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Surfgrass Restoration in the Northeast Pacific

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PURPOSE: This technical note summarizes the current status of our knowledge regarding restoration of surfgrasses (*Phyllospadix* spp.) in the northeastern Pacific, and identifies research needs to improve the success of future restoration efforts.

BACKGROUND: Seagrass populations are declining in many areas around the world, due to anthropogenic stress and habitat alteration (Short and Wyllie-Echeverria 1996, Orth et al. 2006). Due to the universal recognition of seagrasses as valuable coastal habitats, efforts to mitigate these losses and restore seagrass communities have been underway for several decades (Fonseca et al. 1998). However, seagrasses in the genus *Phyllospadix*, also known as “surfgrasses,” differ from others in that they inhabit exposed, rocky shore intertidal and subtidal environments (Figure 1) (den Hartog 1970, Phillips and Menez 1988). As a result, restoration techniques developed for other seagrass species may not be appropriate for *Phyllospadix* spp. (Reed et al. 1998).

Restoration of *Phyllospadix* spp. has rarely been attempted, and a comprehensive review of seagrass restoration in the United States (Fonseca et al. 1998) was able to offer only limited guidance on restoration and transplantation of these species. Recently, a few studies have begun to investigate methods to restore *Phyllospadix* species (Bull et al. 2004, Holbrook et al. 2002, deWit et al. 1998, Reed et al. 1998).

Species Descriptions: Three *Phyllospadix* species occur in the northeastern Pacific, *P. scouleri*, *P. torreyi* and *P. serrulatus* (den Hartog 1970, Wyllie-Echeverria and Ackerman 2003). Unlike other seagrasses, these plants can firmly attach to rock surfaces in high-energy environments (den Hartog 1970, Cooper and McRoy 1988, Kuo and den Hartog 2006). *Phyllospadix* rhizomes attach with short, closely spaced roots to rocks (Stewart 1991). Their emergent roots are extremely short, covered with dense root hairs, and occur in two groups at rhizome nodes (Phillips and Menez 1988).

Northeastern Pacific species can be differentiated by variation in leaves, roots, spathes and the generative axis (Table 1). *P. torreyi* (Figure 2) and *P. scouleri* (Figure 3) have leaves with three nerves and the generative axis has one to several internodes with 6-10 roots. *P. scouleri* and *P. torreyi* can be differentiated by their generative shoots: *P. scouleri* has one spathe and *P. torreyi* has several spathes on each generative shoot (Figure 2) (Phillips and Menez 1988). A spathe is a leafy bract enclosing a cluster of flowers (spadix). Leaves are narrow (0.5-1.5 mm), compressed and wiry for *P. torreyi* while *P. scouleri* has 1- to 4-mm-wide, blade-like leaves. *P. serrulatus* has 2- to

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8-mm-wide leaves up to 1 m long that are serrated along the edges with 5-7 veins (Figure 4), and rhizome internodes with two roots (Table 1).



Figure 1. Mixed stand of *P. scouleri* and *P. serrulatus* on Vancouver Island, British Columbia. Photo by M. Morris.



Figure 2. Flowering shoot of *P. torreyi* at Pacific Grove, CA. Key identification characteristics are the narrow, wiry leaves and two or more spadices per generative shoot. Photo: R. C. Phillips.



Figure 3. *P. scouleri* at Cattle Point, San Juan Island, Washington. Key identification characters are the broad leaves and only one spadix per generative shoot. Photo: R. C. Phillips.



Figure 4. Veins are visible in the leaves of *P. serrulatus*. Photo by M. Morris.

Table 1
Key Characters used to Identify *Phyllospadix* spp. in the Northeastern Pacific (den Hartog 1970; Phillips and Menez 1988).

Species	Leaf Width/ Morphology	Leaf Veins	Leaf Length	# Roots/ Internode	#Spaths/Shoot (# Flowers)
<i>P. scouleri</i>	1-4 mm, flat	3	to 2 m	6-10	1-rarely 2 (14-26)
<i>P. torreyi</i>	0.5-1.5 mm, wiry	3	to 2 m	6-10	2-5 (14-20)
<i>P. serrulatus</i>	1.5-4 mm, serrated	5-7	30-100 cm	2	1 (8-10)

Geographic Range: *P. scouleri* has the broadest latitudinal range, from Sitka, Alaska to Isla Santa Margarita (Phillips 1979) on the Baja, California coast (Figure 5) (Ramirez-Garcia et al. 2002). *P. torreyi* occurs from the northern tip of Vancouver Island, Canada to Isla Santa Margarita (Phillips 1979, Ramirez-Garcia et al. 2002), Baja, California, with its primary abundance south of Monterey, California (Phillips 1979) (Figure 5). *P. serrulatus* has the most restricted distribution, from Cape Arago, Oregon northward to Chirikof Island near Kodiak, Alaska (Phillips and Menez 1988) (Figure 5). All three species co-occur from northern Vancouver Island, British Columbia to Cape Arago, Oregon.

Tidal Zonation: *P. serrulatus* is typically distributed from +1.5 m to -6.0 m MLLW, and may be found growing in cobble overlain by silt and sand in subtidal areas (Phillips and Menez 1988). Where all three species co-occur, *P. serrulatus* grows highest on the tidal gradient (Phillips and Menez 1988). *P. scouleri* is distributed from the lower intertidal zone to the shallow subtidal zone on wave-exposed coasts. Ramirez-Garcia et al. (1998) found that *P. scouleri* occurs significantly shallower than *P. torreyi* with its maximum coverage 30-40 cm above *P. torreyi*. When it occurs with congeners, it grows at an elevation lower than the other two *Phyllospadix* species, down to a depth of -15 m MLLW.

Reproductive Biology: All species in the genus *Phyllospadix* are dioecious, with male and female flowers on separate plants (Cox 1988, Kuo and den Hartog 2001, Ackerman 2006). Fruits have been described for *P. torreyi* and *P. scouleri*. They have two hooked wings (Figure 6) that lodge around coralline algae or other host algae (Gibbs 1902, den Hartog 1970, Blanchette et al. 1999, Dethier 1984). Some species in this genus can produce large numbers of seeds (e.g., up to 10,000 seeds m⁻² for *P. torreyi* (Williams 1995)). The timing of seed production varies among species as well as across latitudes (Phillips 1979, Walker et al. 2001) (Table 3).

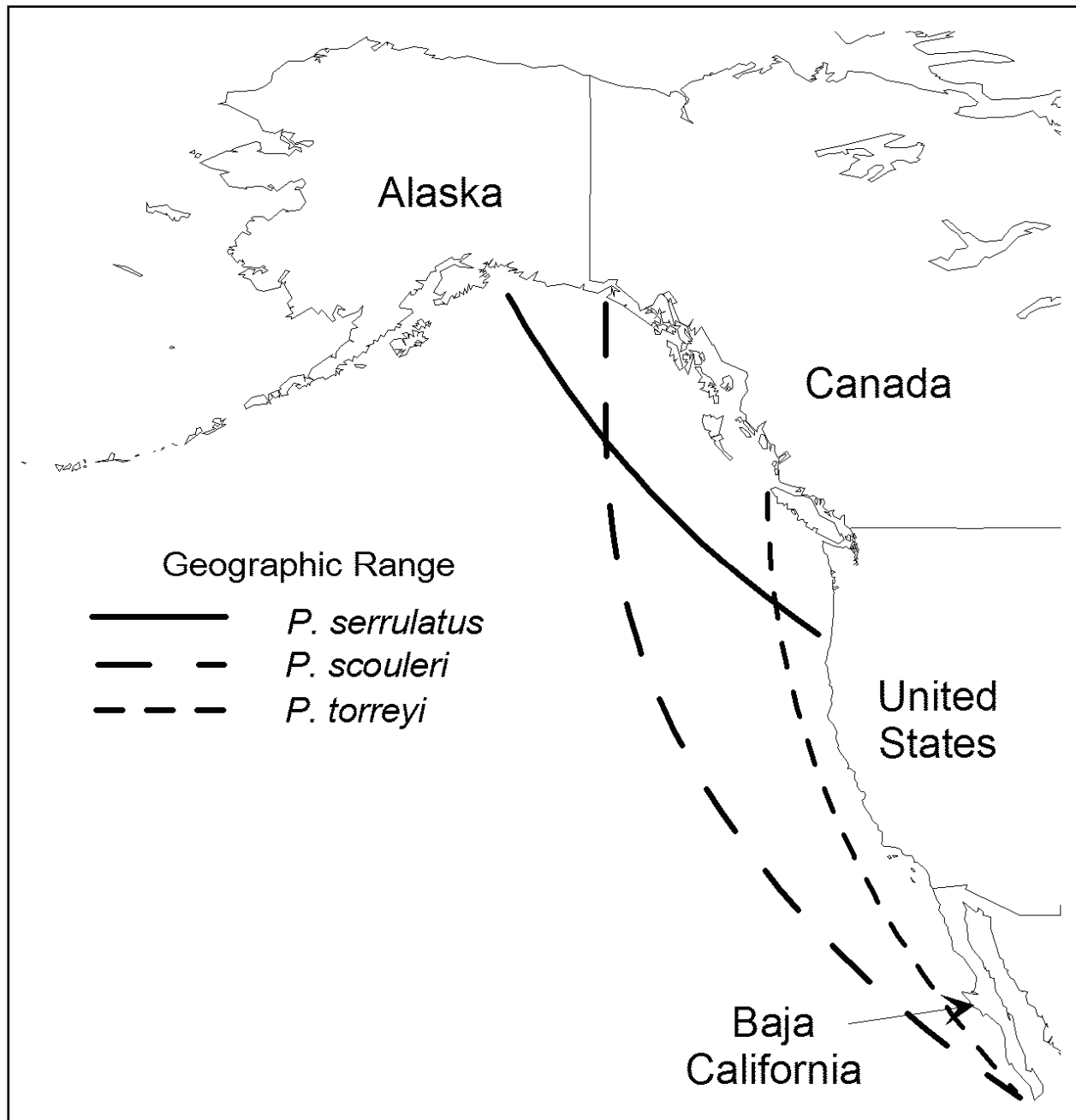


Figure 5. Distribution of northeastern Pacific surfgrasses (*Phyllospadix* spp.). *P. scouleri* has the widest range; from Sitka, Alaska to Isla Santa Margarita, Baja California, Mexico. *P. torreyi* ranges from northern Vancouver Island, British Columbia, Canada to Isla Santa Margarita. *P. serrulatus* has the most restricted range, from Kodiak Island, Alaska to Cape Arago, Oregon. All three species co-occur between northern Vancouver Island and Cape Arago.

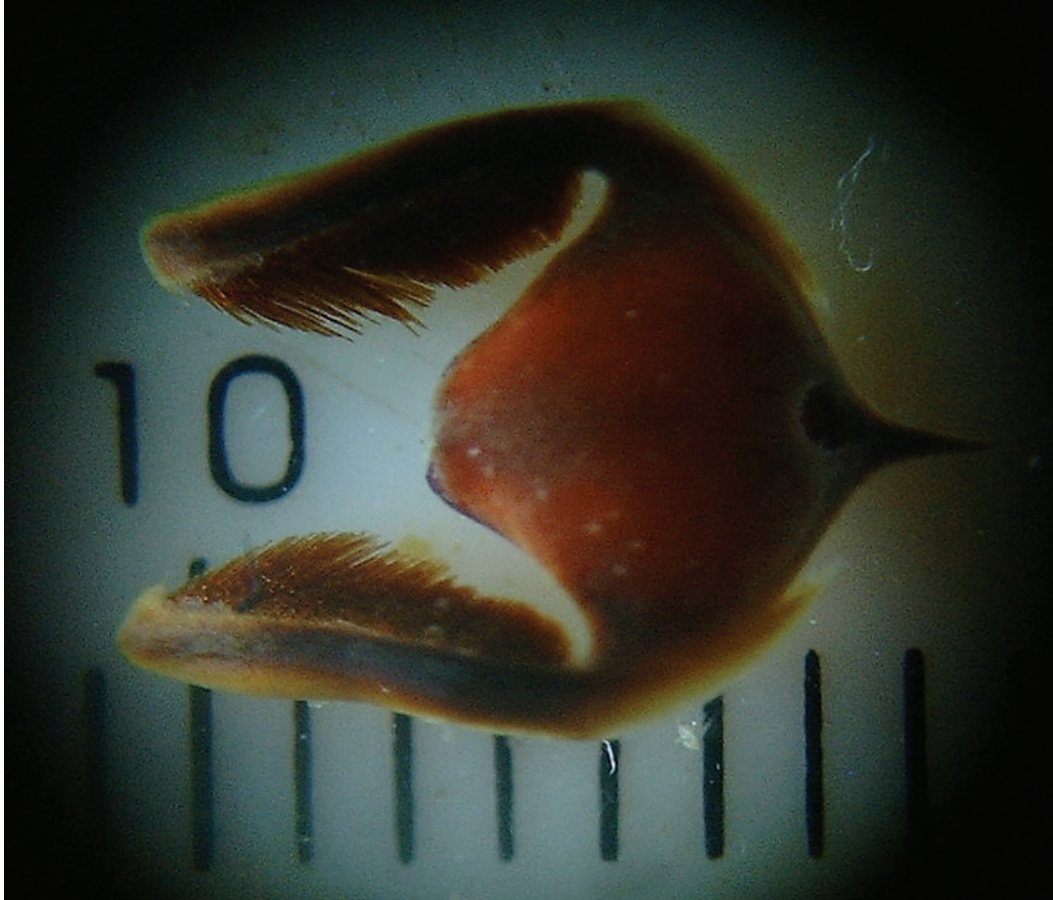


Figure 6. The fruit of *P. scouleri* showing the bristles that allow the seed to anchor to “host” algae. Units = mm. Photo: T. Wyllie-Echeverria.

Habitat Requirements: Compared to other seagrass species, very little is known about the habitat requirements of *Phyllospadix* spp. Information characterizing the optimal range of environmental conditions for *P. serrulatus* is currently lacking. *P. scouleri* and *P. torreyi* grow in regions where winter temperatures are below 21°C and summer sea surface temperatures are below 27°C (Ramirez-Garcia et al. 2002). Optimal growth occurs in more wave-exposed sites (Menge et al. 2005).

In a laboratory study that investigated environmental factors affecting growth of *P. torreyi*, optimal growth was achieved at a salinity of 29 psu, a temperature range of 12-14 °C, and 12 hr of sunlight per day (Drysdale and Barbour 1975). In a field study off San Clemente, California, no seasonality was noted in the growth pattern of *P. torreyi* (Littler et al. 1979).

Shoot length, biomass, and leaf growth rates of *P. torreyi* increased by 25-50 percent when nutrient concentrations were increased experimentally; however, *P. scouleri* did not respond to nutrient enrichment (Ramirez-Garcia et al. 2002). These authors suggest that *P. torreyi* may have higher nutrient requirements or experience lower nutrient availability than *P. scouleri* off Baja, California. Terrados and Williams (1997) found that nitrogen uptake occurs in the leaves, and not roots or rhizomes.

Table 2
Optimum Habitat Characteristics for *Phyllospadix* spp. as Determined under Laboratory Conditions. (Blank spaces indicate a lack of information. Limits have not been defined for natural populations.)

Species	Temperature	Salinity	Nutrients	Desiccation	Wave Exposure	Light
<i>P. scouleri</i>					exposed	
<i>P. torreyi</i>	12-14°C	29 psu	limited	sensitive		12 hours
<i>P. serrulatus</i>					protected	

Reproductive Biology and Seedling Survival: Laboratory Experiments

In the laboratory, highest rates of *P. torreyi* seedling recruitment were achieved under moderate flow regimes ($<85\text{cm sec}^{-1}$) and attachment to the red algae *Chondracanthus canaliculatus* and *Lithothrix aspergillum* (Blanchette et al. 1999). However, seedling recruitment success is highly variable and depends on yearly seed yield and viability in addition to currents and host availability (Blanchette et al. 1999). Population expansion by seed production appears highly inefficient (Dethier 1984; Turner 1985).

Predation may be responsible for the loss of significant numbers (30 percent) of seed stock (Holbrook et al. 2000). Crabs (*Pugettia producta* and *Pachygrapsis crassipes*) are primary predators. These animals eat the seed after release but prior to germination. A few seeds may be consumed in the spathe before release but this apparently occurs infrequently (Holbrook et al. 2000). On Catalina Island, off the coast of southern California, Williams (1995) reported that gender segregation occurs with male plants growing in deeper water than female plants. Male mortality (via displacement of adult plants) was higher than in females; it was suggested that this may result from a weaker attachment to the substrate. However, female reproductive success was apparently not limited by pollen dispersal as there was nearly 100 percent fertilization (Williams 1995).

The timing of seed production varies by latitude (Table 3). For example, *P. torreyi* seeds are dispersed in July in Canada, during August in Oregon, from May- October in California, and April-September in Baja California (Walker et al. 2001). The dehisced seeds are negatively buoyant and drift along the bottom until they become entangled in branched algae such as *Corollina vancouveriensis*, *Bossiella plumose* and *Rhodomela larix* (Dethier 1984, Turner 1983). In addition to providing an attachment surface for seeds, “host” algae also provide cover and moisture during exposure periods of low tides, minimizing seedling mortality due to desiccation (Turner 1983). *Phyllospadix* root and rhizome mats do not appear to serve as a suitable attachment medium for their own seeds (e.g. Blanchette et al. 1999).

P. torreyi was used in laboratory experiments to determine culture conditions for germination (Reed et al. 1998). Reproductive shoots of the plants were collected in September (Santa Barbara, CA) and placed in a flow-through sea water system. After approximately one month, the fruits were dehisced and placed in culture (Reed et al. 1998). Subsequent to at least a 14-day, and as much as an 83-day, dormancy period, germination rate was at least 70 percent after 4 weeks regardless of the length of dormancy. Seeds stored in cold (4°C) and dark conditions germinated within 2 weeks after exposure to ambient light and temperatures. However, germination did occur even in the cold and dark

treatment after 100 days. Reed et al. (1998) found that seeds may have a minimum dormancy period of around 2 weeks and as much as 7 weeks when exposed to cold and dark conditions.

Species	Alaska	Canada	Washington	Oregon	California	Baja CA
<i>P. scouleri</i>	Aug	Aug	Oct	Jun-Oct	Oct	
<i>P. torreyi</i>		Jul		Aug	May-Oct	Apr-Sept?
<i>P. serrulatus</i>	Aug		Jun-Oct	Aug		

¹ Data gaps are indicated by a "?", a "-" indicates that species does not occur at that location.

To test for the effect of fertilizer on transplants, Holbrook et al. (2002) used a single application of a commercially available plant hormone at a concentration of 2 percent. This resulted in a two-fold increase in root mass/total mass ratio in *P. torreyi*. Neither repeated, nor elevated dosages had further effect. In laboratory germination of *P. torreyi*, Holbrook et al. (2002) used 150 seeds per batch. Seeds were placed in 50 ml of filtered seawater and a 50- μ l nutrient stock solution (e.g. Provosoli 1968). The solution was changed weekly and kept at 16°C, a 14:10 light to dark schedule and a light environment of 40-50 μ E m⁻² s⁻¹.

Natural Recolonization Processes: When *Phyllospadix* spp. are displaced, either by natural events or experimental removal, patterns of succession have been documented. At Point Lobos, California, a ship grounding on the rocks denuded a portion of the *P. scouleri* bed, exposing bare rock (deWit et al. 1998, Walder and Foster 2000). Fuel and oil spills associated with the grounding contributed to the habitat damage. During the subsequent two years of monitoring, bare rock was first colonized by diatoms, and by week 36 coralline algae had colonized 12 percent of the area; their cover peaked at 49 percent of the area by week 88 (deWit et al. 1998, Walder and Foster 2000).

Other studies indicate that newly exposed rock is initially colonized by green algae such as *Ulva* spp., and after 5-6 months, mid-successional species of red algae such as *Corallina* spp., *Rhodomela larix*, *Cryptosiphonia woodii* and *Odonthalia floccose* appear (Turner 1983). *Corallina* spp. are able to re-grow after disturbance because the encrusted part of the alga remains attached to rock throughout stormy conditions, making the complete removal of *Corallina* spp. practically impossible (Dethier 1984). Once appropriate 'host' algal species are present, *Phyllospadix* seeds can lodge in the algae, where they attach and germinate (Turner 1983, Menge et al. 2005, Stewart 1989). When *Phyllospadix* spp. co-occur with kelps, it can be crowded out by kelp holdfasts (den Hartog 1970) or shaded out (Turner 1983, Menge et al. 2005, Stewart 1989).

Menge et al. (2005) examined established rocky intertidal community structure and found that *P. scouleri* is a dominant competitor but a poor colonizer. Colonization of bare patches and newly exposed substrate is dependent upon seedling recruitment; however, attachment and survival rates for seedlings are very low. In a study by Turner (1983), *P. scouleri* seedlings recruited into 28 experimental plots with a mortality rate of 93 percent over seven months, while another study observed recruitment rates less than one seedling m⁻² yr⁻¹ (Turner and Lucas 1985).

At Point Lobos, density of *P. scouleri* in damaged areas after two years was estimated to be only 7 percent, whereas density at control plots was 87 percent. Bed expansion is influenced by rhizomal growth; however, growth rates are slow, averaging only 6-8 cm^{-yr} (Turner 1983, Turner and Lucas 1985). The length of time required for recovery into disturbed areas is approximately 3-4 years in the Northeast Pacific region (Dethier 1984; Turner 1985).

Restoration Efforts: A literature search revealed only three sources that describe surfgrass (*P. scouleri* and *P. torreyi*) restoration projects (deWit et al. 1998, Holbrook et al. 2002, and Bull et al. 2004), all located in central California. Plugs, sprigs, and seedlings have been used as planting units.

Plugs as Planting Units

Two studies describe the use of *Phyllospadix* plugs as transplant units. In the first study, 10- by 10-cm² plugs were removed from a donor site with a paint scraper and attached to 14- to 18-kg boulders with epoxy (deWit et al. 1998). Sites were monitored for five years (1993-1997). Initial losses were very high. Of the 105 boulders that were used for transplants, only 22 could be relocated following the first winter's storms. The total area transplanted decreased by 45 percent, but remaining transplants expanded by 57 percent by the end of the study. Flowers were observed after one year. Loss of transplant substrate (boulders), detachment of transplant units by turbulence, predation by urchins and shading by kelp were identified as the major limiting factors to transplant persistence and expansion. Attachment to larger boulders and clearing away of kelp and algae were recommended as measures that could increase survival of transplants. Experimenting with urchin exclusion cages may be worthwhile but would also provide attachment places for algae.

Bull et al. (2004) compared the effectiveness of three different sizes of *P. torreyi* plugs near Santa Barbara, California: Plugs consisting of a rhizome and shoots in three sizes (5 cm², 10 cm² and 20 cm²) were extracted using a wide-blade putty knife from the center of an established bed. Plugs were prepared for transplanting by pulling leaves through a piece of 2.5-cm stretch mesh nylon net that was slightly larger than the area of the plug. The edges of the net were secured to a cleared area of rock with marine epoxy. Leaves were trimmed to a length of 20 cm to minimize drag and dislodgement.

Most transplanted plugs survived after 6 months, but survival varied with size. Small and medium-sized plugs had 100 percent survival during the experiment and rhizome coverage increased significantly in the intertidal for small plugs and in the subtidal for medium plugs. Five of the six large plugs in the intertidal zone were dislodged within days of the beginning of the experiment. The single surviving large plug increased in rhizomal coverage by 9 percent. Although survival of plugs was highest, the potential for donor bed degradation and the cost of preparing the transplanting unit make this technique the least promising. After 6 months, some regrowth into the areas where plugs had been harvested was evident (67 percent of the original area remained bare). In other areas, the size of the cleared areas increased by more than five times the original plug area, resulting in additional losses. Losses were greater for plugs harvested from the intertidal zones and may have been a result of water motion undermining the cut edges of the rhizomes (Bull et al. 2004).

Sprigs as Planting Units

In a study near Santa Barbara, California that compared the effectiveness of different types of *P. torreyi* planting units, sprigs were harvested from the periphery of an established bed with a knife and transplanted immediately after collection using marine epoxy putty (Bull et al. 2004). Rhizomes were at least 5 cm in length and contained several lateral shoots and a terminal shoot. Sprigs were attached to cleared rocks so that at least 1.5 cm of the terminal end of the rhizome was not in contact with the epoxy. Leaves were trimmed to 20 cm to minimize drag and dislodgement.

Survival of sprigs was significantly greater at subtidal sites (71.4 percent) compared to intertidal sites (47.6 percent). Loss of transplanted sprigs appeared to be from necrosis and loss of leaves rather than being dislodged. The number of leaves increased nearly 200 percent by the end of the 6-month experimental period. Rhizome coverage increased by 42 percent in the intertidal, and by 86 percent in the subtidal. By the end of the experiment, cut rhizomes at the donor site (where sprigs had been harvested from the edge of the bed) had regrown to nearly equal the area lost to harvest.

Seedlings as Planting Units

Two studies have attempted to transplant *P. torreyi* seedlings (Holbrook et al. 2002, Bull et al. 2004). Bull et al. (2004) sprouted seedlings in the laboratory and prepared them for transplanting approximately one month after germination, once a single emergent leaf was 2 cm long. Seedlings were secured to a double-braided nylon line, 7 cm in length, so that one arm of the seed coat was secured between the two strands of the line. The line was transported to the transplant site in plastic bags filled with sea water. Marine epoxy putty was used to attach each transplant unit onto rock that was cleared of algae and sand. Nearby algae were also trimmed to prevent abrasion and dislodgement. Transplants occurred in both intertidal and subtidal zones; survival and growth of the transplants as well as recovery at the donor site were monitored for 6 months. Only 1 and 2 percent of the seedlings survived in the subtidal and intertidal zones, respectively. However, the number of leaves in the few surviving seedlings increased by nearly 300 percent and plants had developed small rhizomes by the end of the 6-month study period.

Another study compared survival rates of seedlings 1) recruited naturally, 2) placed on nylon string, and 3) placed on nylon mesh. Highest survival rates (30 percent) were observed in naturally recruited seedlings, followed by seedlings attached to nylon mesh (20 percent), and 10 percent for seedlings attached to nylon string (Holbrook et al. 2002). All treatments were attached to bare rock and algal host plants were trimmed. The increased survival of seedlings on the nylon mesh substrate may have been due to higher seedling densities and reduced losses to abrasion and dislodgement resulting from the direct attachment of the mesh to the substrate. For this bioregion, the optimum transplanting unit for seedlings seems to be 20 to 105 seedlings per 20- by 20-cm² nylon mesh netting, attached by one of the seed's hooked arms into the twisted braid of the netting. The netting should be secured with marine epoxy directly to the substrate in the subtidal zone over clipped *Corallina* algae or bare rock.

From the perspective of planting unit survival, expansion, recovery of donor sites and economics, sprigs appear to be the most effective planting unit. Transplanting using seedlings needs further refinement. Although initial seedling loss was almost complete, this life history stage is worth pursuing because losses seemed to be due to predation and death of the sprouting shoot, not the

technique. Additionally, surviving subtidal seedlings increased in biomass by 300 percent, adding the most biomass of all treatments after a 6-month period. Seedlings have the additional benefit of increasing genetic diversity, which may influence restoration success (Williams 2001). To date, no attempts have been made to evaluate the effects of seed removal on natural recruitment processes.

Considerations for Restoration

Selection of an appropriate site is probably the single most important decision in the restoration planning process (Fonseca et al. 1998). If historical records indicate a lack of seagrass presence at the proposed restoration site, the site should be considered marginal at best, and should probably be rejected. For further information on planning and implementing seagrass restoration projects, see Fonseca et al. (1998).

Given the paucity of surfgrass restoration projects, an experimental approach to restoration such as that proposed by Zedler and Callaway (2000) for tidal wetlands would be extremely valuable. Incorporating research into individual restoration projects would allow for more rapid development of successful restoration techniques, and identify factors limiting restoration success. The results of these experiments could be used to improve the success of future surfgrass restoration projects.

The reproductive timing of the target species should be considered when planning a restoration project, both for the availability of seeds (if seedlings are used) and correct environmental conditions for growth. Gender bias may also influence project success in restoration projects. For *P. torreyi*, male plants dominate different habitats than female plants, and transplant losses may also be higher for male plants (Williams 1995).

Although Fonseca et al. (1998) caution that managers should not rely on natural recolonization to restore seagrass coverage, the potential for natural recolonization should be considered. If the restoration site is adjacent to existing healthy beds, colonization by rhizomal growth could occur. Natural recolonization of disturbed patches by rhizomal growth takes about 3-4 years (Dethier 1984, Turner 1985, Williams 1995).

Restoration success might be increased by employing a multi-layered approach, since the survival of seedlings, for both *P. scouleri* and *P. torreyi*, is enhanced by the presence of suitable “host” algae (Turner 1983, Menge et al. 2005, Stewart 1989). These algae not only serve as an anchor for seedling attachment, but also provide shade and moisture retention for intertidal populations during low tides (Turner 1983). Establishment of such “host” algae as *Corallina* spp. could ensure a substrate for future reseedling if either *P. scouleri* or *P. torreyi* populations are lost due to natural or anthropogenic disturbance.

Given the amount of information currently available, transplanting sprigs seems to be the most cost-efficient and effective mode of transplanting *P. torreyi* into both intertidal and subtidal zones in central California. See Bull et al. (2004) for additional details of this method.

Restoration Research Needs: The use of seeds or seedlings for restoration seems to warrant further investigation. Although seeds offer a potentially cost-effective approach for restoring large, genetically diverse seagrasses and aquatic angiosperms, their use in restoration has been limited to date (Ailstock and Shafer 2006). Recently, eelgrass (*Zostera marina*) seeds have been used for

planting and restoring large acreages (Pickerell et al. 2005, Orth et al. 2003, Granger et al. 2002). Seeds have not been used in restoring species of *Phyllospadix* and only two published accounts describe the use of *P. torreyi* seedlings. Although Bull et al. (2004) reported very low survival of seedlings, increased success (e.g., 20 percent recruitment rate) was achieved when seedlings were attached to braided nylon netting and glued to a substrate (Holbrook et al. 2002). Sources of seedling mortality in the initial stages of establishment need to be identified in order to increase success. Physical factors such as shading and current flow may also play a critical role in seedling recruitment and establishment (Blanchette et al. 1999).

Although the regional distribution of *Phyllospadix* spp. in the Northeast Pacific is established, population ecology data are lacking (except for Dethier's studies in Washington and Turner's studies in Oregon). This may handicap the development of restoration techniques and limit restoration success (see Fonseca et al. (1998) and Fonseca et al. (2007, in press) for a discussion of the importance of ecological knowledge to support restoration planning for the seagrass *Zostera marina* in this region).

The authors recommend the following research to enhance the success of *Phyllospadix* species restoration along the Pacific Coast of the United States:

- (1) Develop conceptual models that elucidate optimum growing conditions for all three species throughout their respective distributional ranges.
- (2) Describe the relative contribution of seed dispersal and rhizome expansion, not only to sustain existing patches but also to colonize adjacent sites.
- (3) Encourage region-wide studies to investigate locally adapted life history patterns (e.g. seasonal biomass allocation; rates of leaf growth) to establish appropriate planting seasons for discrete bioregions (e.g. Southern California versus Northwestern Washington).
- (4) Combine land-based mesocosm studies with field trials to identify the most appropriate restoration technique (e.g. seeds, seedlings, whole plants) for all species in the variety of habitats (intertidal, subtidal) and locations (southern, central and northern) within the distributional range of each species.
- (5) Develop cost estimates for the various restoration alternatives to provide resource managers with information to determine whether protection or restoration is the most cost-effective method to ensure species diversity and productivity (Kenworthy et al. 2006).

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