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Restoration of the bull kelp *Nereocystis luetkeana* in nearshore rocky habitats

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ABSTRACT: Anthropogenic disturbances such as shoreline development and sediment loading can reduce or eliminate *Nereocystis luetkeana* populations and commercially important species associated with *N. luetkeana.* Hence, kelp restoration will become increasingly important in urbanized nearshore areas. Techniques to establish *N. luetkeana* populations in the northwestern waters of Washington State, USA, were examined and compared: (1) out-planting recently settled zoospores and microscopic sporophytes (0.5 to 1.0 mm blade length) grown in laboratory culture, in the field onto natural substrate, and at elevated positions, and (2) transplanting juvenile sporophytes (<15 cm stipe length) from natural populations, bypassing the culturing phase. Juvenile transplants were found to be more successful than cultured out-plants. The restoration cost for juvenile transplants was 12 US dollars (USD) per installed plant with a maximum cost estimate of 200 USD m^{-2}. These had a 10 to 30% higher survival rate than previously reported kelp transplant efforts using larger individuals. The collection of smaller individuals for transplanting imposes smaller ecological costs to natural populations than does the collection of larger, established plants. Stipe breakage caused by the grazing gastropod *Lacuna vincta* posed the largest limiting factor on transplant survival. Lack of survival among the out-planted zoospores and microscopic sporophytes indicates that other methods will be more successful. Restoration efforts in the nearshore marine environment will benefit from an adaptive management approach in which techniques can be tailored to the specific physical and biological conditions at the restoration site.

KEY WORDS: Kelp restoration · *Nereocystis* · Adaptive management · Transplanting kelp · Out-planting kelp · Sedimentation · Grazing

INTRODUCTION

Nereocystis luetkeana (Mertens) Postels et Ruprecht is the structurally dominant, canopy-forming, macroalgal species in the Pacific Northwest of North America. It occurs along rocky shores from below the lowest low tide to 18 m (Kruckeberg 1991). *N. luetkeana* populations support herbivores, detritivores, and their associated food webs (Duggins 1988). The forest structure common to *N. luetkeana* provides critical habitat for a number of important commercial and sport species including salmonids *Oncorhynchus* spp., juvenile surf smelt *Hypomesus pretiosus*, rockfish *Sebastes* spp., lingcod *Ophiodon elongatus*, Dungeness *Cancer magister* and rock crab *Cancer productus* (Duggins 1988, Shaffer & Parks 1994, Shaffer 2004). Detached *N. luetkeana* also provides habitat as beach wrack (Kozloff 1993) and drift mats (Shaffer et al. 1995). Kelps play an important role in regulating nutrients by assimilating nitrogen and phosphorus directly from the water for thallus growth (Lobban & Harrison 1994). This process is utilized by operators of fish farming enterprises who have used kelps to ameliorate nutrient loading (Ahn et al. 1998, Lüning & Pang 2003). By taking up carbon dioxide and releasing oxygen, kelp forests can also offset oxygen depletion from biological and chemical

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oxygen demand (B.O.D. and C.O.D.) processes, and can serve as both a carbon sink (Merrill & Gillingham 1991a, Delille et al. 2000) and a source of dissolved organic carbon (Eckman & Duggins 1991).

Like most nearshore marine vegetation, kelp beds are adversely impacted by a wide variety of human-caused disturbances including sedimentation (Merrill & Gillingham 1991a, Cheney et al. 1994, Shaffer & Parks 1994), oil spills (Antrim et al. 1995), increased levels of metals, herbicides and detergents in the water column (Hopkins & Kain 1978, Chung & Brinkhuis 1986), ultraviolet radiation (UVR) (Swanson & Druehl 2000, Hoffman et al. 2003), and invasions by non-native species (Thom & Hallum 1990, Britton-Simmons 2004). Due to the increasing frequency and severity of these impacts, it is prudent to investigate cost-effective and adaptive methods for restoring kelp beds and the communities they support.

Large-scale kelp restoration projects have been successful but require large budgets or excessive monitoring and maintenance commitments, and therefore are not feasible for smaller-scale projects. The San Onofre Nuclear Generating Station (SONGS) mitigation used a substrate-based technique (Ambrose 1994). SONGS budgeted 4 to 6 million US dollars (USD) to establish 61 ha of kelp forest over a 2 yr period (Southern California Edison (2004) Kelp reef project; www.sce.com/PowerandEnvironment/PowerGeneration/MarineMitigation/KelpReefProject.htm). Additional reviews of this technique were done by Jara & Cespedes (1994), Reimers & Branden (1994), and Terawaki et al. (2001). Long-line cultivation was used for the Elliot Bay Marina (EBM) mitigation in Seattle, WA (Merrill 1991, Merrill & Gillingham 1991a) and though the results were rapid, the managers reported that a large amount of time was spent maintaining the long-line structure and repairing damages caused by pelagic debris (D. Cheney pers. comm.).

As the need for restoration increases, smaller-scale projects will become more common and will benefit from methods (1) that are less costly, (2) logistically easy to implement, and (3) do not require constant monitoring and maintenance. Simpler and less costly restoration methods are described by Devinny & Leventhal (1979) who cultured *Macrocystis pyrifera* (Linnaeus) C. Agardh sporophytes on 5000 m of twine that were then tied directly to rocks in a breakwater in Los Angeles Harbor, CA. This method was adapted from North's technique (1971, 1976) of culturing *M. pyrifera* sporophytes on plastic sheets and then scraping them off at the out-plant site. It was estimated that only 1 out of 100000 embryonic sporophytes developed into a mature plant (North 1976). Transplanting larger sporophytes has also been successful. Hernandez-Carmona et al. (2000) reported that by using transplanting alone, 2 divers could establish a 1875 m^2 *M. pyrifera* kelp forest in 2 yr.

In the Pacific Northwest, juvenile *Nereocystis luetkeana* (<30 cm stipe length) and other kelps tend to be most abundant in the early spring months, generally between late February and early March (Maxell & Miller 1996, L. T. Carney, J. R. Waaland, T. Klinger, pers. obs.). Many of these plants recruit in the mid to low intertidal zone (0 to −3 m MLLW) but do not survive the low spring tides that occur after the vernal equinox in this region. Because these shallow populations have a very low probability of surviving to maturity, their collection for transplanting is less likely to negatively impact the persistence of natural populations than are collections made from deeper populations. During these months, small juveniles can also be found growing under established *N. luetkeana* canopies, some of which are unlikely to survive. Although larger, established plants are available over a longer seasonal period, their collection for transplantation purposes is more likely to have a negative effect on natural populations.

For purposes of studying brown macroalgae in the field, other methods including out-planting and transplanting have been employed and are reviewed by Carney (2003). We adapted several of these techniques for restoration purposes, specifically to establish an initial generation of *Nereocystis luetkeana*, the propagules of which could sustain the population in the next generation. Because culturing the microscopic sporophyte stage from spores can require up to 4 wk in the laboratory, eliminating this culture requirement by out-planting recently settled zoospores would be advantageous in large-scale restoration efforts. Accordingly, we tested the hypothesis (H_1) that, when out-planted, recently settled zoospores and microscopic sporophytes of *N. luetkeana* will develop into macroscopic sporophytes with equal success. Because benthic microscopic stages are at risk of being consumed by herbivores and buried by sediments, we also tested the hypothesis (H_2) that *N. luetkeana* out-plants (zoospores and microscopic sporophytes) will have greater survival when elevated above the substratum, where they have a spatial refuge from herbivory and are less vulnerable to sediment deposition. To address the potential use of smaller juveniles in restoration, we hypothesized (H_3) that small juvenile *N. luetkeana* transplants (<15 cm stipe length) will re-establish and persist to reproductive maturity.

MATERIALS AND METHODS

Study sites. Two study sites in northwestern Washington, USA (Fig. 1) were chosen to represent areas

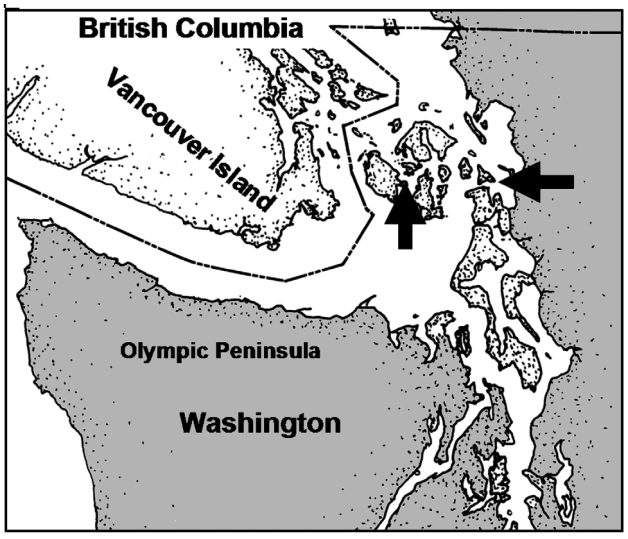

Fig. 1. Map of Washington State, USA, showing Cantilever Point (left arrow) and Saddlebag Island (right arrow)

where *Nereocystis luetkeana* might establish and survive to maturity. *N. luetkeana* forms a natural persistent bed in the north cove of Saddlebag Island (48° 32.93′ N, 122° 33.41′ W) in Padilla Bay. At a second site, *N. luetkeana* previously was established experimentally (Duggins et al. 2001) at Cantilever Point on San Juan Island (48° 32.84′ N, 123° 0.23′ W) in the San Juan Archipelago. Both sites are characterized by serpentine bedrock that is covered in places by shale and silt. Saddlebag Island is dominated by an assemblage of large brown algae, including *Laminaria bongardiana* Postels et Ruprecht, *L. saccharina* (Linnaeus) Lamouroux, *Costaria costata* (C. Agardh) Saunders, *Sargassum muticum* (Yendo) Fensholt, various species of filamentous algae (mostly Ceramiales, phylum Rhodophyta), and *Ulva* spp. (phylum Chlorophyta). The assemblage at Cantilever Point has been characterized by Neushul (1967) and by Duggins & Eckman (1994, 1997) for rocky substrate in the shallow subtidal zone of the San Juan Archipelago.

Site characterizations. A 15 m transect was established along the north-facing bank of Saddlebag Island and the southwest-facing bank of Cantilever Point, between –3.5 to –5.0 m MLLW (U.S. tidal datum). The most conspicuous grazer species observed along each transect throughout the study were identified to species.

Light and temperature were recorded along each transect every 2 h for June and July 2003. Light readings were recorded in lumens ft^{-2} (reported here in lumens m^{-2}) by 3 synchronized HOBO® LI data loggers (Onset Computer) deployed at the mid- and endpoints of each transect. These light measurements were averaged and used to characterize and then compare the study sites, and were not used to quantify light availability for photosynthesis. Although it is most informative to report light measurements as irradiance (μE m^{-2} s^{-1}), we were limited by the instrumentation available to us. To avoid reporting irradiances based on rough and possibly inaccurate conversions, we have reported only the maximum irradiance for each site using an approximate conversion from Lüning (1980) for which data (lumens m^{-2}) are divided by 49.5. Temperature was recorded by 2 synchronized HOBO® H8 data loggers (Onset Computer) deployed along each transect.

Turbidity was measured every 2 wk from September 2002 to August 2003 with a 30 cm marine Secchi disk (Secchi depth).

Seawater salinity was measured in the laboratory on an automatic temperature-compensated hand refractometer (American Optical, Scientific Instrument Division) from seawater samples (120 ml) that were collected every 2 wk by a diver during the spring and summer of 2003.

Sediment accumulation was measured from December 2002 to July 2003 using 3 sediment traps installed at the endpoints and midpoints of each transect. These were constructed by wedging a 14 ml (17 × 100 mm) polypropylene centrifuge tube into a leveled upright section of PVC pipe (5 cm in length) attached to the substrate with epoxy. The centrifuge tubes used for the traps had a height to width (H/W) ratio of 5.6. A H/W ratio between 4.4 and 6.4 is ideal for sites with moderate current velocity (Gardner 1980). Although not measured in this study, Duggins et al. (2001) found average current speed at Cantilever Point (–8 m MLLW) to be less than 10 cm s^{-1} and velocities at Saddlebag Island were suspected to be similar (authors' pers. obs.). Sediment height in the tubes was measured in the field every 2 wk with a ruler by a diver. After measurement, the tubes were cleared of all sediment and repositioned in the PVC pipe base. Data were standardized by dividing the total sediment height for each measurement by the number of full days it was deployed, not counting day of deployment or measurement. Comparisons were made between sites by averaging height-per-day measurements to get a monthly average for each site.

Out-plant experiments. To test H_1, we out-planted experimental substrates seeded either with recently settled zoospores (Z treatment), or with microscopic sporophytes (MS treatment: 0.5 to 1.0 mm blade length). Control treatments consisted of identical experimental substrates to which no seed material was added (control treatment, C). In order to test H_2, we compared survival success between out-plants attached at substrate level versus at elevated positions (7 cm above substrate).

Twenty 30 cm^2 plots were marked along transects at both sites with numbered stainless-steel washers. All plots had slopes less than 45°, similar aspects and surfaces which were smooth enough for an epoxy attachment. Prior to all epoxy applications, the rock surface was cleared by hand of macroalgae and diatom/silt cover then brushed with a stainless-steel wire brush to remove barnacles *Balanus* sp. and any fleshy algae remaining on the substrate. At Cantilever Point, which was generally covered with encrusting coralline algae, a chisel and hammer were used to remove the top layer of rock. Three 7 cm sections of 1.3 cm thick wall PVC pipe were installed in each plot at both sites. Plots were kept clear of macroalgae throughout the study.

In May of 2003, we initiated MS treatment cultures from fragments from a unialgal vegetative seed stock of *Nereocystis luetkeana* gametophytes collected in 1996 at Minnesota Reef (48° 32.14′ N, 122° 59.16′ W), near Friday Harbor. These had been previously separated into male and female gametophyte stocks and maintained vegetatively under low-light conditions at 10°C as part of the University of Washington culture collection (E. C. S. Duffield pers. comm.). Equal amounts of seed stock from separate batches of male and female gametophytes were pipetted into a chilled Waring® blender whose cutting blade had been replaced with a double-edged razor blade. Sterilized seawater (125 ml) was added and the suspension was blended for 45 s in 5 to 10 s pulses. This method is commonly used to induce fertility in kelp gametophytes (Vadas 1972, Bolton & Lüning 1982, Tom Dieck 1992, Duggins et al. 2001). Sample drops of the blended seed stock were examined microscopically to confirm densities of at least two 3 to 5 cell fragments per 0.15 mm^2. The suspension was used to inoculate 86 polystyrene sterile/gamma irradiated Petri dishes (35 × 10 mm style), each containing 4 ml of enriched seawater, with an inoculum volume of 0.25 ml seed stock per dish. This amount yielded an approximate settlement density of 5 reproductive gametophytes per 1 mm^2 in each dish. Full-strength (3.5 ml enrichment l^{-1} of seawater) Guillard's f/2 algal original recipe culture medium (McLachlan 1973) was used for the first 2 wk of the culture phase to increase nutrient availability to developing gametophytes. This had been observed to increase gamete production in earlier trial dishes (L. T. Carney pers. obs.). Medium was changed weekly and reduced to half strength enrichment (1.75 ml enrichment l^{-1} of seawater) for the third week in culture. Cultures were grown at 10°C under long day conditions (16L:8D), with a light level of approximately 70 µE m^{-2} s^{-1}. Microscopic sporophytes developed within 2 wk of inoculation. These were out-planted 21 to 23 d after inoculation, when at least 3 microscopic sporophytes (blade less than 1 mm in length) were observed in each dish.

In early June 2003, Z treatment cultures were started from sori collected from 5 individuals of *Nereocystis luetkeana* from Turn Rock (48.536° N, 122.963° W) near Friday Harbor, San Juan Island, WA. Only ripe, healthy-looking sori were taken. Sori were wrapped in moist paper towels and desiccated at 4°C for 24 h. Zoospore release was induced by soaking the desiccated sori in 1 l of sterilized 10°C seawater for 30 min. Sori were then removed and discarded. This seed stock was left to settle at 10°C for 30 to 40 min and then decanted through a sieve into a sterilized beaker. The spore concentration of the seed stock was measured using a Spotlite™ hemacytometer (1/400 mm^2, 1/10 mm deep) under a microscope (10× objective). An additional 86 Petri dishes were inoculated at a concentration of 1×10^4 spores ml^{-1} as suggested by Reed (1990) for *Macrocystis pyrifera*. The dishes were grown as described above, except that half-strength seawater medium was used from the time of inoculation. These were out-planted 3 to 5 d after inoculation. Zoospore treatments had a zoospore settlement density of 100 spores mm^{-2}.

In mid-June 2003, Petri dishes for both Z and MS treatments were installed along the transect at each site. Transportation to the field and installation methods are described by Carney (2003). Some Petri dishes were brought to the field but not out-planted. These served as a control for the effect of transportation to the field site and were monitored in the laboratory through the end of July in order to observe the effect of transport to the field, as well as culture viability. Blades developed on all monitoring dishes.

After out-planting, each plot contained 2 sets of the C, Z, and MS treatments, 1 set at substrate level and 1 elevated. Presence or absence of blades was noted for each out-planted Petri dish during 2 censuses separated by 2 wk in July 2003. Presence and absence was measured instead of total blade number because each dish would be pruned down to 1 blade in order to reduce mortality by competition if this method was used for restoration purposes. On the final census in July 2003, all remaining dishes were collected from the field and transported on ice to the laboratory where presence of *N. luetkeana* was determined using a dissecting microscope.

Out-planting experiments followed a 2 × 2 × 3 randomized block design and the levels were site, elevation and life stage.

Juvenile transplant experiment. To test H_3, juvenile *Nereocystis luetkeana* plants were transplanted from a natural kelp bed along the shoreline of Shaw Island in the San Juan Archipelago to the experimental transect at Cantilever Point. In March 2003, a diver collected 46 juvenile plants (6 to 12 cm stipe length, Fig. 2a) from the shallow edge (–3 m MLLW) of a kelp bed just south of Point George (48° 33.66′ N, 122° 59.22′ W) on the

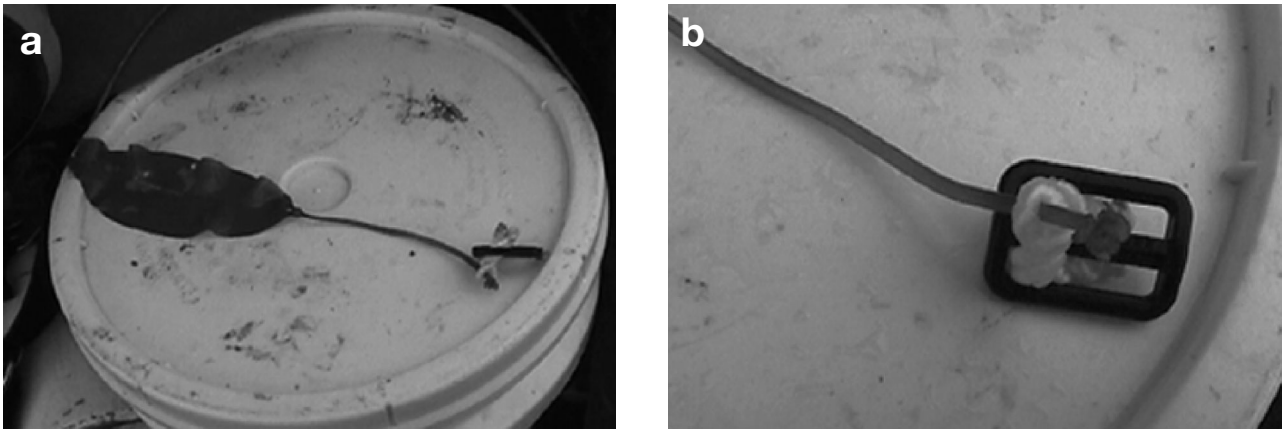

Fig. 2. *Nereocystis luetkeana*. (a) Juvenile transplant with 10 cm stipe length. (b) Close-up of a holdfast prepared for attachment and inserted into rope section and clip

southwestern shore of Shaw Island (across the San Juan Channel from Cantilever Point). At the surface, each juvenile holdfast was inserted through the middle of a 7 cm nylon rope section (0.6 cm diameter). The nylon rope previously had been soaked for several hours in distilled water, then overnight in a sodium carbonate (Washing Soda) solution (20 g l^{-1}) and then rinsed several times in distilled water in order to remove any dyes and other toxic compounds that may have been added by the manufacturer. Holdfasts were inserted into the rope in such a way that part of the holdfast was touching the rope (Fig. 2b).

Extra care was taken to avoid any damage to the stipe or holdfast, as even a small nick could cause future stipe or holdfast failure (Duggins et al. 2001). The rope sections were each threaded through a hard plastic clip and transplants were placed into a seawater-soaked pillowcase and transported to Cantilever Point, across the San Juan Channel. Within 1.5 h of collection, a diver transported the juveniles to Cantilever Point and out-planted 32 individuls along the transect. Each clip, with juvenile, was attached with marine epoxy directly to the cleared substrate, taking special care to avoid getting fresh epoxy on any part of the juvenile thallus. Once attached, the juvenile holdfast was within a few centimeters of the substrate.

Percent survival was calculated on each subsequent visit through July 2003. Reason for failure, when it occurred, was recorded for each transplant loss. A method failure was recorded if the clip, rope, or epoxy failed. Holdfast, stipe, or bulb failure was determined based on remnant tissue (Duggins et al. 2001). Stipe length was recorded for each surviving transplant 24 and 119 d after transplanting. Grazers (gastropods only) were counted and identified on each remaining transplanted stipe at Cantilever Point during a dive 119 d after transplanting. Echinoderms were never observed in the plots at either site.

Cost benefit analysis. The time requirement and monetary costs for each restoration method were determined and weighed against establishment success. The cost per plant was estimated by dividing the total cost of each method by the number of plants installed for each technique rather than the number that actually established. This was done because there is a cost involved with installing plants regardless of survival. The establishment success was then compared in light of the implementation costs.

RESULTS

Biological and environmental site conditions

At Cantilever Point, we continually observed grazers in the plots. The most conspicuous of these were identified as *Lacuna vincta*, *Margarites pupillus*, *Calliostoma ligatum*, *Bittium eschrichtii* and *Tonicella lineata*. Two weeks after the June 2003 out-planting, we observed these species in the majority of the Petri dishes.

Average daylight irradiances are shown in Fig. 3. For both sites, maximum irradiances (1370 lumens m^{-2} or approximately 27.6 µE m^{-2} s^{-1} for Saddlebag Island and 4500 lumens m^{-2} or approximately 90 µE m^{-2} s^{-1} for Cantilever Point) reached saturating levels (1000 to 2000 lumens m^{-2} or approximately 20 to 40 µE m^{-2} s^{-1}) reported for *Nereocystis luetkeana* growth by Vadas (1972). It should be noted that irradiances were lower at Saddlebag Island than at Cantilever Point on average; however, light was not limiting at either site.

Average temperatures are shown in Fig. 4. Temperature ranged from 10 to 16°C for Saddlebag Island and

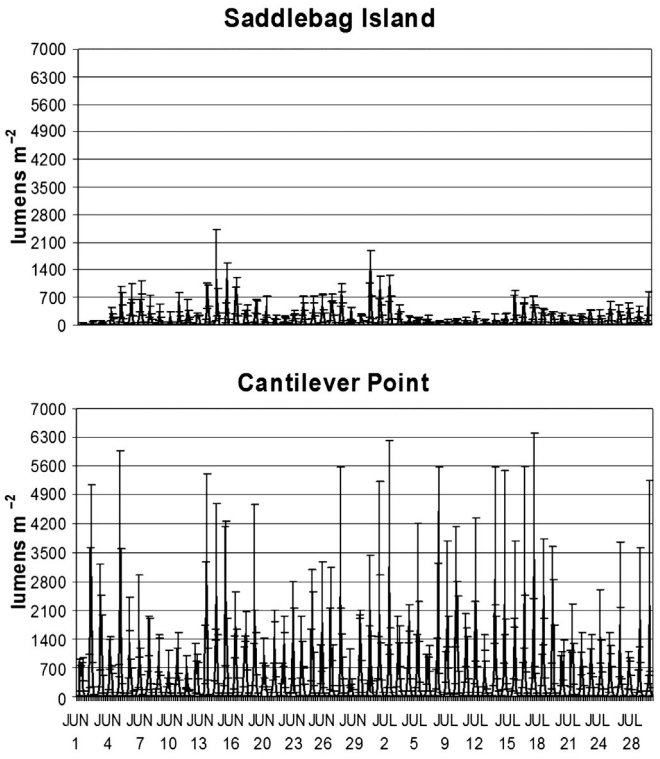

Fig. 3. Light quantity. Average light quantities recorded along the transect at each study site between June and July 2003. These data were recorded in lumens ft^{-2} and reported in lumens m^{-2} by multiplying original data by 10.76. Error bars indicate the standard deviation (SD)

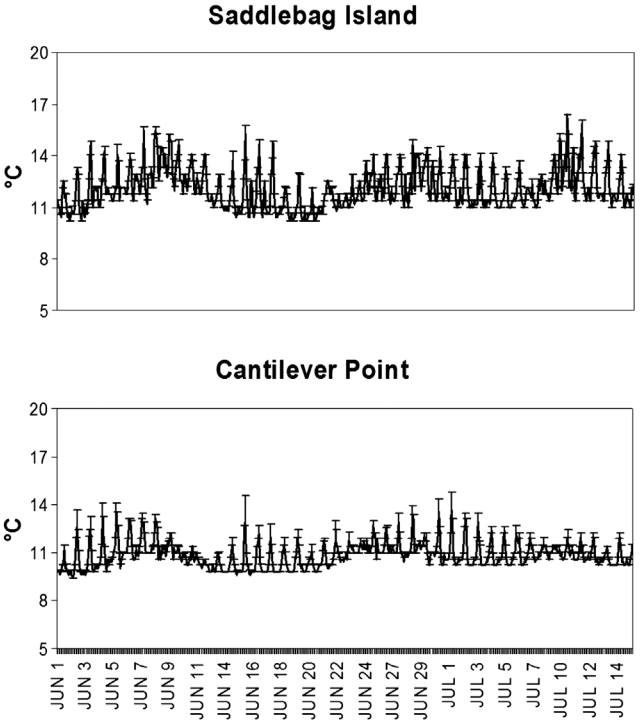

Fig. 4. Temperature. Average temperatures recorded along the transect at each study site between June and mid-July 2003. Error bars indicate the standard deviation (SD)

from 9 to 14°C for Cantilever Point. These temperatures are within the range in which *Nereocystis luetkeana* is known to develop and recruit (Vadas 1972, Maxell & Miller 1996). Slightly higher temperatures were recorded at Saddlebag Island than at Cantilever Point. This is likely due to the fact that Saddlebag Island is located in Padilla Bay, an expansive area of shallow mudflats, while Cantilever Point is influenced by deeper, well-mixed water.

Seawater sample salinity showed continuous readings of 29‰ for Saddlebag Island and 30‰ for Cantilever Point. These values are conducive to *Nereocystis luetkeana* development and within the range reported for populations in the Puget Sound region (Maxell & Miller 1996).

Average monthly Secchi depth and sediment accumulation are shown in Fig. 5. Secchi depth averaged 4.2 m for Saddlebag Island (mean ± 1.3 SD) and 7.7 m for Cantilever Point (mean ± 1.6 SD). The sites were significantly different in terms of Secchi depth (paired-samples *t*-test, p = 0.000) and sedimentation (paired-samples *t*-test, p = 0.003). Secchi depth was consistently more shallow, i.e. turbidity was higher, at Saddlebag Island than at Cantilever Point. Average sediment accumulation per day was 0.097 cm (mean ± 0.016 SE) at Saddlebag Island and 0.051 cm (mean ± 0.011 SE) at Cantilever Point. Accumulation at Saddlebag Island was approximately twice that for Cantilever Point.

Cultured out-plant survival

No recruitment was observed at either site on the dishes out-planted in June 2003 during the first and second July 2003 censuses. Over the experimental period, 52.5% (42 out of 80) of all out-planted cultured dishes were lost at Saddlebag Island. Sparse fouling macroalgae, chain-forming diatoms and juvenile barnacles were observed on most of the out-planted dishes. A layer of sediment (~1 cm) was present in all dishes. In contrast, only 11% (9 out of 80) of all out-planted Petri dishes were lost at Cantilever Point. Half of the remaining dishes were clean of all algal growth except for chain-forming diatoms and gastropod grazers which were observed on a third of the dishes. Because *Nereocystis luetkeana* was not observed on any of the substrates out-planted with cultured kelp in this study, H_1 and H_2 could not be tested.

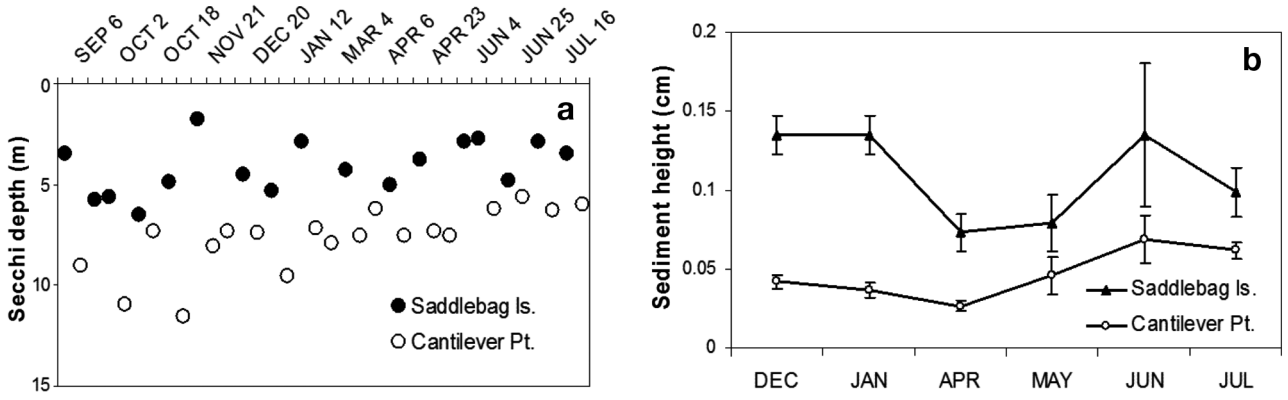

Fig. 5. (a) Secchi depth and (b) sediment height measured at both study sites from 2002 to 2003. Note the different start dates. Error bars indicate the standard error (SE) for monthly data (monthly values are based on the average of all sampling dates during the month, calculated as the average of the 3 sediment traps along the transect)

Juvenile transplant establishment

The number of transplants that survived through the study and the reasons for failure among those that did not survive are shown in Table 1. Average stipe length is reported when available. Nine of the original 32 transplants (28%) survived throughout the study period. These individuals produced and shed sori for at least 80 d, a conservative estimate considering sori were first observed on the blades 56 d after transplanting and their production could have been initiated anytime between then and the time of the previous site visit, 37 d after transplanting. The mean number of days the transplants survived was 56 d, although the 9 surviving at the end of the study persisted longer than others.

A mortality rate of 56% occurred for the first 24 d and was primarily due to method failure. The majority of the method failures (97%) were due to a break in the epoxy bond between the clip and substrate. The holdfasts of all remaining transplants were observed to have established within 56 d after transplanting.

Aside from the period between 10 and 24 d after transplanting, stipe failure remained constant at 3% throughout the study. Holdfast failure was never observed during the experiment.

During the grazer survey at the end of the study, an average of 14 grazers was counted per transplanted stipe. Of 140 gastropod grazers observed on the stipes of the 10 individuals remaining at the time of the survey, 128 (91%) were *Lacuna vincta* and 12 (9%) were *Margarites pupillus* and *Calliostoma ligatum*. *L. vincta* were also observed (but not quantified) on the pneumatocysts and blades of the transplants and *M. pupillus* and *C. ligatum* were only observed on the lower portions of the stipes (<1 m from holdfast) and on the holdfasts of the transplants.

Cost benefit analysis

Cultured out-plants

To out-plant 80 seeded Petri dishes (potentially yielding 1 plant each after pruning) a total of 50 person hours were required for collecting sori, culturing, site preparation, out-planting the seeded substrate and monitoring and maintaining the out-plants (Table 2).

Table 1. *Nereocystis luetkeana*. Transplant survival and reason for failure surveyed every 2 wk during the 135 d of the study. Data are shown as a percentage of the 32 original transplants, for each survival count. The number of individuals that each percentage represents is shown in parentheses. Stipe length range is included when available

Days after transplanting	Stipe length (m)	Survivors (%)	Failure type (%)		
			Method	Stipe	Pneumatocyst
0	0.06–0.12	100 (32)	–	–	–
10		84.4 (27)	12.5 (4)	3.1 (1)	
24	0.5–1	43.8 (14)	18.8 (6)	18.8 (6)	3.1 (1)
37		40.6 (13)	–	3.1 (1)	–
56	~2–3	37.5 (12)	–	3.1 (1)	–
70		37.5 (12)	–	–	–
80		34.4 (11)	–	3.1 (1)	–
119	2.8–4.4	31.3 (10)	–	3.1 (1)	–
135		28.1 (9)	–	3.1 (1)	–
Total		28.1 (9)	31.3 (10)	37.5 (12)	3.1 (1)

Table 2. Cost breakdown for 2 restoration methods tested. Cost per plant is the total cost for each method at 1 site divided by the best-case potential yield of each method: 80 plants for cultured out-planting and 32 for transplanting method. USD: US dollars

	Rate	Cultured out-plants	Juvenile transplants
Lab time	15 USD h^{-1}	210	–
Dive time (2 divers)	15 USD h^{-1}	270	75
Boat time (1 driver)	15 USD h^{-1}	270	150
Boat fuel	1.50 USD gal^{-1}	100	50
Materials		180	107
Total		1030	382
Cost per plant		12.87 USD	11.93 USD

The cost per installed plant was approximately 13 USD, including materials, fuel and hourly rates for divers, lab techs and boat drivers. Because no recruitment was obtained, it can be concluded that the costs far exceeded the benefits.

Juvenile transplants

To transplant 32 plants, a total of 22 person hours were required for site preparation, juvenile collection, transportation and transplantation (Table 2). The cost per transplanted plant was approximately 12 USD, including materials, fuel, and hourly rates for divers and boat drivers. This method resulted in a 28% survival rate of sexually mature *Nereocystis luetkeana*, all of which contributed propagules to the surrounding area for at least 80 d.

DISCUSSION

Transplanting was found to be the most effective method for establishment of reproductive adults, and had the only positive cost benefit. Although over 70% of the transplants were lost by the end of the study, the survivors all produced sori, and most likely contributed large numbers of spores to the local area for at least 80 d. For the purposes of restoration, we consider losses of this order to be acceptable if surviving individuals promote natural recruitment and interannual persistence at the restoration site.

Factors contributing to the success and failure of juvenile transplants

Stipe failure was the leading cause of transplant mortality. We attributed stipe failures to damage by grazers, particularly *Lacuna vincta*, which were abundant on the thallus tissue (lower stipe and holdfast) remaining after stipe failure. Mortality resulting from damage to stipes by grazing *L. vincta* is consistent with the findings of Duggins et al. (2001), who reported that *Nereocystis luetkeana* juveniles transplanted to Cantilever Point (Cantilever Point at –8 m, MLLW) in 1996 suffered a high degree of stipe failure due to deep incisions caused by grazing *L. vincta*. However, in contrast to the findings of Duggins et al. (2001), grazer abundance on the transplanted stipes was 33% lower in this study and the mean number of days the transplants survived (56 d) was more than twice as long as those transplanted in 1996 as reported by Duggins et al. (2001).

The major differences between the 2 studies were the timing of the transplant (October [Duggins et al.] vs. March [this study]) and the size of transplanted sporophytes (3 to 4 m [Duggins et al.] vs. 6 to 12 cm [this study]). Light levels and temperature are reduced and may be suboptimal for growth during the late fall, a time when natural populations of *Nereocystis luetkeana* begin to senesce (Kozloff 1993, Maxell & Miller 1996). Additionally, increased storm surge in the fall increases the risk that transplants will be lost before they become naturally established. Optimal light and temperature conditions and lower storm surge occur during the spring, making it the best season for transplanting small sporophytes.

The late fall timing of transplanting and the larger size class used may have interacted to increase grazing pressure among Duggins et al.'s 1996 transplants. Martel & Chia (1991) found that juvenile *Lacuna vincta* are most abundant in the canopy layer of kelp beds in April through May and then again in the late summer through fall months after the larvae are released by the adults in the understory. After this period, they move down to the understory zone via the stipes. Because Duggins et al. (2001) transplanted older juveniles in the fall, at a time when canopy kelps support large populations of juvenile *L. vincta* on their fronds, stipe grazing may have been more intense after transplanting. Fewer larvae would be present on plants collected prior to recruitment in April, leading to small populations among the transplanted stands. Furthermore, slower kelp thallus growth rates in the fall could allow higher numbers of grazers to develop on the blades, compared with faster growing plants collected in the spring. In this study, smaller juveniles were transplanted and were noted to be free of grazers along their thalli. Consequently, the timing of transplanting may be an important factor in the success of transplantation efforts in which *L. vincta* or another canopy recruiter is the dominant grazer.

It should be noted that a portion of the reported stipe failures in this study could have been caused by damage incurred during collection and transplantation. Young juveniles are highly susceptible to small injuries (nicks and scratches), which can propagate as the plants grow and can cause breakage. Extreme care was taken not to damage the plants during collection, transport and transplanting, and juveniles that showed any signs of damage at the time of installation were discarded. However, it cannot be ruled out that some individuals were transplanted with undetected damage.

Method failure was the second leading cause of mortality and was due to a break in the epoxy hold on the substrate. Attachment via growth of haptera onto the natural substrate corresponded to an immediate decrease in mortality caused by method failure. Similar findings are reported by Hernandez-Carmona et al. (2000) for juvenile *Macrocystis pyrifera* transplants attached to cut but intact holdfasts of an understory kelp with rubber bands. Establishment by growth and attachment to natural substrates is the primary goal of transplantation. Survival may have been considerably higher in this study if a method that does not rely on an epoxy bond had been used. Duggins et al. (2001) never observed method failure when *Nereocystis luetkeana* transplants were secured to the bottom with nylon cable ties. However, abrasion from the cable tie could be problematic for younger transplants and would need to be modified. Other mechanical attachment methods that might be adapted for use in restoration are described by Druehl (1978).

Transplant size

Other researchers have either used or recommended the use of larger-sized transplants (>1 m stipe length) for increased survival (Druehl 1978, Hernandez-Carmona et al. 2000, Duggins et al. 2001, Kawamata 2001, G. Hernandez-Carmona pers. comm.). In this study, transplanting smaller plants was just as effective as larger-sized plants, if not more so, with approximately 20% more surviving after 45 d than in previous efforts using larger plants (Duggins et al. 2001).

Individuals collected from areas where they are unlikely to survive to maturity might reasonably be used for these purposes. However, we offer this suggestion with caution, and emphasize that we do not advocate decimation of healthy, established beds for purposes of transplantation. Such action would be inconsistent with the intended purposes and long-term benefits of transplantation for restoration.

Smaller plants are easier to work with due to their size; consequently, a larger number of individuals can be transplanted given a fixed amount of economic resources. Higher drag forces are exerted on larger plants (Denny & Gaylord 2002) and therefore, mortality rates could be increased for larger transplants prior to natural establishment and depending on the attachment method used. Further, due to morphological differences between blades from high and low current areas (Koehl & Alberte 1988) adult transplants cannot withstand being moved from low to high current sites (Druehl 1978, Kawamata 2001). It may be best to transplant only small (<30 cm stipe length) plants that do not have mature blades of a certain morphology and are not already colonized by grazer larvae. Although the availability of younger juveniles limits transplanting to the spring, the present study shows that transplant survival at this time is higher than during other seasons.

Factors contributing to the success and failure of cultured out-plants

In Washington State, sporophtyes of *Nereocystis luetkeana* are first visible in late winter and early spring and shed sori throughout the late spring, summer and fall (Maxell & Miller 1996). In previous trials not reported here, out-planting was performed during the spring, summer and fall months to account for seasonal variation in the success of this technique. No establishment was observed for out-plants regardless of season (Carney 2003). Although the details of the seasonal trials are not reported here, we cannot recommend the use of cultured out-plants for restoration, regardless of season.

Sedimentation was the major limiting factor at Saddlebag Island. Devinny & Volse (1978) reported a 90% mortality rate for *Macrocystis pyrifera* spores covered by a 0.045 cm thick layer of sediment and showed that sediment can also smother an already attached gametophyte. By these estimates, the sediment observed in the Petri dishes after out-planting (~1 cm) and the 0.1 cm d^{-1} accumulation rate at Saddlebag Island was sufficient to prevent recruitment, regardless of elevation above the substratum. It is likely that the Petri dishes amplified the negative effects of sedimentation by collecting and holding sediment and are certainly not ideal under these conditions. However, previous trials performed in this study (Carney 2003) but not reported here used a wall-less plastic substrate with the same result. According to the recommendations of Devinny & Volse (1978), locations such as Saddlebag Island, where rocky substrate is routinely covered with sediment, should be avoided as restoration sites.

Interestingly, natural recruitment is not prevented by sedimentation at Saddlebag Island, and a natural *Nereocystis luetkeana* population persists there. Garbary et al. (1999) hypothesized that in areas where

sediment accumulation is high, microscopic *N. luetkeana* germlings growing endophytically in filamentous red algae may experience higher survival. Such a strategy could reduce the negative impacts of high sediment loads. It is possible that the natural population at Saddlebag Island depends on an endophytic relationship between its microscopic stages and red algae for initial survival. Alternatively, natural recruitment at Saddlebag Island may occur during infrequent windows of low or no sedimentation.

Whereas sedimentation was minimal at Cantilever Point, grazers were noted during every dive in and around the installed features. As described in the literature (Robles & Cubit 1981, Robles 1982, reviewed by Foster & Sousa 1985), elevating out-plants can be effective in deterring less maneuverable grazers but complex elevation structures can provide refuge to other grazers, particularly coiled snails, fish and amphipods, exaggerating their effects. Coiled snails were continuously observed in the elevated Petri dishes, although they may have served as protection from less maneuverable grazers such as chitons, limpets and echinoids, which were never observed in the dishes. The fact that the Petri dishes collected sediment and seemed to capture or retain gastropod grazers did not allow the effect of elevation to be tested properly at either site. However, elevating or suspending out-plants has been found by other researchers to be advantageous (Devinny & Leventhal 1979, reviewed by Foster & Sousa 1985).

The purpose of testing the use of small styrene substrates for restoration was to find inexpensive materials that could be easily installed. Small substrates attached on the bottom to natural rock are less vulnerable to damage caused by pelagic debris than a suspended rope structure but are more vulnerable to sedimentation and grazing. The effects of grazing and silt are largely avoided when out-planting seeded twine (Devinny & Leventhal 1979, Merrill & Gillingham 1991a) because the out-plants are raised above the benthic layer and can later be lowered when the plants are larger and less affected by benthic processes. Biodegradable string or twine has been suggested as the ideal substrate for out-planting kelps (L. D. Druehl pers. comm.) due to its hydrophilic quality and maneuverability during installation.

Although out-planting cultured kelp did not result in recruitment in this study, the method has been used successfully in other studies (Hsiao & Druehl 1973, Devinny & Leventhal 1979, Deysher & Dean 1986, Lee & Brinkhuis 1988, Reed 1990, Merrill & Gillingham 1991b, Duggins et al. 2001) and it may be advantageous to investigate further for kelp restoration purposes. It would be more cost effective to out-plant an earlier stage (e.g. recently settled zoospores) and reduce time spent in the culture phase. Further work could be done to determine the requirements for success of such a method.

Recommendations for kelp restoration

The subtidal rocky nearshore is an unpredictable environment; light, temperature, nutrient availability, turbidity, water motion, salinity and grazing pressure all vary with season, depth, and location. Restoration in this environment will benefit from an adaptive management approach, since variation between and within sites is potentially large and is due to factors that remain largely uncontrollable. The concept of adaptive management is outlined in the literature (Lee 1993, Murray et al. 2000, Marmorek 2003). As uncertainties regarding the outcomes of a restoration method increases, this approach becomes more useful because it is aimed at using experimentation to ameliorate them. To augment this approach, it is desirable to test multiple planting techniques at a restoration site prior to a large-scale planting. Combining multiple restoration techniques, such as transplanting and sorus seeding, is recommended in the literature (North 1976, Hernandez-Carmona et al. 2000) and increases the likelihood of success given a high degree of environmental variability. The experience gained from using multiple adaptive techniques allows managers to design a more effective approach for future efforts.

The results of this study reveal some of the uncertainties associated with marine restoration and demonstrate that using planting techniques can be difficult and some degree of failure should be expected. Considering this difficulty, restoration budgets need to be flexible, leaving room for improvement, and in some cases, replacement of a method. With this in mind, important recommendations can be made from the present study and are highlighted below. These and others are described in more detail by Carney (2003).

A restoration site must be chosen carefully in order to avoid unnecessary mortality. When out-planting the microscopic stages, restoration sites where sedimentation rates are high should be avoided. If these sites cannot be avoided, transplanting young juveniles (<15 cm stipe length) is recommended because these have developed past the size class most impacted by sedimentation. Although it might be anticipated that a high siltation rate would prevent survival of a second generation at the site, a natural population does persist at the Saddlebag Island site, indicating that natural recruitment occurs even in the presence of sedimentation, perhaps via initial endophytism in understory algae.

If cultured microscopic stages must be used because juveniles are not available, the out-plantings should be elevated on a device that excludes sediment and grazers. Suspending seeded twine above the bottom may be the best option; however, this should be firmly secured to avoid abrading the plants during periods of current when twine could be dragged across nearby rocks. Dominant grazers should be identified before planting and modifications made accordingly. Elevated treatments may exclude less maneuverable grazers but are useless against herbivorous fish and some gastropods. Grazer exclusion devices, such as cages or nets, should be weighed for cost benefit if these types of grazers are abundant. If increased loss due to grazer inflicted damage is expected, it may be advantageous to clear both the substrate and transplants of grazers on a weekly basis. Planting may also be timed to avoid periods when the dominant grazers are at their highest densities.

Approximately 60% of all out-planted substrates and 30% of all transplants were lost in this study due to epoxy failure. Failure could have been caused by residual natural material missed during the substrate cleaning before the epoxy was applied; local faunal activity of river otters *Lutra canadensis*, sea stars *Pisaster ochraceous*, Dungeness and red rock crab (*Cancer* spp.) observed on or around the plots; or, increased water motion. We cannot recommend the use of epoxy for restoration purposes without caveats; however, if an epoxy-based method is used it should be tested at a restoration site prior to any large-scale installations. Using seeded twine for cultured out-plants avoids epoxy use entirely. Methods that tie transplants directly to the substrate seem the most effective in promoting fast establishment and eliminating method based failure (see Druehl 1978, Hernandez-Carmona et al. 2000, Duggins et al. 2001, Kawamata 2001).

Given a 30% transplant survival rate and a reported natural maximum density of 3 to 6 ind. m^{-2} (Shaffer 1998), we estimate that *Nereocystis luetkeana* restoration using transplanting will cost approximately 120 to 200 USD m^{-2}. This calculation is based on the cost per plant reported in Table 2 and is likely an overestimate since it is quite easy to both collect and install a larger number of individuals given the same amount of resources because juveniles are found at high densities in the field. The cost per plant could be markedly reduced by both transplanting more juveniles per unit area and by using a non-epoxy based attachment method as described above. We suggest this due to both the high rate of epoxy failure observed in this study and the high market cost of marine epoxy (approximately 40 USD l^{-1} for Woolsey®/Z•SPAR® epoxy). When transplanting is called for, pilot studies should be performed to identify areas and planting densities that have the appropriate cost–benefit ratios. With practice, greater efficiencies and economies of scale are likely to reduce the cost per plant.

Although it is possible to establish *Nereocystis luetkeana* at sites lacking kelp beds, restoration may be most effective when combined with conservation efforts, especially when the goal is to enhance an existing system. We caution, though, that one must consider population genetic effects when using transplants to enhance and conserve natural populations, in order to maintain adequate levels of population-genetic diversity. Once restoration methods are chosen, plantings should be dense and may have to be repeated each spring for several years in order to offset a high failure rate from any of the above-mentioned factors. We anticipate that the restoration of kelp and other macroalgal communities will become increasingly necessary as coastal development expands and as global change alters the nearshore environment. New restoration methodologies must be developed in response to these needs, and the transplant methodologies tested here provide an important first step.

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