998, Engle and Miller 2005). Compared to eelgrass meadows along the mainland coast, meadows at the mostly uninhabited Channel Islands are minimally impacted by humans; these impacts are restricted to anchoring and mooring activities associated with recreational boating which utilize sheltered coves harboring extensive meadows. Equally important are seasonal storms and/or heavy surf, which remove biomass, increase sedimentation and burial, and limit the upper depth range of subtidal meadows.

Eelgrass (*Zostera pacifica* and *Zostera marina*) occurs at approximately 40 locations around 6 of the 8 Channel Islands, with the largest meadows on Santa Cruz Island (Engle and Miller 2005). Substantial *Z. pacifica* meadows were present from 1980 to 1982 in 7–12-m depth along the north side of West and Middle Anacapa Islands, with scattered patches at East Anacapa Island (Engle et al. 1998, Engle and Miller 2005). Subtidal surveys in 1991 revealed the absence of a formerly present meadow at Frenchy's Cove (West Anacapa Island) and high densities of white urchins (*Lytechinus anamesus*). In 1995, only 2 small eelgrass patches were present at Cathedral Cove, East Anacapa Island; subsequently, one disappeared in 1998 and the other in 1999. Local extinction of *Z. pacifica* meadows from Anacapa Island by 1999 was most likely due

to overgrazing by white urchins following an extraordinary post-El Niño recruitment event in the 1980s (Engle et al. 1995).

Annual surveys from 1991 to 2001 at Frenchy's Cove revealed no eelgrass seedlings, adult plants, or drift material. Although the density of white urchins gradually declined during this period ( $60 \text{ m}^{-2}$  in 1992 to  $0.4 \text{ m}^{-2}$  in 2000), eelgrass remained absent. Long-distance dispersal of eelgrass can occur via drifting spathes and/or reattachment of dislodged rhizomes (Reusch 2002, Rhode and Duffy 2004, Coyer et al. 2008), but neither mechanism was likely for Frenchy's Cove because the nearest meadow (Smugglers Cove, Santa Cruz Island) was  $>12 \text{ km}$  distant and separated by deep water ( $>75 \text{ m}$ ) and strong currents.

In 2002, we transplanted approximately 450 *Z. pacifica* shoots from 2 meadows on Santa Cruz Island to Frenchy's Cove as described in Altstatt (2005). Initial losses were high, but after 2 years the surviving shoots began to expand. In this study, we report spatial and temporal dynamics of the transplanted meadow, track the spread of eelgrass along the north side of Anacapa Island, compare shoot density with 3 reference meadows at Santa Cruz Island, and describe changes in fish species composition and densities at Frenchy's Cove.

## METHODS

### Site Description

Anacapa Island (ca. 32 km south of Ventura, California), the easternmost and smallest of the 4 northern California Channel Islands, is comprised of 3 small islets. Frenchy's Cove ( $34^{\circ}00.595' \text{ N}$ ,  $119^{\circ}24.690' \text{ W}$ ) is a small cove at the junction of Middle and West Anacapa islets (Fig. 1), with moderate protection from prevailing wind and swell. The formerly present eelgrass meadows occurred on sandy substrates  $>6 \text{ m}$  depth; shallower substrates were too coarse and unsuitable (gravel, rock, and shell hash). The study site borders a brown pelican nesting area that is seasonally closed to boaters and is within the Anacapa State Marine Conservation Area created in 2003.

### Monitoring

The Channel Island Research Program established a permanent 60-m transect in Frenchy's Cove in 1991, parallel to shore at

the 10-m contour and in the middle of the historic meadow. The site was surveyed yearly between May and July for the density and percent cover of seagrass, kelps, and macroinvertebrate species using band transects (6 bands,  $1 \text{ m} \times 20 \text{ m}$ ) and quadrats ( $0.25 \text{ m}^2$ , placed every other meter along the fixed transect). In 2005, a 30-m transect (7-m depth) was established upslope from and parallel to the existing transect and was sampled in the same manner. This transect was located at the depth of the original shallow edge of the historic meadow and is the focus of this paper.

### Harvesting Donor Meadows

Details on the eelgrass transplantation methods can be found in Altstatt (2005). In brief, both harvesting and transplanting work occurred on 2 July 2002. Single shoots were harvested by divers from 3 locations (shallow edge, middle of meadow, and deep edge) within large meadows at Smugglers Cove and Prisoners Harbor near the east end of nearby Santa Cruz Island (Fig. 1). These meadows were selected based on their proximity to Anacapa Island and their large size. The donor meadows differed in genetic makeup, exposure, and depth range (see discussion in Engle et al. 1998, Engle and Miller 2005, Coyer et al. 2008). Analysis of water quality or sediment was outside the scope of this study. Divers swam along haphazardly placed transects of up to 100 m in length and moved at least 1–3 m between harvesting individual shoots. Plants were held for a period of several hours in sea water aboard ship during transport to Anacapa Island and were replanted the same day.

### Planting

We adapted the "bare shoot" transplant technique developed by Orth et al. 1999. An estimated 450 eelgrass shoots were transplanted into an area of approximately  $300 \text{ m}^2$  and into 3 different depths: deep (10-m depth), shallow (7-m depth), and swath ( $\sim 50 \text{ m}$  in length, running perpendicular to shore from 6- to 13-m depth). We thereby covered a representative area and depth range of the historic meadow. Along the swath, shoots were spaced 1 m apart for a density of 1.1 shoots  $\text{m}^{-2}$ . In the shallow and deep patch areas, shoots were spaced at 30 cm for a density of 11 shoots  $\text{m}^{-2}$ . The shallow and deep patches

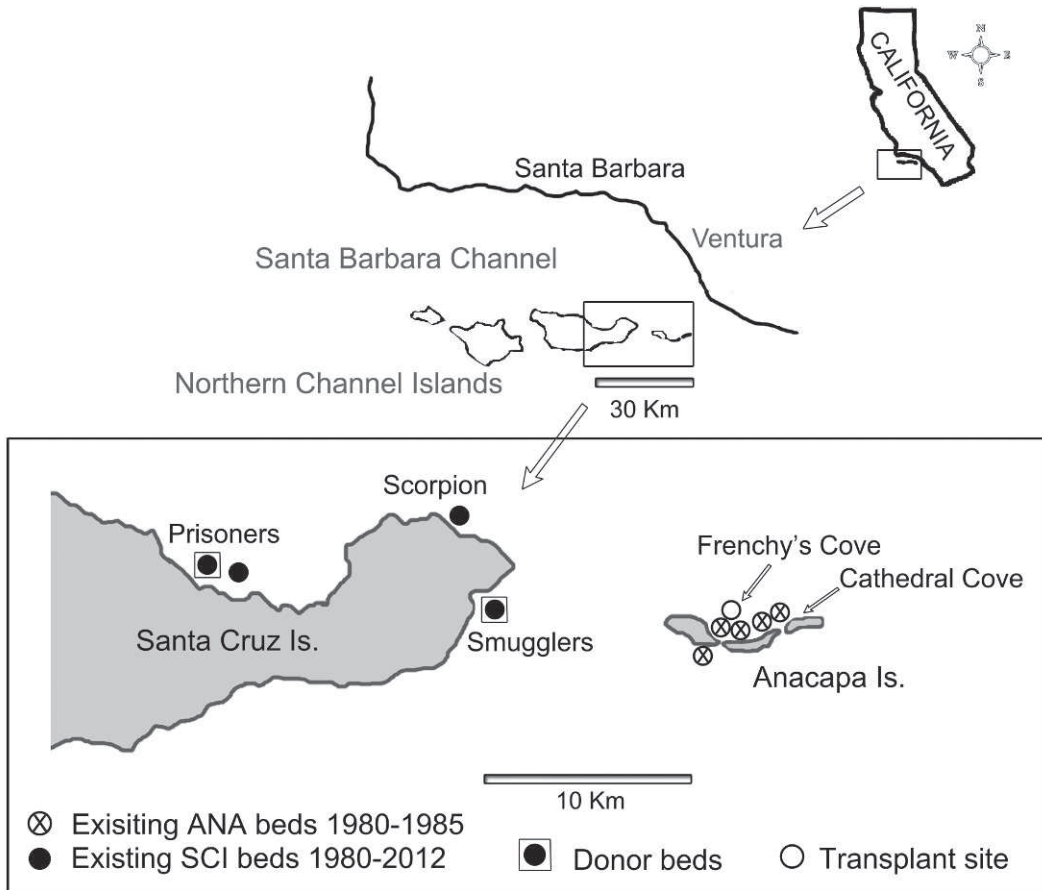


Fig. 1. Location of study sites: (solid circle) large and persistent eelgrass (*Zostera pacifica*) beds on Santa Cruz Island; (solid circle within a box) the 2 donor beds at Prisoners Harbor and Smugglers Cove; (X) historic bed locations along northern Anacapa Island; (open circle) the transplant site at Frenchy's Cove.

received 100 shoots each and the swath received approximately 250. Shoots were not labeled according to source and were randomly selected by divers when planted. Additional details can be found in Altstatt (2005).

#### Shoot Density

Divers counted all individual shoots from 2002 to 2004 (initial sampling interval ranged from weeks to months) until the number of shoots increased to a level precluding individual counting. From 2005 to 2012, we counted individual shoots within fifteen 0.25-m<sup>2</sup> quadrats placed every other meter along the fixed shallow transect. Counts were extrapolated to shoots per m<sup>2</sup>. An analysis of variance (one-way ANOVA) was conducted to test for significant differences in shoot densities

between sampling dates (years). From 2006 to 2012, divers measured the extent of eelgrass along the shallow transect out to 10 m perpendicular to the transect at regular intervals both inshore and offshore, thus mapping an area of 600 m<sup>2</sup> (20 m × 30 m).

Divers also made observations on eelgrass outside of this immediate area. The fixed 30-m shallow transect line was scored yearly for proportion of eelgrass, sand, and worm tubes (*Chaetopterus* sp.). In 2005, 2008, 2009, and 2012, shoot density was determined from haphazardly placed quadrats within the middle of the meadow in 8-m water depth, in addition to along the fixed 7-m-depth transect. In 2009 and 2012, divers mapped the extent of the entire eelgrass meadow by swimming along the edge of the densest eelgrass observed

TABLE 1. Diver reconnaissance surveys from 1980 to 2012 for eelgrass (*Zostera pacifica*) in 6 different areas at Anacapa Island, California. An asterisk (\*) denotes no survey. Shoots = <10 individual shoots, Patches = 1–3 m<sup>2</sup> (10–100 shoots); Ana = Anacapa. Bold face type denotes the date of transplant.

Dive date	Frenchy's Cove West Ana	East Frenchy's W. Middle Ana	Mid Middle Ana	E. Middle Ana	NW end East Ana	Cathedral Cove mid East Ana
Oct 1980	meadow	*	meadow	*	meadow	*
Jun 1981	*	meadow	*	*	*	patches
Mar 1982	*	*	meadow	*	*	*
Jun 1982	meadow	*	*	*	*	*
June 1985	*	*	*	*	*	patches
Jul 1991	none	*	*	*	*	*
Jun 1992	none	*	*	*	*	*
Jul 1993	none	*	*	*	none	none
Jul 1994	none	*	*	*	*	*
Jun 1995	*	*	*	none	*	*
Aug 1995	none	*	*	*	*	*
Dec 1995	*	*	*	*	*	2 patches
Jun 1996	none	*	*	*	*	1 patch
Jul 1997	none	*	*	*	*	1 patch
Jun 1998	none	*	*	*	*	1 patch
Jul 1999	none	*	*	*	*	none
Jun 2000	none	*	*	*	*	none
Jul 2001	none	*	*	*	*	none
<b>Jul 2002</b>	<b>transplant</b>	*	*	*	*	*
Jun 2003	shoots	*	*	*	*	*
Jun 2004	shoots	shoots	none	none	*	*
Jun 2005	patches	patches	*	none	*	*
Jun 2006	patches	patches	*	*	*	*
Jun 2007	meadow	patches	shoots	*	*	none
Jun 2008	meadow	meadow	*	*	*	*
Jun 2009	meadow	meadow	*	*	*	*
Jun 2010	meadow	meadow	*	*	*	*
Jul 2011	meadow	meadow	patches	patches	*	none
Jun 2012	meadow	meadow	*	patches	shoots	*

within Frenchy's Cove while towing a GPS unit on a surface float; the resulting track polygon shape was then converted to hectares. We compared changes in shoot density at Frenchy's Cove with the 3 largest natural meadows at Santa Cruz Island—Prisoners Harbor (3–9-m depth), Scorpion Anchorage (5–8-m depth), and Smugglers Cove (9–16-m depth). Individual shoots were counted in 0.25-m<sup>2</sup> quadrats established every other meter along haphazardly placed 30-m transects throughout the meadows in October 2001, 2005, 2008 and 2009.

#### Reconnaissance Surveys

Diver surveys for the presence of eelgrass focused on 4 locations along northern Anacapa Island where eelgrass was documented in 1980–1981 prior to the period of high white urchin abundance in nearshore habitats: 0.5 km east of Frenchy's Cove, North–Middle Anacapa Island, Northwest–East Anacapa Island, and Cathedral Cove. Reconnaissance

surveys occurred yearly during the summer, from 1981 to 2012. Teams of divers scouted in different directions at each location. If eelgrass was present, then the shoot count or patch size, inshore and offshore depth range, and the lateral extent along the shoreline were recorded. On the surface, a GPS position was determined at diver-deployed floats marking the patches, although there were often scattered shoots beyond these points. In some instances when there was not a definable meadow, a position was taken on the middle of the scattered shoots and divers noted patch size, shoot count, and condition.

#### Roving Diver Fish Counts

We conducted 30-min roving diver fish counts (CINP Kelp Forest Monitoring Program 1997) to determine indices of species presence, abundance, and diversity. Fish species were scored both on (1) the 5-min time intervals during which they were encountered and (2) abundances recorded during the overall 30-min

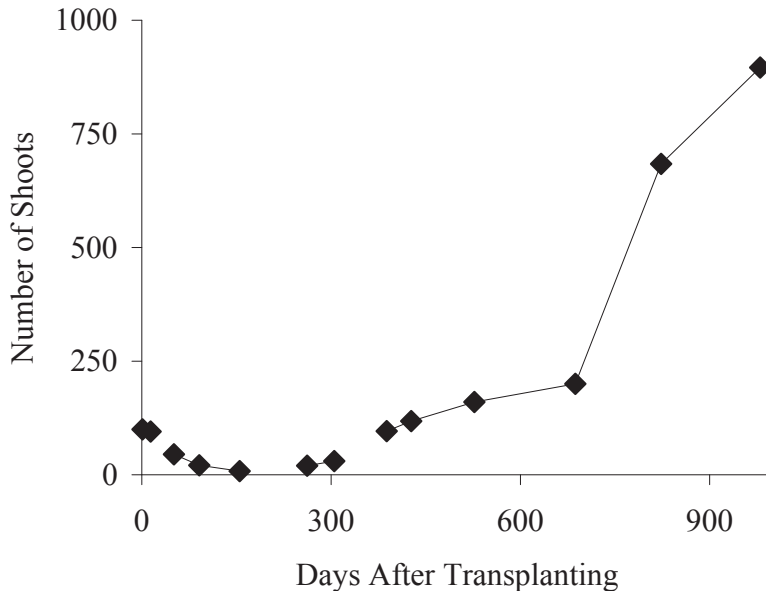


Fig. 2. Total number of observed eelgrass (*Zostera pacifica*) shoots in shallow transplant area at Frenchy's Cove, Anacapa Island, California, from July 2002 to April 2005.

survey. Abundances during the survey were described using the following 4 categories: single (1), few (2–10), common (11–100), and many (>100). Divers remained within a set depth range, geographical area, or habitat type (eelgrass or sand plain). In 2012, we conducted additional fish counts over sandy plains at Cathedral Cove. For analysis, we created a weighted abundance index that combined the “Time Interval Code” and “Abundance Code” (if a species was not tallied, the Abundance Code was 0). The index was  $(TIC/10) \cdot AC$ . This formula gives more weight to fish seen earlier in the 30-min count; so for example, a species with an overall abundance of “common” (3) seen in the second time interval (9) would have a weighted index of 2.7.

#### White Urchin Density

From 2005 to 2012, we measured white urchin density within fifteen 0.25-m<sup>2</sup> quadrats placed along the shallow transect. We searched the sediment, eelgrass, and drift material in order to capture cryptic urchins or recent recruits.

## RESULTS

A total of 182 person-dives were made at Frenchy's Cove and along the north side of Anacapa Island for eelgrass surveys and

reconnaissance between the years 2002 and 2012 (Table 1). In summary, 97% of shoots were lost within the first 6 months, but survivors expanded so that by 1.5 years, shoots in the shallow plot more than doubled from the original planting (Fig. 2). There was little regrowth in the swath and deep plots.

#### Shoot Density

We observed 3 distinct phases of shoot density (Fig. 3). From 2005 to 2007, there was no significant change in density along the shallow transect; but there was a significant difference (ANOVA,  $df = 1$ ,  $MS = 14287.62$ ,  $P = 0.002$ ) between 2007 (41.9) and 2008 (86.3) when density doubled. Shoot density stayed high from 2008 through 2010 but declined by half in 2011 and was further reduced to a mean of 23 m<sup>-2</sup> by 2012 when much of the inner edge of the previously dense meadow was missing. A third of the transect in 2012 showed signs of disturbance and consisted of sparse shoots (<1 m<sup>-2</sup>; Fig. 4) but with seedlings evident nearby (seedlings were not included in density estimates). There was no significant difference in density between 2007 (first phase) and 2012 (third phase); however, there was a significant difference ( $df = 1$ ,  $MS = 25579.2$ ,  $P = 0.0004$ ) between 2010 (second phase) and 2011 (third

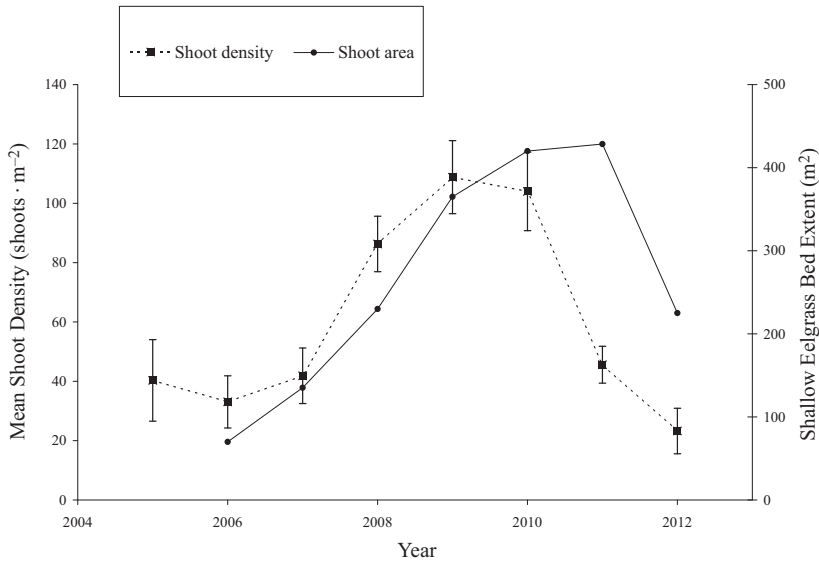


Fig. 3. Eelgrass (*Zostera pacifica*) shoot density and meadow extent at Frenchy's Cove, Anacapa Island, California, from 2005 to 2012. Solid squares indicate shoot density along a fixed shallow (7-m depth) transect. Error bars are  $\pm 1$  SE. Small circles indicate total area (m<sup>2</sup>) of eelgrass bed around fixed transect from 2006 to 2012.

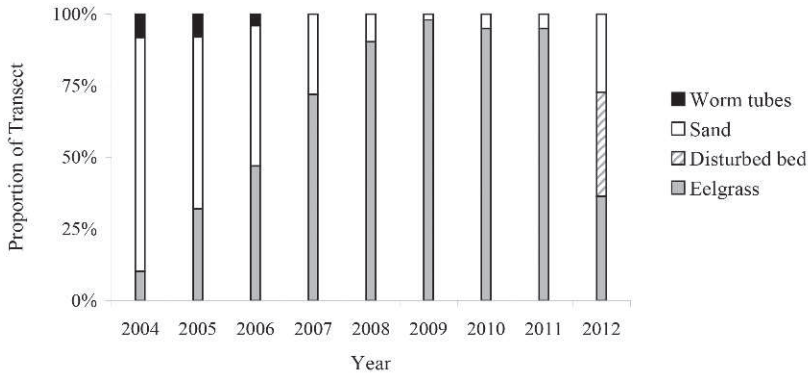


Fig. 4. Eelgrass (*Zostera pacifica*), sand, and worm tubes (*Chaetopterus* sp.) at Frenchy's Cove, Anacapa Island, California, from 2004 to 2012, as a proportion of the permanent shallow transect (7-m depth, 30-m length). Shoot density in the disturbed bed in 2012 was  $< 1$  m<sup>-2</sup>.

phase) and between 2011 and 2012 ( $df = 1$ ,  $MS = 3867.271$ ,  $P = 0.03$ ). In 2012, shoot density along the fixed transect ( $52.3$  m<sup>-2</sup>) was significantly lower ( $df = 1$ ,  $MS = 11213.33$ ,  $P < 0.0001$ ) than within quadrats placed within the meadow slightly downslope ( $90.9$  m<sup>-2</sup>,  $n = 15$ ).

#### Comparison of Shoot Density with Santa Cruz Island Meadows

Shoot density displayed considerable variation between sites and between years (Fig. 5)

with no clear trend evident. Between the 4 meadows, shoot density ranged from a mean high of  $169$  m<sup>-2</sup> at Scorpion Anchorage in 2001 to a mean low of  $39$  m<sup>-2</sup> at Frenchy's Cove in 2009. Among the 3 Santa Cruz Island meadows, the highest densities were found at Scorpion Anchorage and the lowest at Smugglers Cove. In 2009, density increased at Prisoners Harbor and Scorpion Anchorage and decreased at Frenchy's Cove. By 2012, density at Frenchy's Cove had rebounded to 2008 levels.



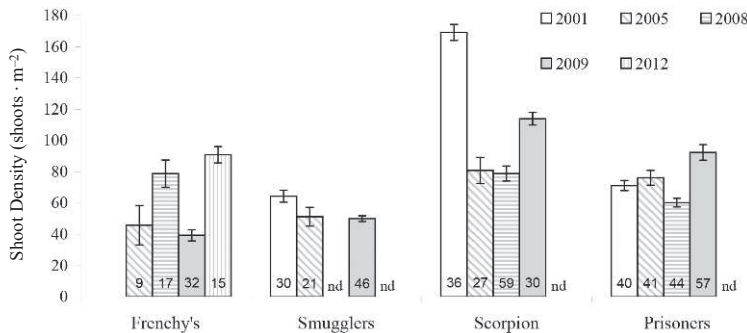


Fig. 5. Eelgrass (*Zostera pacifica*) mean shoot density from 2001 to 2012 at 4 sites: Anacapa Island transplant site (Frenchy's Cove), 2 donor beds (Smugglers Cove and Prisoners Harbor, Santa Cruz Island), and another natural bed (Scorpion Anchorage, Santa Cruz Island). Counts were made in 0.25-m<sup>2</sup> quadrats haphazardly placed within eelgrass meadows or patches. The number of quadrats per site per year is represented within each bar. Sampling in 2001 was before the transplant. Smugglers Cove was not sampled in 2009, and only Frenchy's Cove was sampled in 2012. Error bars are  $\pm 1$  SE.

### Meadow Expansion

The meadow surrounding the shallow transect expanded from 2006 to 2012 (Fig. 3). Shallow meadow size increased steadily from 20 m<sup>2</sup> in 2005 to a high of 428 m<sup>2</sup> in 2011. Loss of eelgrass along the 7-m transect (Fig. 4) accompanied the overall decline in area by 2012. Although the inshore edge of the meadow had shifted slightly downslope by 2012, eelgrass patches extended out through an area approximately 60 m  $\times$  30 m (1800 m<sup>2</sup>) and spanned depths from 8 m to 10 m. Over the study period, individual shoots spread into expanding patches, which grew past the area that we were mapping along the fixed shallow transect and eventually coalesced into an overall meadow at Frenchy's Cove of 8700 m<sup>2</sup> (0.87 ha) in 2009, retracting slightly to 6200 m<sup>2</sup> (0.62 ha) in 2012.

### Spread of Eelgrass along Anacapa Island

Two years after the 2002 transplant, scattered shoots of eelgrass were found approximately 300 m across the cove and up to 1000 m east of the original transplant site (Fig. 6, Table 1). Little expansion of eelgrass was observed east along Middle Anacapa Island in 2004 ( $\sim$ 850 m searched) or 2005 ( $\sim$ 1000 m searched). By 2006, the shoots at both Frenchy's Cove and east of the cove formed large patches ( $>4$  m<sup>2</sup>), some of which contained flowering shoots, and scattered shoots appeared along the 9-m depth contour between the 2 areas. In 2007 at Middle Anacapa Island, approximately 20 shoots were observed. By 2011, patches and scattered

individuals were observed 1.3 km and 2 km, respectively, from the transplant site. In 2012, there were additional patches 200 m to the east, and scattered shoots were observed at the west end of East Anacapa Island—a distance of 2.5 km from the transplant site. No eelgrass was observed during the dives furthest east in Cathedral Cove in either 2007 or 2011.

### Fish Diversity and Species Richness

Seventy-two individual roving diver fish counts were performed between 1997 and 2012 within the meadow area, comprising 36 hours of observations at Frenchy's Cove. A total of 42 different species were observed during roving diver fish counts (Table 2). The average number of fish species observed ranged from 5 to 14 (Fig. 7). Before the transplant, the average number of fish species observed during the survey ranged from 5 (2001) to 11 (1999). After the transplant, average fish species increased from 7 species (2003) to 14 (2011) and 11 (2012).

The 3 most commonly observed fish (average abundance index) at Frenchy's Cove before the transplant were the blackeye goby (*Rhinogobiosoma nicholsii*), señorita (*Oxyjulis californica*), and kelp bass (*Paralabrax clathratus*; Table 2). Some species were observed on only one occasion: Pacific herring (*Clupea pallasii*) in 1999, smallhead flyingfish (*Cheilopogon pinnatibarbatus*) in 2002, California lizardfish (*Synodus lucioceps*) in 1998, barracuda (*Sphyraena argentea*) in 2009, yellowtail (*Seriola lalandi*) in 2009, and white seabass (*Atractoscion nobilis*) in 2003. Other species were common

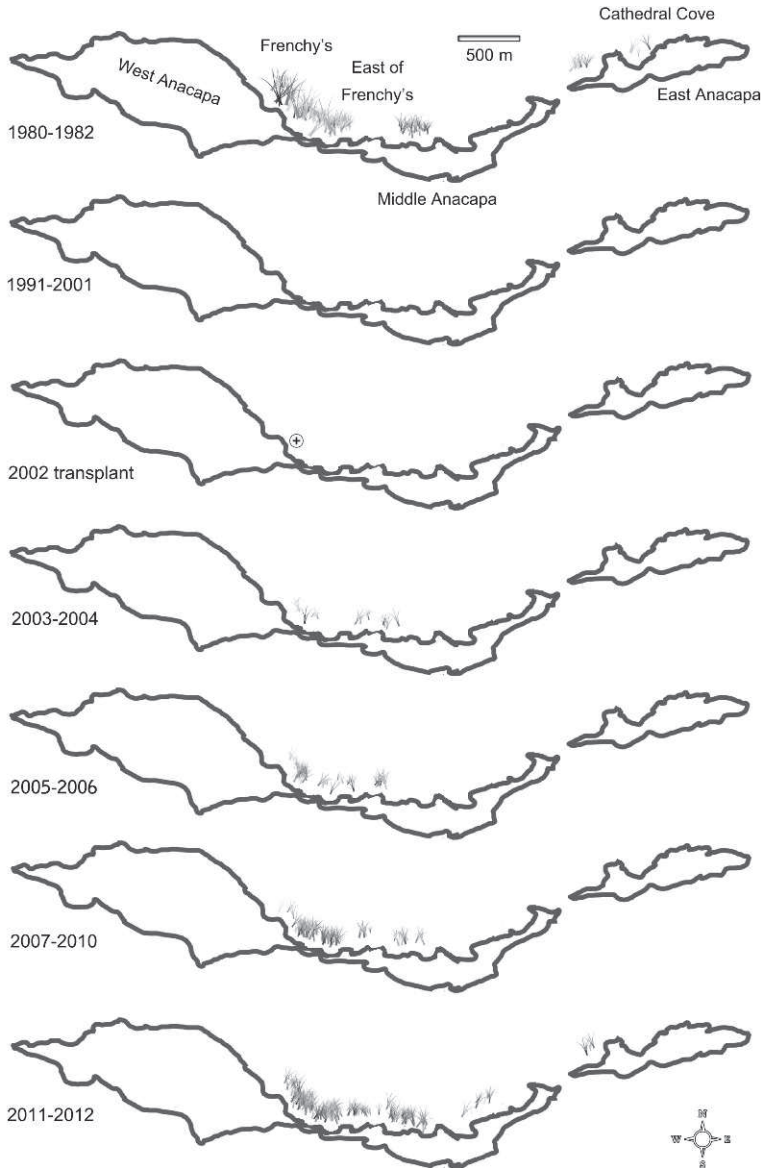


Fig. 6. Geographic spread of eelgrass (*Zostera pacifica*) eastward across Anacapa Island, California. Data represent diver observations from 1980 to 2012.

on adjacent sandy substrates yet were not found in the meadow, such as sanddab (*Citharichthys stigmaeus*) and C-O turbot (*Pleuronichthys coenosus*) that occurred in 2001 and 2002 and then in 6 out of 10 years after the transplant.

In addition to number of fishes, there was a change in functional guilds (Fig. 8). Surfperches, including the black, pile, and shiner surfperches (*Embiotoca jacksoni*, *Rhacochilus*

*vacca*, *Hyperprosopon argenteum*, respectively; all common in eelgrass meadows at other locations), did not occur in surveys at Frenchy's Cove before the transplant but were commonly encountered afterwards. The herbivorous halfmoon (*Medialuna californiensis*) was found in every survey from 2005 to 2012. Opaleye (*Girella nigricans*), another herbivore, was more commonly encountered after the transplant.

TABLE 2. Fish mean yearly abundance index from 1997 to 2012 from roving diver surveys at Frenchy's Cove, Anacapa Island, California. Species are presented by index rank. Surveys were combined for shallow (7-m) and deep (10-m) areas. Index rank describes the relative abundance seen for each species, using the following codes: 0 = absent, 1 = single, 2 = few (2–10), 3 = common (11–100), 4 = abundant (>100). Years after eelgrass (*Zostera pacifica*) transplant are indicated in bold.

Fish species	1997	1998	1999	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	Average
<i>Oxygilis californica</i>	2.67	0.00	3.00	0.00	0.00	1.12	1.20	3.25	3.00	1.98	3.00	3.00	3.00	3.40	3.06	2.11
<i>Rhinogobius nicholsii</i>	2.90	3.00	0.95	4.00	3.50	4.00	3.00	2.00	0.00	2.51	0.00	0.00	1.55	0.58	1.99	2.00
<i>Paralabrax clathratus</i>	2.67	1.00	2.40	0.00	0.94	1.20	2.00	2.00	3.00	1.79	3.00	3.00	2.78	3.00	3.08	1.99
<i>Embiotoca jacksoni</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.75	3.00	0.27	3.00	1.00	2.78	3.00	2.93	1.12
<i>Rhacochilus vaeca</i>	0.00	0.00	0.00	0.00	0.00	0.24	0.00	2.55	0.00	0.32	1.60	1.00	1.10	2.94	3.21	0.86
<i>Neoclinus blanchardi</i>	0.87	1.30	0.90	2.45	1.67	1.60	1.15	0.68	0.00	0.71	0.00	0.00	0.95	0.00	0.42	0.85
<i>Medialuna californiensis</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.43	3.00	0.45	1.60	3.00	0.50	1.02	0.93	0.80
<i>Chaenopsis alepidota</i>	1.00	2.23	2.00	0.70	0.73	0.12	0.00	0.58	0.00	2.14	0.00	0.00	0.00	0.00	0.00	0.63
<i>Girella nigricans</i>	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.60	0.00	0.50	2.70	1.49	0.62
<i>Migilobatis californica</i>	1.00	0.75	0.25	0.00	0.08	0.52	0.30	0.00	1.80	1.07	1.00	1.00	0.23	0.00	0.19	0.55
<i>Senecossiphus pulcher</i>	0.83	0.00	1.35	0.00	0.00	0.00	0.00	0.00	0.00	0.28	0.00	0.00	0.51	1.12	1.08	0.34
<i>Chromis punctipinnis</i>	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.10	0.00	0.00	0.00	0.00	0.34
<i>Pleuronichthys coenosus</i>	0.00	0.00	0.00	0.85	0.57	0.34	0.00	0.00	0.00	0.13	0.00	0.80	0.28	0.90	0.22	0.27
<i>Heterostichus rostratus</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.12	1.80	1.00	0.00	0.00	0.91	0.27
<i>Halichoeres semicinctus</i>	0.00	0.00	0.53	0.00	0.00	0.00	0.00	0.25	0.00	0.08	0.90	0.00	0.53	0.54	0.26	0.20
<i>Chupea pallasi</i>	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20
<i>Leiocottus hirundo</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.90	0.00	0.56	0.13	0.17
<i>Citharichthys stigmaceus</i>	0.00	0.63	1.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16
<i>Atherinops affinis</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	1.80	0.00	0.00	0.00	0.00	0.15
<i>Pardalichthys californicus</i>	0.00	0.00	0.40	0.00	0.33	0.00	0.00	0.00	0.60	0.00	0.00	0.00	0.00	0.38	0.41	0.14
<i>Anisotremus davidsonii</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13
<i>Sardinops sagax</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.13
<i>Trachurus symmetricus</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.53	0.00	0.00	1.20	0.00	0.00	0.00	0.00	0.12
<i>Aulorhynchus flavidus</i>	0.00	0.00	0.00	0.00	0.00	1.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10
<i>Rhacochilus toxotes</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.88	0.14	0.08
<i>Brachyistius frenatus</i>	0.00	0.00	0.00	0.00	0.00	1.10	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08
<i>Scorpaena guttata</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.80	0.00	0.20	0.00	0.07
<i>Sphyræna argentea</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.07
<i>Scorpaenichthys marmoratus</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.80	0.04	0.06
<i>Pleuronichthys verticalis</i>	0.00	0.00	0.00	0.00	0.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
<i>Sebastes rastrelliger</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.32	0.31	0.04
<i>Caudolatus princeps</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.54	0.00	0.00	0.00	0.00	0.08	0.04
<i>Seriola lalandi</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.03
<i>Syngnathus</i> sp.	0.00	0.00	0.00	0.00	0.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
<i>Albichthys holderi</i>	0.00	0.00	0.00	0.43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
<i>Xystreus holepis</i>	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
<i>Synodus lacticeps</i>	0.00	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
<i>Heterodontus francisci</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.06	0.01
<i>Cupselarus californicus</i>	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
<i>Squatina californica</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.01
<i>Atractoscion nobilis</i>	0.00	0.00	0.00	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
<i>Gibbisia elegans</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00

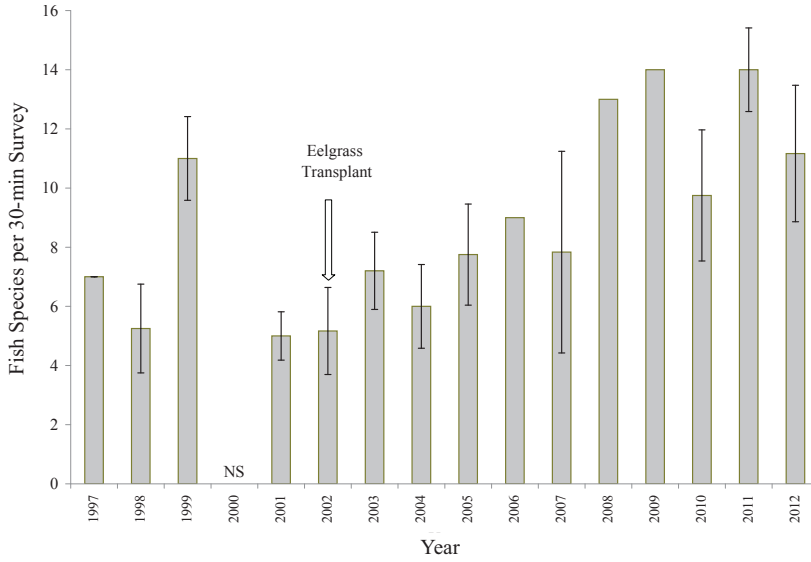


Fig. 7. Mean fish species richness at Frenchy’s Cove, Anacapa Island, California, from 1997 to 2012, as estimated from roving diver fish counts. Data are for adults only. Error bars are  $\pm 1$  SD; values with no error bars either are all the same (1997) or indicate only a single count (2008, 2009).

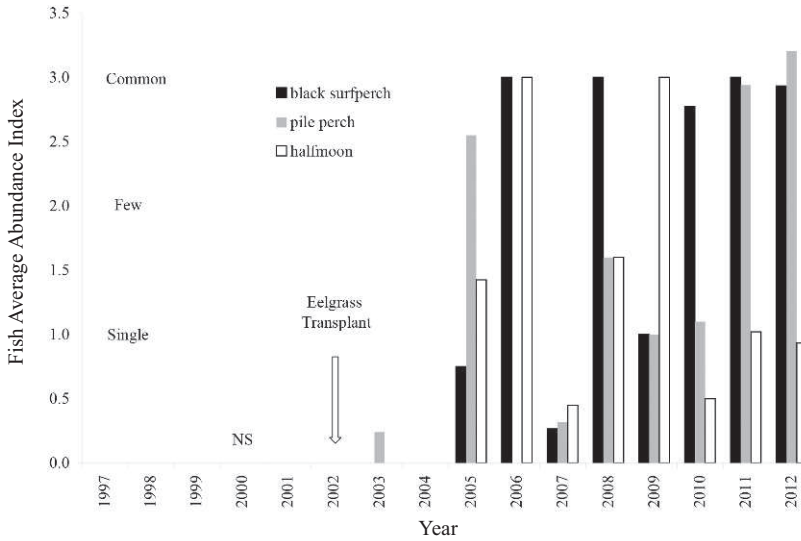


Fig. 8. Relative abundance of 3 fish species, representing different fish guilds, from 1997 to 2012 at Frenchy’s Cove, Anacapa Island, California. The eelgrass (*Zostera pacifica*) transplant occurred in 2002. Data shown are calculated from roving diver fish counts. The average abundance index = (time interval code/10)\*abundance code. The 3 fish species are black surfperch (*Embiotoca jacksoni*), pile perch (*Rhacochilus vacca*), and halfmoon (*Medialuna californiensis*).

To compare fishes found in eelgrass habitat with those found over sandy substrates, we performed roving diver surveys on 2 adjacent days in July 2011 over the eelgrass meadow at Frenchy’s Cove and at Cathedral Cove, where

scattered patches had existed until the late 1990s but are no longer present. Out of 22 species overall, 17 were observed at Frenchy’s Cove (eelgrass) and 10 were observed at Cathedral (sand; Fig. 9). In order of abundance, 5 species

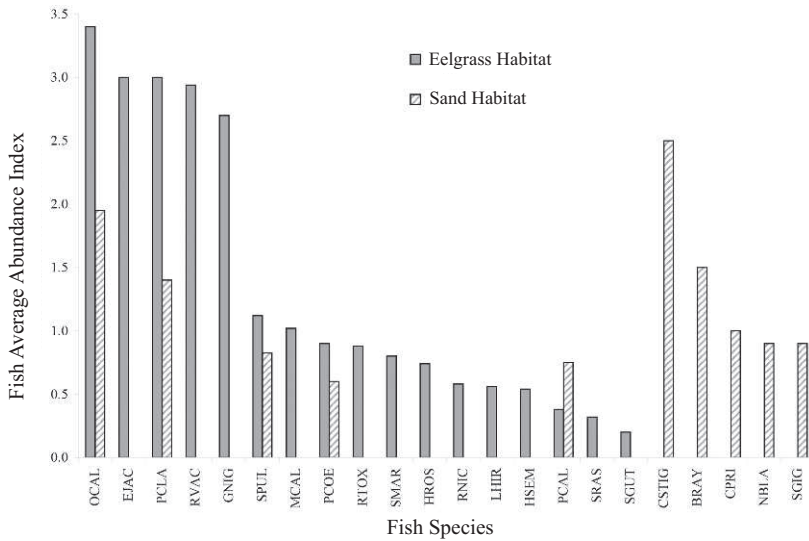


Fig. 9. Fish species in eelgrass (*Zostera pacifica*) at Frenchy's Cove and sand habitats at Cathedral Cove (both on Anacapa Island, California). Data represent roving diver fish counts on consecutive days in July 2011. The average abundance index = (time interval code/10)\*abundance code. Species abbreviations from left to right: *Oxyjulis californica*, *Embiotoca jacksoni*, *Paralabrax clathratus*, *Rhacochilus vacca*, *Girella nigricans*, *Semicossyphus pulcher*, *Medialuna californiensis*, *Pleuronichthys coenosus*, *Rhacochilus toxotes*, *Scorpaenichthys marmoratus*, *Heterostichus rostratus*, *Rhinogobiops nicholsi*, *Leiocottus hirundo*, *Halichoeres semicinctus*, *Paralichthys californicus*, *Sebastes rastrelliger*, *Scorpaena guttata*, *Citharichthys stigmaeus*, *Myliobatis californica*, *Caulolatilus princeps*, *Neoclinus blanchardi*, *Stereolepis gigas*.

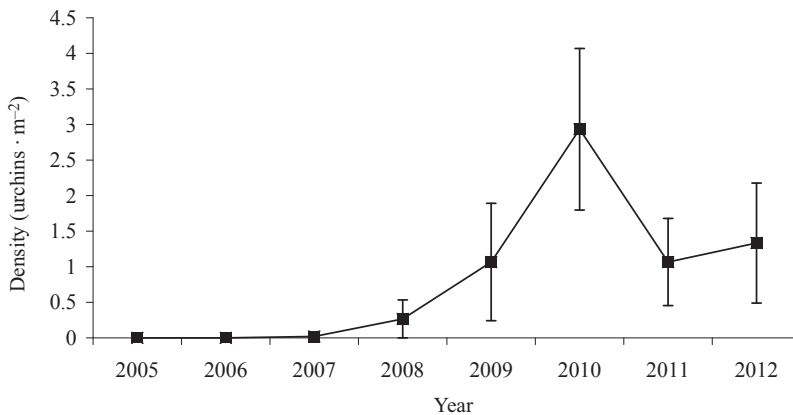


Fig. 10. White sea urchin (*Lytechinus anamesus*) density along permanent shallow transect (7-m depth, 30-m length), Frenchy's Cove, Anacapa Island, California. Quadrats were placed every other meter. Error bars are  $\pm 1$  SE.

were only found on sand (sand dab, bat ray [*Myliobatis californica*], ocean whitefish [*Caulolatilus princeps*], giant seabass [*Stereolepis gigas*], and spotted kelpfish [*Gibbonsia elegans*]), 12 only found over eelgrass (black surfperch, pile perch, opaleye, halfmoon, rubberlip perch [*Rhacochilus toxotes*], cabezon [*Scorpaenichthys marmoratus*],

giant kelpfish [*Heterostichus rostratus*], lavender sculpin [*Leiocottus hirundo*], rock wrasse [*Halichoeres semicinctus*], grass rockfish [*Sebastes rastrelliger*], scorpionfish [*Scorpaena guttata*] and 5 at both sites (senorita, kelpbass, sheep-head [*Semicossyphus pulcher*], C-O turbot, and halibut [*Paralichthys californicus*]).

### Urchin Density

White urchin density gradually increased along the shallow transect, from 0 m<sup>-2</sup> in 2005, peaking at 3 m<sup>-2</sup> in 2010, and declining to 1.3 m<sup>-2</sup> in 2012 (Fig. 10). Distribution of white urchin throughout the meadow was patchy, as evident by the large error bars. In most years, fewer than 100 urchins were found site-wide.

### DISCUSSION

We initiated a restoration of eelgrass, *Zostera pacifica*, in response to local extinction of a small meadow at Frenchy's Cove, Anacapa Island, in 1991. The transplant was successful, with shoots presently ranging from 7- to 10-m depth along >60 m of shoreline; but the goals of our transplant effort differed from those required by the Eelgrass Mitigation Policy benchmarks. The California Eelgrass Mitigation Policy requires that (1) "restored habitat will develop . . . such that within 36 months following planting, it meets or exceeds the full coverage and not less than 85% of the density relative to the initial condition of affected eelgrass habitat" and (2) "restored habitat is expected to sustain this condition through at least 60 months following initial planting." At 3 years posttransplant, individual patches started to coalesce into a measurable meadow, and density was half that found at donor meadows (Fig. 3). By these benchmarks, therefore, the transplant effort was not successful. However, after 5 years, the meadow greatly increased both in shoot density and spatial expansion, which would have been unrecorded if monitoring had ceased at the 60-month benchmark of mitigation projects. By way of comparison, 87% of 43 eelgrass restoration projects from 1989 to 2009 in southern California have been successful or satisfied permit conditions but did not necessarily reach a full recovery at the time of evaluation (National Marine Fisheries Service 2011). It is important to note that the Eelgrass Mitigation Policy was written specifically for *Z. marina* found in shallow embayments such as San Francisco and San Diego bays and not for the open-coast species *Z. pacifica*, and there may be species-specific ecological differences.

### Eastward Spread

By 1992, eelgrass was extinct on Anacapa Island and the nearest meadow was on Santa

Cruz Island, a distance of >12 km and across a deep and exposed channel with strong tidal currents. However, in 2004, new shoots appeared 300 m across the cove and eastward from our transplant at Frenchy's Cove. There are only 2 possible mechanisms for this reappearance: reattachment of dislodged/broken ramets or seed dispersal from upcurrent meadows, either from our transplant or Santa Cruz Island. Free-floating fragments of *Z. marina* can remain viable for at least 1 month (Biber 2006), and seagrass fragments have been shown to survive and regenerate after dislodgement (Balestri et al. 2011). A high degree of genotype sharing in geographically separated *Z. marina* meadows along Santa Catalina Island was due to reattachment of dislodged rhizomes (Coyer et al. 2008), demonstrating that vegetative fragments are redistributed and can colonize new areas. While some of the >90% loss of transplanted shoots occurring within the first 6 months at Anacapa Island were attributed to grazing, some shoots likely were dislodged by foraging bat rays and may have colonized new areas. Mean current flow along Anacapa Island is 1 cm · s<sup>-1</sup> toward the east-southeast (Partnership for Interdisciplinary Studies of Coastal Oceans, unpublished data).

The 11 scattered small patches (<1 m<sup>2</sup>) of *Z. pacifica* found approximately 300 m from the transplant site in 2004 suggested a recent introduction (<2 years), as they were similar in size (1–13 shoots per patch) and width (8–12 mm; ~3 mm were considered seedlings) to the small patches that were expanding from single shoots at the transplant site. Estimates of annual rhizome elongation rates for *Z. marina* range from 22 to 31 cm · year<sup>-1</sup> (Marbà and Duarte 1998), and if equivalent for *Z. pacifica*, these rates support the transplanted shoots as the source population. Furthermore, a single adult shoot near the shallow transect expanded to 11 shoots in 12 weeks and to a patch (~1 m<sup>2</sup>) of 45 shoots in 1.5 years (Altstatt unpublished data). Based on this observation, it is likely that the small patches encountered east of Frenchy's Cove were of similar age or younger (<2 years old) and thus did not precede the transplant experiment.

It is possible that reproductive seed-bearing material rafted to Anacapa Island independently of, but concurrently with our transplant program. Coastal bays in Virginia lost eelgrass

in the 1930s due to wasting disease and had not recovered after nearly 70 years (Orth et al. 2012), with the closest seed source 50 km distant. Although other species of seagrasses have seeds that float on the surface and may travel long distances (~55 km) before sinking (Ruiz-Montoya et al. 2012), eelgrass seeds are negatively buoyant. The seed-bearing spathes, however, frequently raft with other floating vegetative material and can colonize distant areas, as discussed by Kendrick et al. (2012). For example, rafting material of *Z. marina* with viable seeds has been found up to 34 km from the nearest source (Harwell and Orth 2002), and spathes were observed to float for at least 26 days (Kallstrom et al. 2008). Genetic assignment tests of *Z. marina* revealed that gene flow (and seed dispersal) via rafting shoots occurred up to 54 km (Reusch 2002). Depending on surface currents, seed-bearing spathes of *Z. marina* may be transported up to 150 km, but most were retained within a few kilometers of the starting point, with approximately 50% within 500 m (Kallstrom et al. 2008).

The predominant near-surface current pattern within the southern Santa Barbara Channel is from west to east (Winant et al. 2003), as is the predominant wind and swell direction. Three source populations of *Z. pacifica* (Smugglers Cove, Scorpion Anchorage, and Prisoners Harbor) lie to the west of Anacapa Island. In order to reach the north side of Anacapa Island, however, drift material from these meadows must cross strong tidal currents perpendicular to and between Santa Cruz and Anacapa Islands. A recent genetic study indicated potential seed dispersal between Santa Catalina and San Clemente islands—lands that are separated by 63 km and a deep channel similar to that between Santa Cruz and Anacapa islands (Coyer et al. 2008). Consequently, rafting from Santa Cruz Island to Anacapa Island cannot be categorically dismissed.

Although we did not observe any seedlings outside the transplanting area across the cove and east of Frenchy's Cove in 2003 and 2004, we found a small number of seedlings at the transplant site during those years (Altstatt unpublished data). Some of the transplanted shoots (<5%) were reproductive at the time of harvest and were likely the source, as the seedlings were only in the immediate area of the transplant and horizontal dispersal of seagrass

seeds is usually <1 m (Koch et al. 2010). Eelgrass seeds that become buried in sediment may persist and remain viable for at least 3 years, thus providing a seed source (Lee et al. 2007) and a new source of genetic diversity (Zipperle et al. 2009). Orth et al. (2012) successfully reestablished eelgrass meadows in 4 Virginia coastal bays following widespread distribution of more than 38 million seeds and suggest that seed availability was the limiting factor for 7 decades. The existence of a >10-year *Z. pacifica* seed bank at Anacapa Island, however, is unlikely; thus the observed seedlings in 2003 and 2004 undoubtedly derived from transplanted shoots that became reproductive.

Even though Frenchy's Cove is the most sheltered spot along the north side of Anacapa Island, it can be affected by long-period, high-energy northwest ground swell from the North Pacific Ocean. An unusually large winter swell (4-m, 15-s period) occurred in April 2012 (National Data Buoy Center website). Large ground swells may increase localized currents (Schwartz 2006), which could change sediment transport and either bury or uproot seedlings and plants (Marion and Orth 2012). Oscillatory flows from a long-period swell may prevent blades from shielding the sediment, as is the case in laminar (current) flow regimes, and instead increase turbulence and scour of sediments (Lawson et al. 2012). Indeed, it has been suggested that long-period wave energy may not be attenuated by eelgrass meadows (Hansen and Reidenbach 2012). We observed thinning throughout the shallowest edge of the meadow in 2012; scattered seedlings throughout this area indicated recolonization from recently dispersed seeds or germination from a buried seed bank. Wave action may affect the shallow edge of the historic bed (location of the 7-m-depth fixed transect) to a greater degree than the rest of the meadow further downslope.

#### Transplant versus Natural Meadows

Comparing shoot density in planted eelgrass plots relative to natural meadows can show resilience to or effects of changing environmental conditions (Thom et al. 2012). Meadows at Santa Cruz Island showed some variable temporal and spatial patterns, but shoot densities remained similar to those of 1994–1997: 116–140 m<sup>-2</sup> at Scorpion to 36–76 m<sup>-2</sup>

at Smugglers Cove (Engle et al. 1998). High variation at Scorpion Anchorage was likely due to a period of rapid recovery after damaging floods carrying sediment buried the bed in 1998 and due to periodic disturbance from mooring chains. There is no historic density information for Frenchy's Cove. By 2008, shoot density at Frenchy's Cove had met or exceeded densities found at Smugglers Cove and Prisoners Harbor, the 2 donor sites.

### White Urchins

Urchin grazing can dramatically alter seagrass habitat structure for years by continually removing shoots and eventually exhausting rhizome nutrient stores (Heck and Valentine 1995). The recruitment pulse of white urchins at Anacapa Island after the 1983 El Niño resulted in island-wide densities of  $>40 \text{ m}^{-2}$  from 1986 to 1988 (Richards et al. 1997, Carroll et al. 2000) and  $60 \text{ m}^{-2}$  at Frenchy's Cove in 1992 (Engle unpublished data). This intense grazing pressure was apparently enough to remove eelgrass shoots and buried rhizomes.

Urchin grazing is an important feature of seagrass biology. For example, based on feeding rates of *L. variegates*, densities greater than  $42 \text{ m}^{-2}$  exceed the production capacity of *Thalassia testudinum* and lead to overgrazing (Greenway 1976). *Lytechinus* grazing fronts with densities of up to  $636 \text{ m}^{-2}$  denuded 20% of a large Florida seagrass meadow (Camp et al. 1973), and a front with a density of  $167 \text{ m}^{-2}$  overgrazed to  $0.81 \text{ km}^2$  in 9 months (Rose et al. 1999). Urchin herbivory at densities of  $10\text{--}30 \text{ m}^{-2}$  largely exceeded seagrass production in a coastal Mediterranean lagoon (Fernandez et al. 2012); but once the front diminished, recovery of eelgrass was rapid, within 10 months. At Frenchy's Cove, white urchin density in 2012 was an order of magnitude lower than in 1992. Consequently, it does not appear that urchin grazing influenced density and meadow size during the study period.

### Fish Surveys

The number of fish species present and overall fish abundance at Frenchy's Cove were positively associated with the expansion of the meadow. On the simplest level, eelgrass provides 3-D structure in which fishes associate or hide (Jackson et al. 2001), and losses in eelgrass habitat may result in a shift in fish assemblages (Pihl et al. 2006). Additionally,

greater shoot density may lead to higher levels of epiphytes and epifauna, which in turn increase trophic subsidies (Heck et al. 2008). Higher shoot density (structural complexity) may be important for ambush predators such as giant kelpfish (*Heterostichus rostratus*; Tait and Hovel 2012), a species that increased at Frenchy's Cove as the eelgrass expanded. Additionally, several of the species that showed the greatest increase were benthic microcarnivores (black and pile perch) or herbivores (halfmoon; Horn and Ferry-Graham 2006) that would benefit from the rise in local productivity from eelgrass. One species that decreased over time was the orangethroat pikeblenny (*Chaenopsis alepidota*). The worm tubes that provide shelter for this fish declined after 2007 as eelgrass expanded. Frenchy's Cove is the northern reported edge of the pikeblenny's geographical range, so factors other than eelgrass may be at play.

### CONCLUSIONS

Meadows of *Z. pacifica* nearly a hectare in size are now present at Frenchy's Cove at Anacapa Island. The eelgrass meadows found along the north side of Anacapa Island originated from an initial transplant site established 0.3 to 3 km distant in 2002. Expansion of the meadow was due to reattachment of uprooted plants and/or reproductive material drifting from the initial transplant site. Additionally, the biotic assemblage associated with these meadows increased in abundance and diversity. Our study supports McGlathery et al. (2012), who stated that at least a decade is required for eelgrass meadow ecosystem services to be fully restored. We expect to see further expansion of patches and meadows along Anacapa Island. These meadows will provide an increasing level of structural and functional ecological attributes and serve as an example for future restoration efforts around the Channel Islands and elsewhere.

### ACKNOWLEDGMENTS

We thank the many Channel Islands Research Program volunteers who helped with the surveys, particularly S. Lee, P. Owens, D. Richards, and S. Whitaker. The surveys and cruises were made possible with the help of Tatman Foundation staff H. Chomeau, J. Chomeau, and C. Bungener, and other crew of



the *R/V Cormorant*. Thanks to the Channel Islands National Marine Sanctuary and crew of the *R/V Shearwater* for vessel support, and thanks also to the Channel Islands National Park and the California Department of Fish and Wildlife. We are grateful for the comments of the editor and an anonymous reviewer that helped us improve the manuscript. This work was supported primarily by the Tatman Foundation.

#### LITERATURE CITED

- ALTSTATT, J. 2005. Restoration of a historic eelgrass (*Zostera marina*) bed at Frenchy's Cove, Anacapa Island. Pages 397–404 in D.K. Garcelon, C.A. Schwemm, editors, Proceedings of the Sixth California Islands Symposium, Institute for Wildlife Studies, Arcata, CA.
- BALESTRI, E., F. VALLERINI, AND C. LARDICCI. 2011. Storm-generated fragments of the seagrass *Posidonia oceanica* from beach wrack—a potential source of transplants for restoration. *Biological Conservation* 144:1644–1654.
- BIBER, P.D. 2006. Hydroponic versus rooted growth of *Zostera marina* L. (eelgrass). *Hydrobiologia* 568: 489–492.
- CAMP, D.K., S.P. COBB, AND J.F. BREEDVELD. 1973. Overgrazing of seagrasses by a regular urchin, *Lytechinus variegatus*. *BioScience* 23:37–38.
- CARROLL, J.C., J.M. ENGLE, J.A. COYER, AND R.F. AMBROSE. 2000. Long-term changes and species interactions in a sea urchin-dominated community at Anacapa Island, California. Pages 370–378 in Proceedings of the 5th California Islands Symposium.
- CINP KELP FOREST MONITORING PROGRAM. 1997. Kelp forest monitoring handbook. Volume 1, Sampling protocol. Channel Islands National Park, Ventura, CA. Available from: [http://science.nature.nps.gov/im/units/chis/Reports\\_PDF/Marine/KFM-HandbookVol1.pdf](http://science.nature.nps.gov/im/units/chis/Reports_PDF/Marine/KFM-HandbookVol1.pdf)
- COLE, L.W., AND K.J. MCGLATHERY. 2012. Nitrogen fixation in restored eelgrass meadows. *Marine Ecology Progress Series* 448:235–246.
- COYER, J.A., K.A. MILLER, J.M. ENGLE, J. VELDSINK, A. CABELLO-PASINI, W.T. STAM, AND J.L. OLSEN. 2008. Eelgrass meadows in the California Channel Islands and adjacent coast reveal a mosaic of two species, evidence for introgression and variable clonality. *Annals of Botany* 101:73–87.
- DEN HARTOG, C. 1970. The sea-grasses of the world. North-Holland, Amsterdam, Netherlands.
- DUFFY, J.E. 2006. Biodiversity and the functioning of seagrass ecosystems. *Marine Ecology Progress Series* 311:233–250.
- ENGLE, J.M., R.F. AMBROSE, P.T. RAIMONDI, K.D. LAFFERTY, D.L. MARTIN, AND J.M. ALTSTATT. 1998. Inventory of coastal ecological resources of the northern Channel Islands and Ventura/Los Angeles counties. Draft report for the California Coastal Commission.
- ENGLE, J.M., K.D. LAFFERTY, J.E. DUGAN, D.L. MARTIN, N. MODE, R.F. AMBROSE, AND P.T. RAIMONDI. 1995. Second year study plan for inventory of coastal ecological resources of the Northern Channel Islands and Ventura/Los Angeles counties. Report to the California Coastal Commission. June 1995. 51 pp.
- ENGLE, J.M., AND K.A. MILLER. 2005. Distribution and morphology of eelgrass (*Zostera marina* L.) at the California Channel Islands. Pages 405–414 in D.K. Garcelon and C.A. Schwemm, editors, Proceedings of the Sixth California Islands Symposium. Institute for Wildlife Studies, Arcata, CA.
- FERNANDEZ, C., L. FERRAT, G. PERGENT, AND V. PASQUALINI. 2012. Sea urchin–seagrasses interactions: trophic links in a benthic ecosystem from a coastal lagoon. *Hydrobiologia* 699:21–33.
- FONSECA, M.S., W.J. KENWORTHY, D.R. COLBY, K.A. RITTMASER, AND G.W. THAYER. 1990. Comparisons of fauna among natural and transplanted eelgrass *Zostera marina* meadows: criteria for mitigation. *Marine Ecology Progress Series* 65:251–264.
- FOURQUREAN, J.W., C.M. DUARTE, H. KENNEDY, N. MARBA, M. HOLMER, M.A. MATEO, E.T. APOSTOLAKI, A. KENDRICK, D. KRAUSE-JENSEN, K.J. MCGLATHERY, AND O. SERRANO. 2012. The grazing of *Thalassia testudinum* in Kingston Harbor, Jamaica. *Aquatic Botany* 2: 117–126.
- HANSEN, J.C.R., AND M.A. REIDENBACH. 2012. Wave and tidally driven flows in eelgrass beds and their effect on sediment suspension. *Marine Ecology Progress Series* 448:271–287.
- HARWELL, M.C., AND R.J. ORTH. 2002. Long-distance dispersal potential in a marine macrophyte. *Ecology* 83:3319–3330.
- HECK, K.L., JR., T.J.B. CARRUTHERS, C.M. DUARTE, A.R. HUGHES, G. KENDRICK, R.J. ORTH, AND S.W. WILLIAMS. 2008. Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers. *Ecosystems* 11:1198–1210.
- 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 Ecology* 189:205–217.
- HEMMINGA, M.A., F.J. SLIM, J. KAZUNGU, G.M. GANSEN, J. NIEUWENHUIZE, AND N.M. KRUYT. 1994. Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). *Marine Ecology Progress Series* 106:291–301.
- HOFFMAN, R.S. 1986. Fishery utilization of eelgrass (*Zostera marina*) beds and non-vegetated shallow water area in San Diego Bay. National Marine Fisheries Service, Southwest Region Admin. Rept. SWR-86-4.
- HORN, M.H., AND L.A. FERRY-GRAHAM. 2006. Feeding mechanisms and trophic interactions. Pages 387–410 in L.G. Allen, D.J. Pondella, and M.H. Horn, editors, The ecology of marine fishes: California and adjacent waters. University of California Press, Berkeley, CA.
- JACKSON, E.L., A.A. ROWDEN, M.J. ATTRILL, S.J. BOSSEY, AND M.B. JONES. 2001. The importance of seagrass beds as habitat for fishery species. *Oceanography and Marine Biology: An Annual Review* 39:269–303.

- KALDY, J. 2006. Carbon, nitrogen, phosphorus and heavy metal budgets: how large is the eelgrass (*Zostera marina* L.) sink in a temperate estuary? *Baseline/Marine Pollution Bulletin* 52:332–356.
- KALLSTROM, B., A. NYQVIST, P. ABERG, M. BODIN, AND C. ANDRE. 2008. Seed rafting as a dispersal strategy for eelgrass (*Zostera marina*). *Aquatic Biology* 88:148–153.
- KELLER, B.D. 1983. Coexistence of sea urchins in seagrass meadows: an experimental analysis of competition and predation. *Ecology* 64:1581–1598.
- KENDRICK, G.A., T.J.B. CARRUTHERS, L. MARION, M.L. CAMBRIDGE, R. HOVEY, S.L. KRAUSS, P.S. LAVERY, D.H. LES, R.J. LOWE, O.M.I. VIDAL, J.L.S. OOI, R.J. ORTH, D.O. RIVERS, L. RUIZ-MONTOYA, E.A. SINCLAIR, J. STATTON, J.K. KORNELIS VAN DIJK, AND J.J. VERDUIN. 2012. The central role of dispersal in the maintenance and persistence of seagrass populations. *BioScience* 62:56–65.
- KOCH, E.W., M.S. AILSTOCK, D.M. BOOTH, D.J. SHAFER, AND A.D. MAGOUN. 2010. The role of currents and waves in the dispersal of submerged angiosperm seeds and seedlings. *Restoration Ecology* 18:584–595.
- LAWSON, S.E., K.J. MCGLATHERY, AND P.L. WIBERG. 2012. Enhancement of sediment suspension and nutrient flux by benthic macrophytes at low biomass. *Marine Ecology Progress Series* 448:259–270.
- LEE, K.S., J.I. PARK, Y.K. KIM, S.R. PARK, AND J.H. KIM. 2007. Recolonization of *Zostera marina* following destruction caused by a red tide algal bloom: the role of new shoot recruitment from seed banks. *Marine Ecology Progress Series* 342:105–115.
- MARBÀ, N., AND C.M. DUARTE. 1998. Rhizome elongation and seagrass clonal growth. *Marine Ecology Progress Series* 174:269–280.
- MARION, S.R., AND R.J. ORTH. 2012. Seedling establishment in eelgrass: seed burial effects on winter losses of developing seedlings. *Marine Ecology Progress Series* 448:197–207.
- MCGLATHERY, K.J., L.K. REYNOLDS, L.W. COLE, R.J. ORTH, S.R. MARION, AND A. SCHWARZSCHILD. 2012. Recovery trajectories during state change from bare sediment to eelgrass dominance. *Marine Ecology Progress Series* 448:209–221.
- MERKEL, K.W. 1991. The use of seagrasses in the enhancement, creation and restoration of marine habitats along the California Coast: lessons learned from fifteen years of transplants. Technical Advisory Panel presentation to Marine Board, National Research Council Committee on the role of technology in marine habitat protection and enhancement. 20 March 1991. San Francisco, CA.
- NATIONAL MARINE FISHERIES SERVICE. 1997. Summary of eelgrass (*Zostera marina*) transplant projects in California 1976–1997. Southwest Region. Available from: <http://swr.nmfs.noaa.gov/hcd/eeltran.htm>
- \_\_\_\_\_. 2011. Southern California eelgrass mitigation policy. Southwest Region. Available from: [http://www.westcoast.fisheries.noaa.gov/publications/habitat/california\\_eelgrass\\_mitigation/draft\\_cemp\\_122911v.pdf](http://www.westcoast.fisheries.noaa.gov/publications/habitat/california_eelgrass_mitigation/draft_cemp_122911v.pdf)
- ORTH, R.J., T.J.B. CARRUTHERS, W.C. DENNISON, C.M. DUARTE, J.W. FOURQUREAN, K.L. HECK JR., A.R. HUGHES, G.A. KENDRICK, W.J. KENWORTHY, S. OLYARNIK, F.T. SHORT, M. WAYCOTT, AND S.L. WILLIAMS. 2006. A global crisis for seagrass ecosystems. *BioScience* 56:987–996.
- ORTH, R.J., M.C. HARWELL, AND J.R. FISHMAN. 1999. A rapid and simple method for transplanting eelgrass using single, unanchored shoots. *Aquatic Botany* 64:77–85.
- ORTH, R.J., K.L. HECK JR, AND J. VAN MONTFRANS. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator–prey relationships. *Estuaries* 7: 339–350.
- ORTH, R.J., AND K.J. MCGLATHERY. 2012. Eelgrass recovery in the coastal bays of the Virginia Coast Reserve, USA. *Marine Ecology Progress Series* 448:73–176.
- ORTH, R.J., K.A. MOORE, S.R. MARION, D.J. WILCOX, AND D.B. PARRISH. 2012. Seed addition facilitates eelgrass recovery in a coastal bay system. *Marine Ecology Progress Series* 448:177–195.
- PHIL, L., S. BADEN, N. NAUTSKY, P. RONNBACK, T. SODERQVIST, M. TROELL, AND H. WENNHAGE. 2006. Shift in fish assemblage structure due to loss of eelgrass *Zostera marina* habitats in Sweden. *Estuarine, Coastal and Shelf Science* 67:123–132.
- REED, B.J., AND K.A. HOVEL. 2006. Seagrass habitat disturbance: how loss and fragmentation of eelgrass *Zostera marina* influence epifaunal abundance and diversity. *Marine Ecology Progress Series* 326:133–143.
- REUSCH, T.B.H. 2002. Microsatellites reveal high population connectivity in eelgrass (*Zostera marina*) in two contrasting coastal areas. *Limnology and Oceanography* 47:78–85.
- RHODE, J.M., AND J.E. DUFFY. 2004. Relationships between bed age, bed size, and genetic structure in Chesapeake Bay (Virginia, USA) eelgrass (*Zostera marina* L.). *Conservation Genetics* 5:661–671.
- RICHARDS, D.V., C. GRAMLICH, G.E. DAVIS, AND M. MCNULTY. 1997. Kelp forest monitoring: 1982–1989 report. Technical Report CHIS-97-05, Channel Islands National Park, Ventura, CA.
- ROSE, C.D., W.C. SHARP, W.J. KENWORTHY, J.H. HUNT, W.G. LYONS, E.J. PRAGER, F.J.F. VALENTINE, M.O. HALL, P.E. WHITFIELD, AND J.W. FOURQUREAN. 1999. Overgrazing of a large seagrass bed by the sea urchin *Lytechinus variegatus* in Outer Florida Bay. *Marine Ecology Progress Series* 190:211–222.
- RUIZ-MONTOYA, L., R. LOWE, K.P. VAN NIEL, AND G.A. KENDRICK. 2012. The role of hydrodynamics on seed dispersal in seagrasses. *Limnology and Oceanography* 57:1257–1265.
- SCHMIDT, A.L., J.K.C. WYSMYK, S.E. CRAIG, AND H.K. LOTZE. 2012. Regional-scale effects of eutrophication on ecosystem structure and services of seagrass beds. *Limnology and Oceanography* 57:1389–1402.
- SCHWARTZ, M., EDITOR. 2006. *Encyclopedia of coastal science*. Springer, Netherlands.
- SHAFER, D., AND P. BERGSTROM. 2010. An introduction to a special issue on large-scale submerged aquatic vegetation restoration research in the Chesapeake Bay: 2003–2008. *Restoration Ecology* 18:481–489.
- SHORT, F.T., AND S. WYLLIE-ECHEVERRIA. 1996. Natural and human-induced disturbances of seagrasses. *Environmental Conservation* 23:17–27.
- TAIT, K.J., AND K.A. HOVEL. 2012. Do predation risk and food availability modify prey and mesopredator microhabitat selection in eelgrass (*Zostera marina*) habitat? *Journal of Experimental Marine Biology and Ecology* 426–427:60–67.
- THOM, R.M., H.L. DIEFENDERFER, J. VAVRINEC, AND A.B. BORDE. 2012. Restoring resiliency: case studies from Pacific Northwest estuarine eelgrass (*Zostera marina* L.) ecosystems. *Estuaries and Coasts* 35:78–91.

- THOM, R.M., G. WILLIAMS, A. BORDE, J. SOUTHARD, S. SARGEANT, D. WOODRUFF, J.C. LAUFLE, AND S. GLASOE. 2005. Adaptively addressing uncertainty in estuarine and near coastal restoration projects. *Journal of Coastal Research, Special Issue* 40:94–108.
- VALENTINE, J.F., AND K.L. HECK. 1991. The role of sea urchin grazing in regulating subtropical seagrass meadows: evidence from field manipulations in the northern Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology* 154:215–230.
- \_\_\_\_\_. 2005. Perspective review of the impacts of overfishing on coral reef food web linkages. *Coral Reefs* 24:209–213.
- WAYCOTT, M., C.M. DUARTE, T.J.B. CARRUTHERS, R.J. ORTH, W.C. DENNISON, S. OLYARNIK, A. CALLADINE, J.W. FOURQUREAN, K.L. HECK, A.R. HUGHES, G.A. KENDRICK, W.J. KENWORTHY, FT. SHORT, AND S.L. WILLIAMS. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *PNAS* 106(30):12377–12381.
- WILLIAMS, S.L. 2001. Reduced genetic diversity in eelgrass transplantations affects both population growth and individual fitness. *Ecological Applications* 11: 1472–1488.
- WINANT, C.D., E.P. DEVER, AND M.C. HENDERSHOTT. 2003. Characteristic patterns of shelf circulation at the boundary between central and southern California. *Journal of Geophysical Research* 102(C2):3021.
- ZIPPERLE, A.M., J.A. COYER, K. REISE, W.T. STAM, AND J. OLSEN. 2009. Evidence for persistent seed banks in dwarf eelgrass *Zostera noltii* in the German Wadden Sea. *Marine Ecology Progress Series* 380:73–80.

*Received 27 April 2013*  
*Accepted 27 May 2014*