CENTRAL ORANGE COUNTY AREAS OF SPECIAL BIOLOGICAL SIGNIFICANCE

EXPERIMENTAL RE-ESTABLISHMENT OF THE ROCKY INTERTIDAL BROWN ALGA *SILVETIA COMPRESSA* AT LITTLE CORONA DEL MAR

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<u>1.0</u> <u>SUMMARY</u>

Flora and fauna in the rocky intertidal zones in southern California and elsewhere have exhibited changes in abundance and community composition over the past several decades. These changes include declines in mussel populations and mussel-bed-associated species diversity and shifts in seaweed community structure with fleshy seaweeds being replaced by low-lying, turf-forming species. In the Area of Special Biological Significance (ASBS) located in Newport Beach, Orange County, CA at Robert E. Badham Park (also known as Little Corona del Mar (CDM)), changes in seaweed communities are particularly evident including the disappearance of the important habitat-forming, brown-algal rockweed, *Silvetia compressa* (J. Agardh) Serrão, Cho, Boo & Brawley. The purpose of this study was to test the efficacy of several methods for experimentally re-establishing *Silvetia* at CDM and examining the factors that might affect survival. The ultimate goal was to: a) re-establish this rockweed in CDM where it was abundant during the 1950s; b) determine an effective procedure that can be used to re-establish *Silvetia* at this and other sites; and c) to determine the importance of biotic and abiotic factors in the success of re-established thalli. This study was implemented in two Phases.

In Phase I, starting in February 2007, we investigated two methods for re-establishing *Silvetia*. These were: a) the transplantation of juvenile thalli; and b) the relocation of fertile reproductive structures to seed the area with rockweed germlings. Transplantation was accomplished by removing small sections of bedrock to which individual juvenile (< 2.5 cm diameter) *Silvetia* thalli were attached by using mechanized angle-grinding saws. The seeding technique consisted of the removal of fertile reproductive branches from randomly chosen thalli which were then placed in porous containers bolted to the substratum. All donor materials were collected from a healthy population of *Silvetia* at Morning Canyon, a nearby rocky intertidal site. The effects of grazing and canopy-protection, two factors known to influence the success of juvenile and early post-settlement stages of *Silvetia* and other rockweeds, also were examined. To exclude most grazing invertebrates, a ring of marine epoxy coated with a copper-based anti-fouling paint was placed around randomly chosen plots. Canopy-protection was afforded by small sections of acrylic designed to simulate natural frond protection from desiccation stress and wave energy. Phase I studies were conducted at four study sites using a three-way factorial design. The transplanted and seeded replicates were monitored monthly until February 2008. We were not successful in re-establishing recruits from our seeding technique, and transplanted juveniles exhibited relatively low survival. However, survival of juvenile transplants appeared to be enhanced by the presence of the simulated canopy treatment but did not differ among sites or in the presence or absence of grazers.

In Phase II, initiated in January 2008, we transplanted large fertile (15-40 cm in length) thalli and small juvenile (< 2.5 cm diameter) thalli onto both horizontal (< 30°) rock surfaces and the landward sides of vertical (> 45°) surfaces at CDM. Similar sized individuals on both types of surfaces were marked at the Morning Canyon donor site, but not manipulated, to compare transplant survival with natural survival rates. Monthly

monitoring of these transplants and marked plants continued through January 2009. Transplants exhibited moderate survival rates but, not surprisingly, were lower than the rates for natural thalli. In addition, we found that large thalli transplanted onto north-facing vertical surfaces exhibited the highest survivorship.

To attempt to determine reasons for disparate success rates of transplants located on horizontal and north-facing vertical surfaces, we performed an experiment designed to test the relative levels of desiccation stress experienced by *Silvetia* on the two substrata. The results of this experiment supported our hypothesis that less desiccation stress occurs on the vertical surfaces in relation to horizontal surfaces. This implies that transplanted *Silvetia* occurring on vertical surfaces may receive an ecological advantage over transplants on horizontal substrata. Furthermore, we observed that mortality of transplants on horizontal surfaces may be increased due to the negative trampling effects by human visitors.

Although monitoring needs to be continued, it is likely that we have successfully re-established a self-sustaining rockweed population at the site, given the survival rates of transplanted materials and the high number of transplants placed at CDM in Phase II. This is further evidenced by the presence of more than a dozen “naturally” recruited individuals that likely originated from our transplanted thalli.

2.0 INTRODUCTION

Coastal ecosystems are subjected to perturbations from both natural sources, such as changing ocean conditions, sand movement, drying winds, boulder movement, competition, and predation, and anthropogenic sources such as pollution, urban development, and exploitation (Diefenderfer et al. 2003). As the degree and frequency of anthropogenic disturbances intensify, the ecological services provided by important biogenic habitats, such as coral reefs, estuaries, mangroves, kelp forests, and eelgrass beds, are increasingly becoming impacted (Field 1998; Fonseca et al. 1998; Thayer 1992; Turgeon et al. 2002). For instance, global coastal wetlands are declining at a rate of 1% annually due to human reclamation (Nicholls et al. 1999), and coral reefs throughout the Caribbean are becoming dominated by fleshy algae through the combination of nutrient inputs and overfishing (Hughes 1994; McClanahan and Muthiga 1998; McCook 1999).

Anthropogenic perturbations in rocky intertidal ecosystems are evident worldwide. These have been linked to global declines in large conspicuous invertebrates (Keough et al. 1993, Miller and Lawrenz-Miller 1993, Addessi 1994, Pombo and Escofet 1996, Goodson 2003), seagrasses (Short and Wyllie-Echeverria, 1996), and brown fleshy algae (Bokn and Lein, 1978; Bokn, 1979; Vogt and Schramm, 1991; Rodriguez-Prieto and Polo, 1996; Oliveira and Qi, 2003), and a shift towards seaweed communities dominated by disturbance-tolerant turfs (Worm et al., 1999; Benedetti-Cecchi et al., 2001). In California, and particularly in southern California, increased urbanization of coastal regions over the past several decades has resulted in increased anthropogenic disturbance during which many changes in flora and fauna have been observed. For example, Smith et al. (2006) documented significant losses in mussel cover and biomass throughout southern California. Even though the exact cause of mussel loss is not known, the disturbances caused by high populations of humans in coastal areas of southern California are believed to have contributed to these declines (Smith et al. 2006; 2008). Escalating levels of human disturbance in southern California also are hypothesized to have caused significant changes in the structure of rocky intertidal macrophyte communities (Dawson 1959, 1965; Widdowson 1971; Murray and Littler 1984). Many intertidal macrophyte communities near southern California urban centers were once dominated by highly productive, large to mid-sized, fleshy macrophytes but now support high abundances of less productive, small, turf-forming and crustose algae (Dawson 1959, 1965; Widdowson 1971; Thom & Widdowson 1978; Murray et al. 2001; Gerrard 2005; Murray et al., unpublished data). As large, fleshy seaweeds decline in abundance, there are likely cascading effects that impact species abundances, community composition, or ecosystem functioning.

In habitats affected by anthropogenic disturbances, re-establishing or enhancing depleted populations of important biogenic habitat-forming species is a common strategy to restore abundances and ecosystem functioning. Re-establishment or restoration efforts are common in terrestrial (e.g. Larissa et al. 2006) and, to lesser degree, in coastal ecosystems (e.g. The Batiquitos Lagoon dredging project (City of Carlsbad and COE 1990)); however, these efforts have resulted in both success and failure. For example, while Larissa et al. (2006) was successful at re-introducing 24 species of oak woodland understory vegetation to a degraded early-successional woodland in central Iowa, the creation of a tidal wetland at Agua Hedionda Lagoon in San Diego, California, was criticized as being inadequately implemented (Zedler 1996). In some cases, attempts at re-establishing populations have resulted in failure but have led to a further understanding of ecosystem functioning (e.g. The Connector Marsh in San Diego Bay), and have highlighted the need to better understand the factors that affect restoration efforts. Although re-establishment is a common technique to combat ecological change as a result of human influences, to our knowledge only one restoration project has been attempted in the rocky intertidal zone [e.g. the reintroduction of *Fucus* on Alaskan rocky shores following the Exxon Valdez oil spill by Stekoll and Deysher (1996)].

On rocky shores, fleshy seaweeds that have been declining over the past few decades are good candidates for restoring community structure because they are often biogenic habitat-forming species that play an important role in community structure. In southern California, the mid-intertidal rockweed *Silvetia compressa* (J. Agardh) Serrão, Cho, Boo & Brawley [formerly *Pelvetia fastigiata* (J. Agardh) DeToni and *Pelvetia compressa* (J.Agardh) De Toni], is a good candidate for re-establishment because this rockweed is highly productive (Littler 1980), provides a source of food for many grazers (Gunnill 1980), and forms habitat for a diverse assemblage of seaweeds and invertebrates (Hill 1980; Gunnill 1985; Thompson et al. 1996; Sapper and Murray 2003). Reintroducing *Silvetia* into a site may provide a source of local recruitment and facilitate re-establishment of populations of this key species, and lead to enhanced species diversity at the site (Sapper and Murray 2003). Even though only one study has experimentally reintroduced a rockweed for the purpose of ecosystem restoration (see Stekoll and Deysher 1996), projects carried out in terrestrial habitats have shown that it may be possible to restore ecosystem functioning by recovering damaged populations of key species in affected habitats (e.g. Larissa et al. 2006).

Robert E. Badham Park (referred herein as Little Corona del Mar (CDM)) is an Area of Special Biological Significance (ASBS) located in Newport Beach, Orange County, California. This site has exhibited multiple changes in flora and fauna over the past several decades (Nicholson and Cimberg 1971; Thom and Widdowson 1978; Goodson 2003; Murray et al. unpublished data) highlighted by an absence of the rockweed *Silvetia compressa* since the 1970s (Nicholson and Cimberg 1971; Thom and Widdowson 1978; Goodson 2003; Murray et al. unpublished data). Given the importance of this species, we attempted to re-establish a *Silvetia* population at CDM. In addition, because of the lack of literature describing seaweed restoration projects in rocky intertidal habitats, we experimentally tested techniques and factors that may affect re-establishment of this species. We hypothesized that factors such as inter-site differences, age/size of thalli at out-planting, grazer presence, natural canopy accommodations by neighboring thalli, and the orientation of substrata used for out-planting, may play important roles in determining the success of *Silvetia* restoration efforts. Our intention was to implement experimental designs that would test the ability of each of these factors to affect the re-establishment of *Silvetia*. The ultimate goal was to: a) re-establish this rockweed at CDM where it was abundant during the 1950s; b) determine an effective procedure that can be used to re-establish *Silvetia compressa* at this and other sites; and c) to determine the importance of selected biotic and abiotic factors in the success of re-established thalli.

3.0 METHODS

3.1 PHASE I:

3.11: STUDY SITES

Four rocky intertidal sites were established along ~4 km of similar, semi-protected, southwest-facing coastline in Orange County, California during January 2007 (Figure 1). The four study sites, Crystal Cove State Park (CRC), Morning Canyon (MOR), and two locations at Little Corona del Mar (CDM A and B) are characterized by similar geologic origin, and marked by the presence of conglomerate and granitic boulders atop siltstone substrata that form flattened and angled rocky benches (Littler 1977; Moeller 2002). All sites are exposed to similar oceanographic regimes. Surface sea temperatures range from 9.9ºC in March to 24.4ºC in July during the year 2006 and salinities from 28 to 34‰ (Balboa, Newport Beach, California; http://shorestation.ucsd.edu/). Due to the close proximity of the sites to each other, there is little variation in either temperature (≤1ºC) or salinity (≤1‰) among sites at any point in time (Sapper & Murray 2003).

Figure 1. Location of four study sites utilized in Phase I of the study.

The four study sites are subjected to varying levels of anthropogenic disturbance (Littler and Littler 1987, Murray et al. 1999, Goodson 2003; Sapper and Murray 2003). The CDM A and B sites receive disturbance from the activities of human visitors, which are more numerous per linear meter of shoreline than at any other intertidal site in the region (Tenera Environmental 2004). CDM site A, and to a lesser extent site B, are also subjected to continuous run-off from coastal development through Buck Gully (Goodson 2003). CRC is less disturbed by coastal runoff and receives only moderate levels of human use (Sapper and Murray 2003) with approximately one third of the visitors per year experienced by CDM (Tenera Environmental 2004). MOR is subjected to intermediate levels of disturbance since this site receives continuous terrestrial runoff. However, MOR experiences considerably lower levels of human use than CDM (Ware, pers. comm.). All four study sites are located within California Marine Life Refuges (now referred to as State Marine Conservation Areas) where collection of intertidal flora and fauna has been prohibited by law for more than 30 years (McArdle 1997).

In addition to differences in natural and anthropogenic disturbance levels, *Silvetia* abundances also vary markedly among sites. At CDM sites A and B, rockweeds were absent at the beginning of this study despite being noted as common to abundant during Dawson's 1956 survey of site A (Dawson 1959). Subsequent samplings of the same transects used in Dawson's 1956 survey have indicated that *Silvetia* has likely been absent from site A since at least the 1970's (Nicholson and Cimberg 1971; Thom 1976; Goodson 2003; Murray et al. unpublished data). At CRC, *Silvetia* thalli are rare on the rocky platform selected for study and are confined to a single 0.5 m^2 patch. However, it should be noted that rockweeds are abundantly present on an intertidal rocky reef located < 0.5 km upcoast from the platform chosen for study at CRC. At MOR, *Silvetia* is locally abundant and spans large areas of the intertidal. In this study, MOR served as the source for rockweed specimens, fertile receptacles, and also provided a control site for testing re-establishment methodologies.

3.12 OUT-PLANTING TECHNIQUES

Two out-planting techniques were evaluated for restoring *Silvetia*: 1) naturally seeding the substratum by relocating fertile receptacles, and 2) transplantation of small, juvenile rockweed plants.

The natural seeding method was initiated in early February 2007 during the time of year that *Silvetia* thalli are highly fertile (Moeller 2002). The method involved the attachment of porous containers (10 cm x 10 cm; screen size = 1 cm) filled with freshly collected, fertile rockweed receptacles (Fig. 2). These receptacles contain pit-like structures called conceptacles, which in turn, contain the oogonia and antheridia. The oogonia and antheridia produce eggs and sperm, respectively, which are typically released simultaneously during day-time low tidal events (Johnson and Brawley 1998, Brawley and Johnson 1999). The release of largely non-motile gametes during periods of low tide emersion results in low dispersal distances (<1m) from parent populations (Williams and Di Fiori 1996) and very high (≈100%) fertilization rates (Brawley 1990, Johnson and Brawley 1998). Like the early post-settlement stages of many seaweeds, the post-settlement mortality of *Silvetia* recruits is extremely high (Brawley and Johnson 1991, Johnson and Brawley 1998, Moeller 2002). For example, Moeller (2002) estimated mortality of early post-settlement Phases (=zygotes and germlings up to 15 mm in size) of *Silvetia* in southern California to be more than a million fold.

Twenty four of the porous containers containing fertile receptacles were bolted to the substratum using stainless steel hardware at each of the three experimental study sites and at the donor site. The rock surfaces underneath the containers were etched with a mechanized angle-grinding saw to provide cracks and crevices, which are known to facilitate the post-settlement survival of fertilized *Silvetia* eggs (Brawley and Johnson 1991). Reproductive material within the 'receptacle containers' was refreshed approximately every two weeks until late March, when receptacle and conceptacle production in southern California populations of *Silvetia* decreases significantly (see Moeller 2002).

Figure 2. Porous container used to hold fertile receptacles. Note the etched surface of the substratum.

In late February 2007, using mechanized angle-grinding saws, rockweed specimens were transplanted by removing small sections of bedrock to which individual juvenile (< 2.5 cm diameter) *Silvetia* thalli (Fig. 3) were attached. Candidate thalli were haphazardly selected from the donor MOR population. Rock sections with attached thalli were reattached into pre-cut depressions in the substrata at recipient sites using marine epoxy putty (Z spar, Kopper's Co. Los Angeles) (Fig. 4). Twenty four individual juvenile thalli were transplanted onto flat substrata (<30º) at the donor site and also at each of the three recipient sites.

Figure 3. Juvenile *Silvetia* thallus attached to small section of bedrock.

Figure 4. Reattached section of bedrock and juvenile *Silvetia* thallus.

Silvetia and other rockweeds have highly constrained vertical distributions with respect to tidal height. To determine appropriate locations for out-planting, each of the recipient sites was marked simultaneously as the tide receded according to information relayed from the donor site regarding the emersion of upper and lower intertidal boundaries of the MOR *Silvetia* population. Using this method to delineate potential habitat for *Silvetia* accounted for discrepancies among sites that may result from variations in oceanographic conditions and topographical composition. Final out-plant locations at all sites were measured with topographical surveying equipment and were determined to occur between + 1.04 m and + 0.27 m above MLLW. For comparison purposes, the upper and lower intertidal boundaries of the existing *Silvetia* population at the donor site were measured to be +0.99 m and +0.32 m above MLLW, respectively.

3.13 TREATMENTS

Two of the most important factors affecting recruitment, growth, and the survivorship of juvenile or post-settlement stages of seaweeds in intertidal habitats are grazers that consume or damage seaweed thalli (Dethier et al 2005) and canopy fronds that protect vulnerable stages from desiccation stress and wave energy (Davison and Pearson 1996). To test the hypotheses that grazer exclusion and the protective presence of canopy enhance recruitment and survivorship at each of my sites, a crossed design in which combinations of simulated canopy (– and +) and grazer (– and +) treatments were randomly assigned to the two re-establishment techniques. These treatments were also applied in the absence of out-plants to provide a control for natural recruitment that may occur due to the presence of simulated canopies and/or the exclusion of grazers. Six replicates of each of the four treatment combinations (– canopy + grazers, – canopy – grazers, + canopy, + grazers, and + canopy –grazers) were applied at all four sites (Fig. 5).

SITE	CORONA DEL MAR (Upcoast)				CORONA DEL MAR (Downcoast)				MORNING CANYON				CRYSTAL COVE			
GRAZERS	+G		-G		+G		-G		+G		-G		+G		-G	
CANOPY	+C	-C	+C	-C	+C	-C	+C	-C	+C	-C	+C	-C	+C	-C	+C	-C
REPLICATES	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6

Figure 5. Experimental design for the Phase 1 of the study.

To exclude grazers, a ring of marine epoxy (approximately 15 cm in diameter, 2-3 cm wide) coated with a copper-based anti-fouling paint (Trinidad SR Antifouling Bottom Paint, Pettit Paints [Rockaway, New Jersey, USA]) was placed around randomly selected plots (Fig. 6). Copper-based paint is a commonly used method to exclude some mobile intertidal invertebrates, such as chitons and limpets, with little negative impact on the biology of species in the immediate area (e.g. Cubit 1984; Benedetti-Cecchi and Cinelli 1997; Paine 1984, 1992, 2002). The painted barriers are less effective in excluding some types of grazers, including littorines (*Littorina*) and turban snails (*Chlorostoma*, *Agathistoma*), shore crabs (*Pachygrapsus*), hermit crabs (*Pagurus*) as well as many microherbivores. To reduce the impacts of this latter group, all grazers located within rings were removed prior to, and repeatedly after, transplantation throughout the monitoring process.

Figure 6. Grazer-exclusion treatment.

To simulate natural frond protection from desiccation stress and wave energy, canopies made of clear acrylic (1 cm x 10 cm x 10 cm) were attached approximately 3-4 cm above the substratum using stainless steel hardware (Fig. 7). A piece of white fabric (terry cloth) cut to fit each canopy was glued to the bottom of the plexi-glass to reduce irradiance. Photosynthetically active radiation (PAR) measured under and away from the canopies on a cloudless day using a cosine PAR sensor and data logger (LI-COR model LI-1000 [Lincoln, Nebraska, USA]) revealed that irradiance was reduced by 80% under canopies but remained above levels (75-150 $\mu mol \cdot m^{-2} \cdot s^{-1}$) limiting photosynthesis in this rockweed species (Oates and Murray 1983). In addition, using fabric as a material to inhibit irradiance had the added benefit of retaining moisture during tidal emersion (pers. obs.).

Figure 7. Simulated canopy treatment.

3.14 DATA COLLECTION

All out-planted materials were monitored monthly for survival, in the case of juvenile transplants, or successful establishment of recruits. Thalli were only recorded as missing if the entire holdfast became detached. Twelve months following initial transplant, survival/establishment was determined and analyzed statistically.

3.15 DATA ANALYSIS

Qualitative data were obtained to evaluate the success of the two restoration methods. For the procedure involving the transplantation of *Silvetia* juveniles, survivorship was recorded (+ or -). Data were examined for variance homogeneity, transformed where necessary to meet parametric criteria, and analyzed using a nominal logistic regression analysis which can use binomial categorical data to calculate the proportion of thalli surviving the entire 12-month study period. Site, canopy treatment, and grazer treatment were fixed factors. Statistical analysis was performed using JMP software (SAS Institute 2007). For the procedure involving re-located receptacles, success was defined as achieved if *Silvetia* recruits were observed in the study plots. Data for this procedure were recorded using a four-part scale (0 = absent, + = low abundance, ++ = medium abundance, +++ = high abundance).

3.2 PHASE II

3.21 STUDY SITE

In early January 2008, a second Phase was initiated involving the transplantation of additional *Silvetia* thalli (n = 134) into one study site, CDM, location A (Figure 1). The decision to use one study site was based on the results of Phase I where site differences in the survival of juvenile transplants were not detected (see Results, Fig. 9). Transplants were placed in similar tidal ranges as previously discussed with tidal ranges in Phase II ranging from +1.09 m to +0.21 m above MLLW

3.22 OUT-PLANT TECHNIQUE

Similar methodologies to the one utilized in Phase I were applied in this Phase entailing the use of mechanized angle-grinding saws to remove rockweed specimens again with the small sections of bedrock to which they were attached. Candidate thalli were haphazardly selected from the MOR population. Rock sections with attached thalli were reattached at CDM A into natural depressions in the substrata using marine epoxy putty (Z spar, Kopper's Co. Los Angeles).

During Phase I, we observed that rock dust resulting from the cutting procedure may have contributed to the accelerated desiccation of candidate thalli during the early days following transplantation. Therefore, special care was taken during Phase II to ensure that all transplanted thalli were wrapped with cloth prior to being removed and rinsed with water during the transplant process to reduce injury.

3.23 TREATMENTS

Juvenile stages of *Silvetia* experience high post-settlement mortality (Gunnill 1980, Brawley and Johnson 1991). However, mortality rates for *Silvetia* have been shown to decrease with age (Gunnill 1980). Therefore, age at transplantation may play a significant role in the ability of individual *Silvetia* thalli to persist. For Phase II, we tested this hypothesis by transplanting two size classes of *Silvetia*; smaller, non-reproductive (< 2.5 cm diameter) and larger, reproductively fertile (15-40 cm in length) thalli (Fig. 8).

Figure 8. Fertile *Silvetia* thallus.

The slope of the substratum is another factor that may significantly affect the growth and survivorship of *Silvetia* thalli (Gunnill 1980). Vertical surfaces receive less disturbance induced by human trampling compared with horizontal (<30°) surfaces (pers. obs.). Additionally, at this northern hemisphere and southwest-facing site, north-facing vertical surfaces may receive less wave energy, reduced irradiance, and decreased direct sun exposure and therefore reduced desiccation (Brawley and Johnson 1991), than substrata oriented horizontally. Collectively, these conditions possibly provide an ecological advantage for transplanted *Silvetia* thalli growing on such surfaces. Therefore, we tested the hypothesis that north-facing vertical subtrata (> 45°) positively influence transplanted rockweed survivorship and growth rates by placing half of the replicates from both size classes onto horizontal surfaces (< 30°) and the other half onto the landward, north-facing sides of vertically-angled substrata (> 45°) (Fig. 9). To ensure that the original orientation of transplanted material did not affect survivorship, we transplanted thalli into approximately the same orientation on similarly sloped substrata at the recipient site (CDM) as the orientation and substrata from which they were removed at the donor site (MOR).

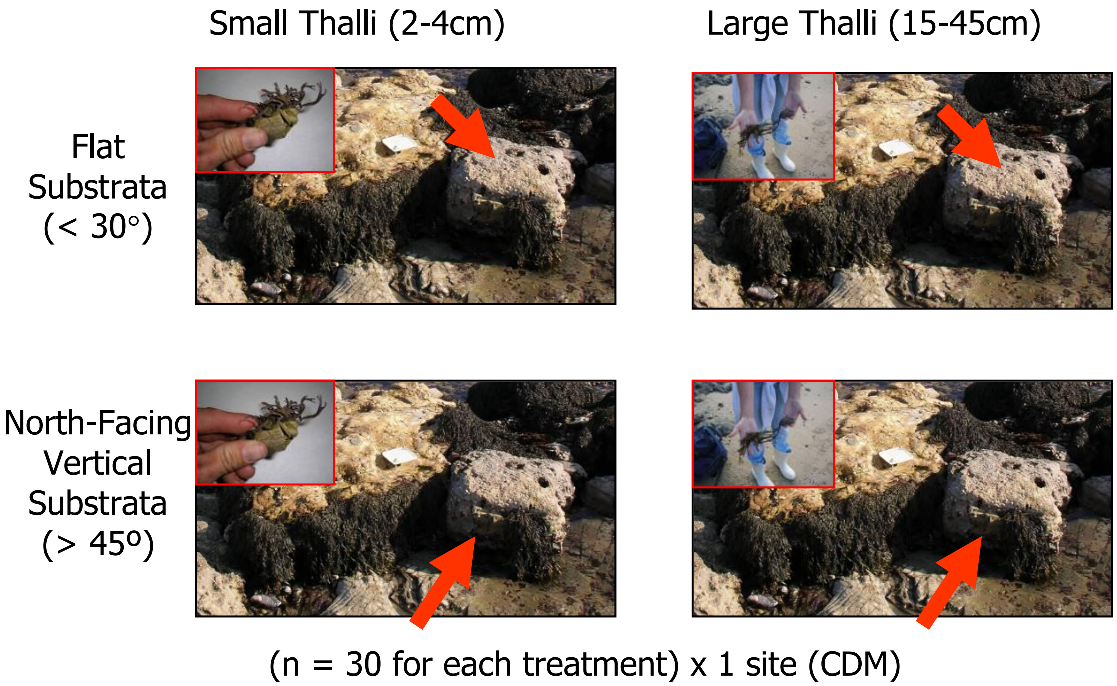


Figure 9. Experimental design for Phase II of the study.

3.24 DESICCATION EXPERIMENT

To determine if horizontal and vertical rock surfaces differ in the degree of desiccation, we measured relative levels of desiccation stress experienced by *Silvetia* on both types of surfaces, as well as that which occurs under the natural canopy provided by large *Silvetia* thalli. This experimental design consisted of weighing similar-sized units of clipped *Silvetia* thalli multiple times throughout two low tidal cycles during the year as they lay in each of the three described microhabitats; clipped materials were only placed underneath canopies during the second low tidal cycle. Conditions on both cloudless days remained similar with temperatures averaging ≈ 18 °C, wind speed < 1.5 m/s, irradiance ≈ 2,000 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and 0% humidity. Clipped thalli were initially weighed at time of emersion and placed on horizontal or vertical surfaces near transplanted materials at CDM, or underneath natural *Silvetia* canopies at CDM. Clipped materials were reweighed every ~ 30 min to determine desiccation rates. The overall change in weight was calculated for each unit over the course of both low tidal cycles.

3.25 NATURAL SURVIVAL RATES

To determine differences in survivorship and growth that may arise temporally and spatially between transplanted *Silvetia* at the recipient site and naturally existing *Silvetia* at the donor site, individual thalli were located and marked at the donor site (MOR) prior to the initiation of the Phase II transplant experiment. These *Silvetia* plants were not manipulated and thus provided natural survival and growth rates within established populations. Both small and large individuals on vertical and horizontal surfaces were used in this study.

3.26 DATA COLLECTION

All out-planted materials and marked thalli at MOR were monitored monthly for survival and quarterly for growth (change in surface area, maximum length, weight) from January 2008 to January 2009. Thalli were only recorded as missing if the entire holdfast became detached. In an effort to help avoid discrepancies between weight measurements of attached thalli and ‘actual’ weights of unattached thalli, a pilot experiment was conducted involving replicated measurements of attached thalli on both horizontal and vertical substrata followed by measurements of the same thalli post-detachment. Data were then examined for variance homogeneity and analyzed statistically.

For small thalli, surface area was calculated using an image processing program (SigmaScan Pro 5.0 [Chicago, Illinois, USA]) to analyze digital photographs taken of individuals that had been flattened against a white sheet next to a scaled object. Twelve months following initial transplant, survival was determined and growth rates were calculated and analyzed statistically.

3.27 DATA ANALYSIS

Qualitative and quantitative data were obtained to evaluate the success of the re-establishment technique involving the transplantation of small and large *Silvetia* thalli. Survivorship was recorded (+ or -) and change in size was determined by the surface area of small thalli and maximum length/weight measurements taken on the large transplanted and marked thalli to provide assessments of growth rates. Data were examined for variance homogeneity, and transformed where necessary to meet parametric criteria. Survival data for both the transplants at CDM and the marked thalli at MOR were analyzed using a nominal logistic regression analysis with thallus status (transplanted or naturally-existing), size class, and substratum orientation as fixed factors. Survival rates of transplants at CDM were then analyzed separately with the same procedure. Quarterly growth assessments were used to calculate percent changes from initial. These were then analyzed using a repeated measures 2-way ANOVA. Additionally, final results for the percent change in growth of all thalli were analyzed using two-factor ANOVAs with thallus status and substratum orientation as fixed factors. Since different parameters were measured for small and large thalli, size classes as well as measurement parameters were analyzed separately. Statistical analyses for survival data were performed using JMP software (SAS Institute 2007). All other statistical analyses were performed using Minitab software (2000).

For the desiccation experiment, the overall change in weight for each sampling unit over the course of both low tidal cycles was used in either a two-sample t-test (in the case of the first experiment involving two treatments) or an ANOVA (for the second experiment involving two treatments and natural canopy) to determine differences between and among treatments.

4.0 RESULTS

4.1 Phase I

By the end of the 12 month-long phase (March 2008), the out-planting technique involving the relocation of fertile receptacles had failed to yield any *Silvetia* recruits in any treatment at any of the four study sites.

For transplanted juveniles, we found low survival rates following completion of the monitoring period (Fig. 10) with only 18 total transplants of 96 (19%) surviving among all sites and treatments. Survival of transplants did not vary significantly among sites or for the grazer treatment, but the presence of canopy did significantly enhance survivorship (Table 1). Note that interaction effects were not included in analysis to reduce issues of multicollinearity. Not surprisingly, we found a peak in mortality during the first several months following transplants (Fig. 11) but continued to observe mortality throughout the experiment.

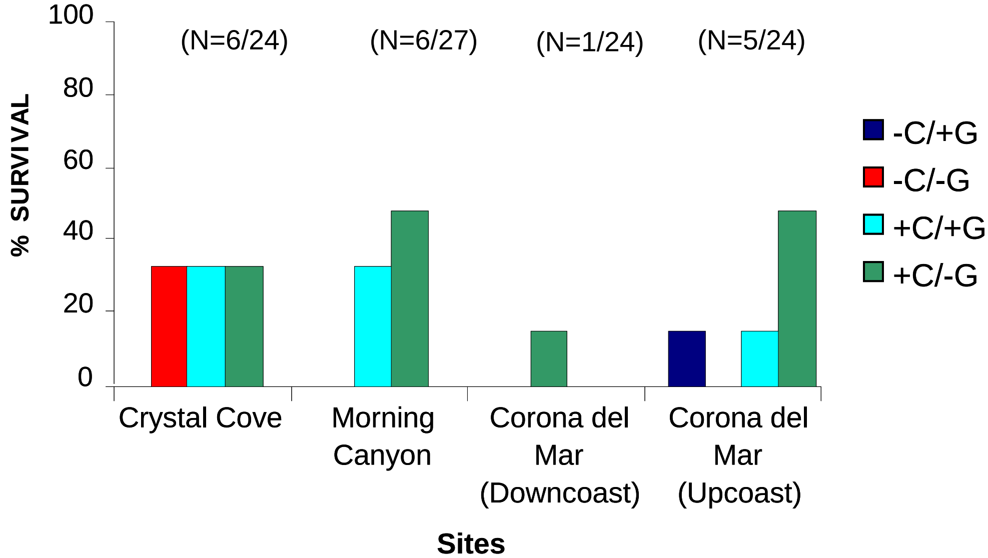


Figure 10. Survivorship (%) of transplanted *Silvetia* juveniles in each of the four treatments after 12-months at each study site. Represented within each site are the four grazer and canopy treatments: -C/+G, canopy absent, grazer control present; -C/-G, canopy absent, grazers removed; +C/+G, canopy present, grazer control present; +C/-G, canopy present, grazers removed.

Table 1. Nominal logistic regression analysis of the 12-month results for survivorship of all the *Silvetia* transplants at the four study sites and treatments.

Source	Nparm	DF	Chi Square	P
Site	3	3	5.844	0.1194
Grazers	1	1	2.232	0.1352
Canopy	1	1	10.776	**0.001**

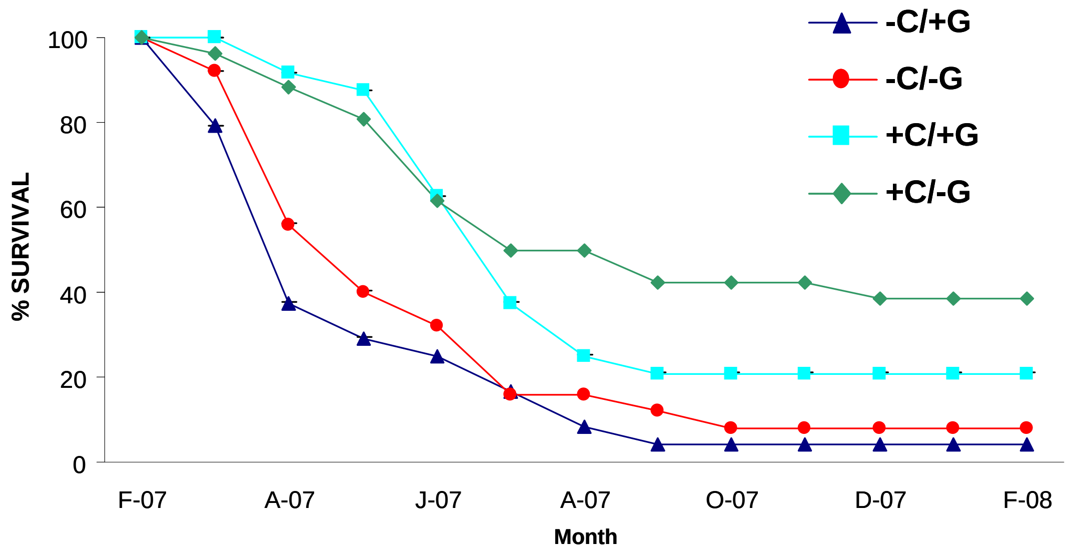


Figure 11. Survivorship (%) of transplanted *Silvetia* juveniles in each of the four treatments across all study sites. Represented are means for the four grazer and canopy treatments: -C/+G, canopy absent, grazer control present; -C/-G, canopy absent, grazers removed; +C/+G, canopy present, grazer control present; +C/-G, canopy present, grazers removed.

4.2 Phase II

<u>Survival.</u> Transplant success of both small and large individuals again was relatively low in Phase II (36 % among all treatments) yet was higher than survival found in Phase I. A nominal logistic regression analysis of the twelve-month results for survivorship of all the *Silvetia* transplants at CDM and the marked *Silvetia* thalli at MOR indicated that there were significant differences in thallus status (transplants from CDM or marked thalli from MOR) (P = < 0.05) in addition to differences in size classes, and orientations (Table 2). There were no significant interactions among factors. Survival of transplants was highest for large thalli placed on vertical surfaces and lowest for small thalli on horizontal surfaces (Fig. 12). In comparison to natural survival rates of non-manipulated thalli at MOR, survival of transplanted materials at CDM was markedly lower. As with transplanted thalli, natural survival was highest for larger thalli on vertical surfaces and lowest for small thalli on horizontal surfaces. A second analysis run on only the transplants at CDM revealed a non-significant difference between the two size classes of transplants and a trend towards significantly different orientations (P=0.0545) (Table 2).

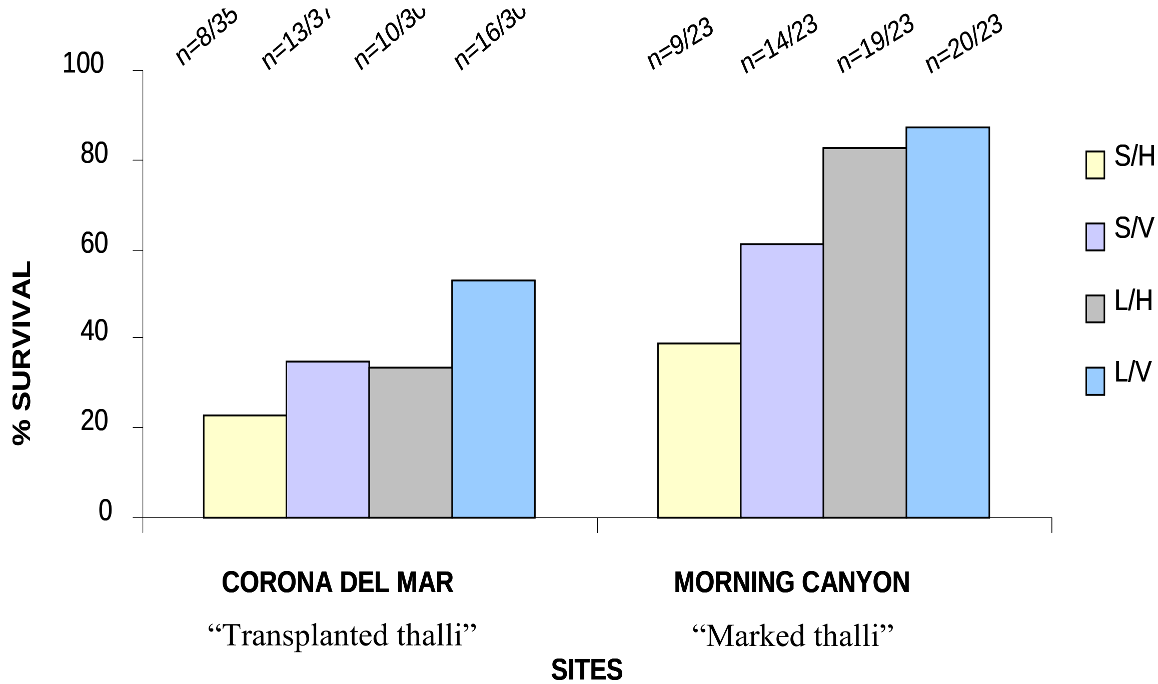


Figure 12. Survivorship (%) of transplanted *Silvetia* thalli at CDM and marked *Silvetia* thalli at MOR in each of the four treatments after 12-months. Represented within both sites are the four size and orientation treatments: S/H, small, horizontal; S/V, small, vertical; L/H, large, horizontal; L/V, large, vertical.

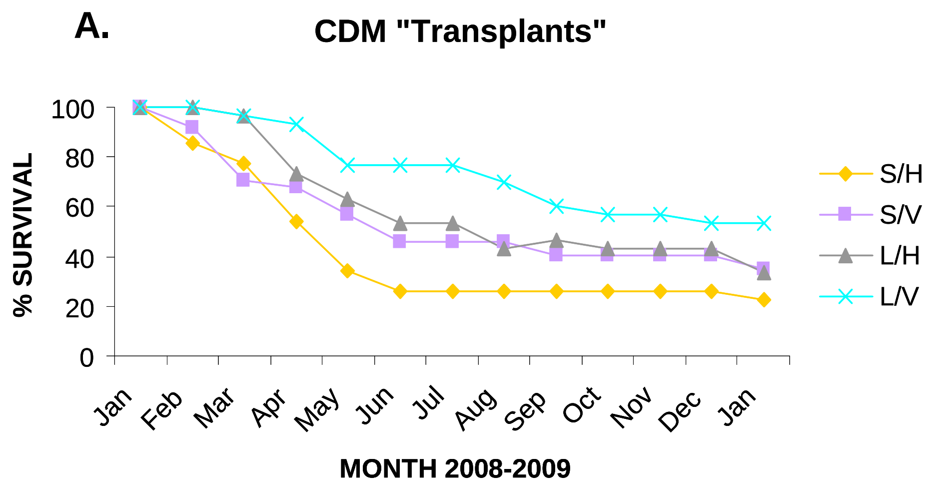
Table 2. Nominal logistic regression analysis of the twelve-month results for survivorship of all the *Silvetia* transplants at CDM and the marked *Silvetia* thalli at MOR.

Source	Nparm	DF	Chi Square	P
Thallus Status (Transplant/Natural)	1	1	16.147	< **0.001**
Size	1	1	13.075	< **0.001**
Orientation	1	1	4.542	**0.033**
Thallus Status*Size	1	1	1.901	**0.168**
Thallus Status*Orientation	1	1	0.105	**0.746**
Size*Orientation	1	1	0.094	**0.759**
Thallus Status*Size*Orientation	1	1	0.474	**0.491**

Table 3. Nominal logistic regression analysis of the twelve-month results for survivorship of all the *Silvetia* transplants at CDM.

Source	Nparm	DF	Chi Square	P
Size	1	1	2.885	0.089
Orientation	1	1	3.700	0.054
Size*Orientation	1	1	0.038	0.766

Attrition of the transplanted population at CDM was relatively uniform across all four treatments throughout the study period (Fig.13A).The same was true for all but one treatment (S/H) of the naturally-existing marked thalli at MOR (Fig.13B). Mortality of the small marked thalli on horizontal surfaces at MOR spiked from March to May and then remained relatively stable during the remaining seven months.



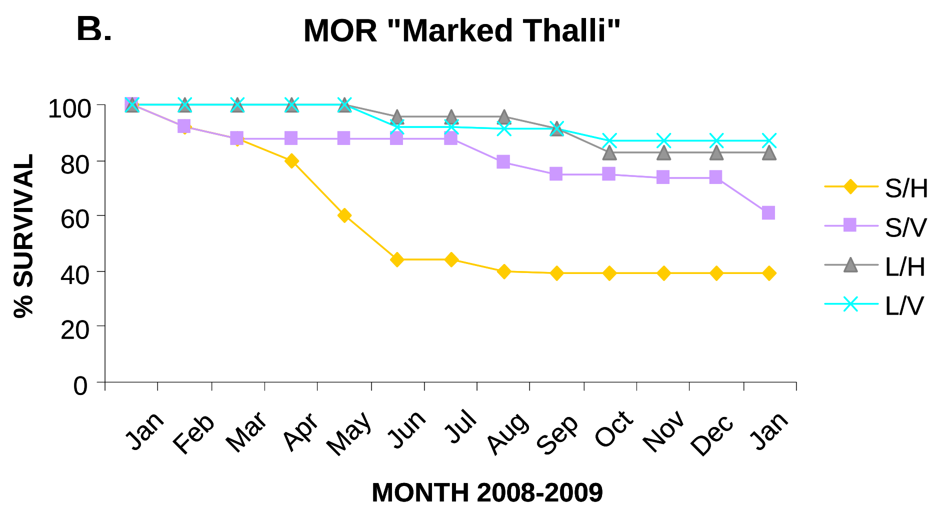


Figure 13. Survivorship (%) of (A) transplanted *Silvetia* at CDM, and (B) marked thalli at MOR in each of the four treatments over the course of 12 months. Represented are means: S/H, small, horizontal; S/V, small, vertical; L/H, large, horizontal; L/V, large, vertical.

Growth of Small Thalli. Over the twelve-month study period, the quarterly growth rates, measured as surface area, for small transplants at CDM and marked thalli at MOR were comparable (Fig. 14; Table 4). Additionally, there were no significant differences between vertically and horizontally-oriented thalli in regard to percent change of surface area. Naturally-occurring thalli at MOR grew continuously throughout the year whereby vertically-oriented thalli became 1,199% larger, and thalli on horizontal surfaces increased in size by 2,430%. Conversely, vertical and horizontally-oriented transplanted thalli at CDM reached their maximum size nine months into the study becoming 1,553% and 1,254% larger respectively, and then decreased in size from September to January 2009, a period following the switch to more desiccating afternoon lower, low tides in the region.

Table 4. Two-Factor ANOVA of the twelve-month results for percent change in growth of the small *Silvetia* transplants at CDM and the marked *Silvetia* thalli at MOR.

Source	**DF**	**Seq SS**	**Adj SS**	**Adj MS**	**F**	**P**
Thallus status (Transplant/Natural)	1	3301743	5090900	5090900	1.65	0.207
Orientation	1	3396983	2716154	2716154	0.88	0.355
Thallus status*Orientation	1	5068205	5068205	5068205	1.64	0.208
Error	38	117494304	117494304	3091955		
Total	41	129261235				

<u>Growth of Large Thalli (Length).</u> Unlike the small thalli in this study, the large transplants at CDM and the naturally-existing marked thalli at MOR did not grow at comparable rates, measured using changes in maximum length (cm) (Fig. 15; Table 5). The combined horizontal and vertically-oriented thalli yielded significantly different percent changes in length between the two populations of *Silvetia* at the second and fourth monitoring periods. When viewed separately, the horizontal transplants grew significantly less during the first and final quarters than the horizontally-oriented marked thalli at MOR. By the end of the twelve months, the horizontally-located marked thalli increased by 39%, while the mean length of transplants on horizontal surfaces remained approximately the same.

The vertically-oriented transplants and marked thalli displayed a similar growing trend. Both populations grew to comparable lengths throughout the first quarter, but the naturally-existing thalli at MOR achieved significantly greater maximum lengths than the transplants at CDM by the end of the study period. Twelve months following the initial measurements, marked thalli had reached a maximum length which was 28% longer than twelve months before, and vertically-oriented transplants had decreased to -12% of their original length.

Table 5. Two-Factor ANOVA of the twelve-month results for percent change in growth (length) of the large *Silvetia* transplants at CDM and the marked *Silvetia* thalli at MOR.

Source	**DF**	**Seq SS**	**Adj SS**	**Adj MS**	**F**	**P**
Thallus status (Transplant/Natural)	1	30234	27578	27578	11.27	0.001
Orientation	1	1338	1248	1248	0.51	0.478
Thallus status*Orientation	1	6	6	6	0.00	0.961
Error	61	149232	149232	2446		
Total	64	180811				

Growth of Large Thalli (Weight). A preliminary experiment designed to determine any discrepancies between wet weight (g) measurements of "attached" thalli and 'actual' wet weights of unattached thalli indicated that the two were comparable for both horizontally-located thalli (SLR; R-Sq = 90.5%; df = 1; F = 28.509, P = 0.013) and vertically-oriented thalli (SLR; R-Sq = 96.9%; df = 1; F = 93.449; P = 0.002). Therefore, all measured values of "attached" thalli were used for analysis.

All thalli from the two orientation treatments (horizontal and vertical) and the two separate populations (transplants at CDM and naturally-existing thalli at MOR) grew to comparable weights at each quarterly monitoring period (Fig. 16; Table 6). By the end of the twelve month study period, both the horizontally-located marked thalli and the transplants weighed approximately 112% and 95% more than initially, respectively. The vertical marked thalli were 54% and the transplants were 63% heavier.

Table 6. Two-Factor ANOVA of the twelve-month results for percent change in growth (weight) of the large *Silvetia* transplants at CDM and the marked *Silvetia* thalli at MOR.

Source	**DF**	**Seq SS**	**Adj SS**	**Adj MS**	**F**	**P**
Thallus status (Transplant/Natural)	1	6341	5199	5199	0.06	0.811
Orientation	1	16361	8712	8712	0.10	0.757
Thallus status*Orientation	1	16891	16891	16891	0.19	0.667
Error	60	5424163	5424163	90403		
Total	63	5463756				

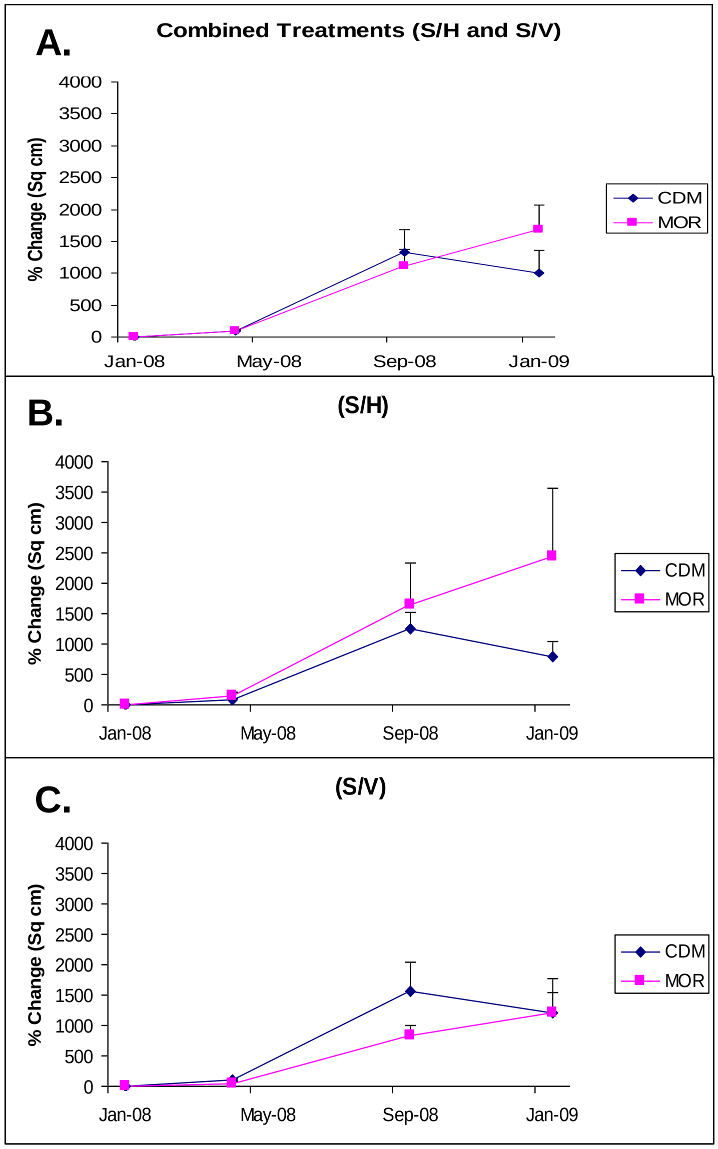


Figure 14. Results for the percent change in surface area (sq cm) calculated from quarterly measurements of small transplants at CDM and naturally-existing marked thalli at MOR: (A) combined vertical and horizontally-oriented thalli; (B) S/H, small horizontal; (C) S/V, small vertical. Figured are means (+ 1 SE) for each parameter. Sample sizes for quarterly assessments of surface area at CDM and MOR respectively were: (A) n = 72 and n = 50 (January 2008), n = 42 and n = 40 (May 2008), n = 24 and n = 27 (September 2008), n = 19 and n = 23 (January 2009); (B) n = 35 and n = 25 (January 2008), n = 16 and n = 20 (May 2008), n = 9 and n = 9 (September 2008), n = 8 and n = 9 (January 2009); (C) n = 37 and n = 25 (January 2008), n = 24 and n = 22 (May 2008), n = 15 and n = 18 (September 2008), n = 11 and n = 14 (January 2009). Significant differences in percent change of surface areas were detected by a repeated measures 2-way ANOVA .

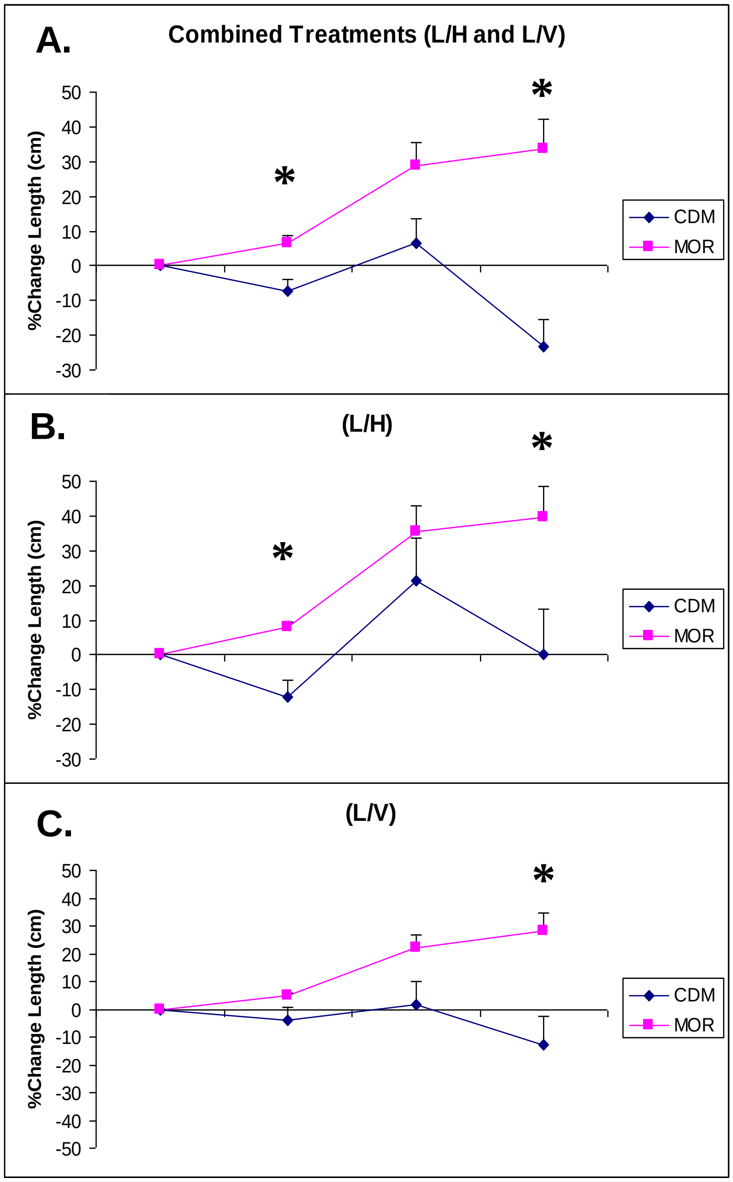


Figure 15. Results for the percent change in maximum length (cm) calculated from quarterly measurements of large transplants at CDM and naturally-existing marked thalli at MOR: (A) combined vertical and horizontally-oriented thalli; (B) L/H, large horizontal; (C) L/V, large vertical. Figured are means (+ 1 SE) for each parameter. Sample sizes for quarterly assessments of maximum length at CDM and MOR respectively were: (A) n = 60 and n = 48 (January 2008), n = 49 and n = 48 (May 2008), n = 32 and n = 44 (September 2008), n = 27 and n = 39 (January 2009); (B) n = 30 and n = 24 (January 2008), n = 21 and n = 24 (May 2008), n = 14 and n = 22 (September 2008), n = 10 and n = 19 (January 2009); (C) n = 30 and n = 24 (January 2008), n = 28 and n = 24 (May 2008), n = 18 and n = 22 (September 2008), n = 17 and n = 20 (January 2009). Significant differences in percent change of surface areas were detected by a repeated measures 2-way ANOVA . Asterisks denote significance (P = <0.05)

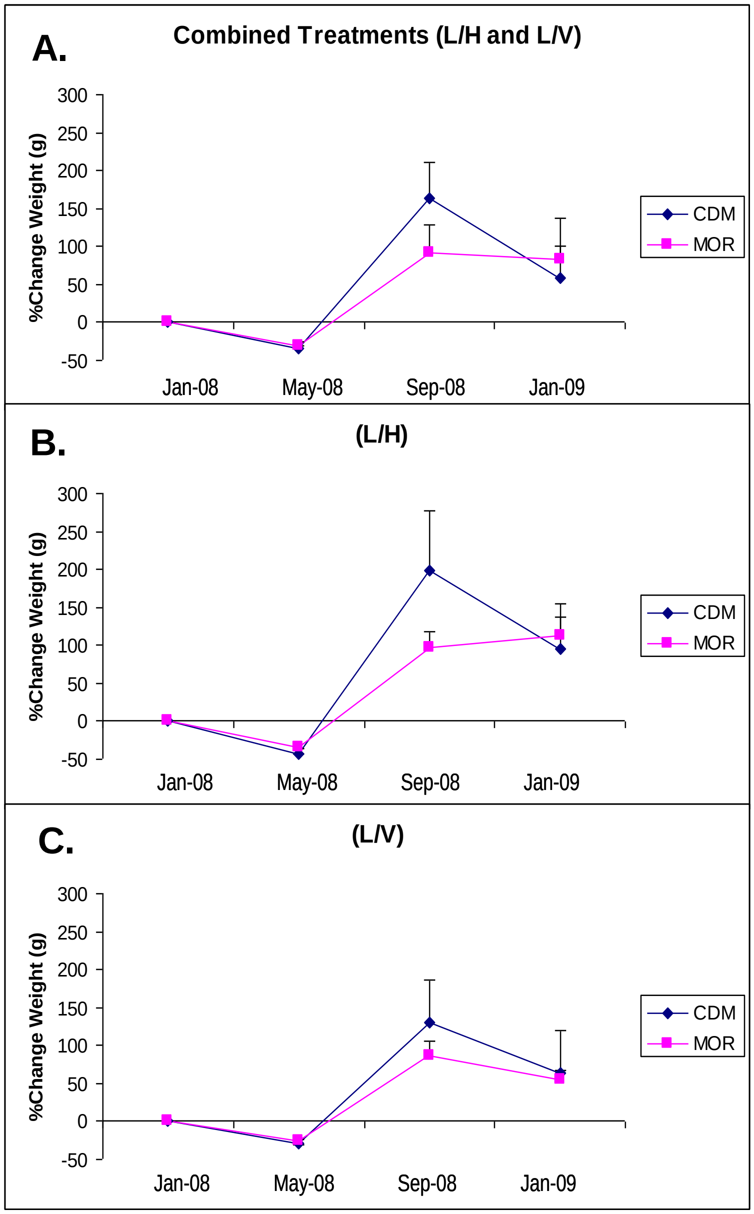


Figure 16. Results for the percent change in maximum weight (g) calculated from quarterly measurements of large transplants at CDM and naturally-existing marked thalli at MOR: (A) combined vertical and horizontally-oriented thalli; (B) L/H, large horizontal; (C) L/V, large vertical. Figured are means (+ 1 SE) for each parameter. Sample sizes for quarterly assessments of maximum weight at CDM and MOR were same as reported for Fig. 13. Significant differences in percent change of surface areas were detected by a repeated measures 2-way ANOVA.

Desiccation Experiment. The results of the experiments conducted to test the relative levels of desiccation stress experienced by *Silvetia* on two different orientations of substrata, horizontal and north-facing vertical surfaces, as well as under the natural canopy provided by large *Silvetia* thalli, supported our hypothesis that less desiccation stress occurs on the vertical surfaces and under canopy in relation to horizontal surfaces (Fig. 17).

A. $P < 0.001$, $DF = 26$, $T = 8.03$

B. $P < 0.001$, $DF = 2$, $F = 39.45$

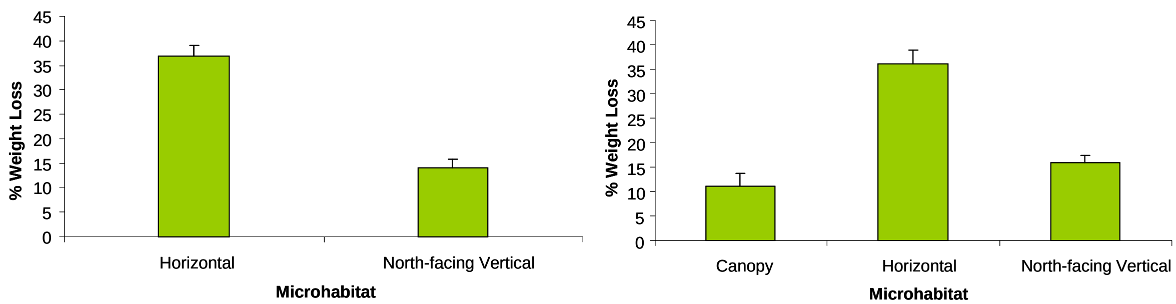


Figure 17. Percent weight loss (g) of *Silvetia* sampling units as they dehydrated over the course of an afternoon low tide period (3 hrs) in (A) March 2008, and (B) January 2009. Bars indicate means (+ 1 SE). Sample sizes for each treatment were n = 15 (A) and n = 10 (B). Significant differences in weight loss were detected by a two-sample t-test (A) or ANOVA (B). Letters above each bar indicate subsets of means based on results of Tukey's *a-posteriori* multiple comparison test.

5.0 DISCUSSION

Ecological restoration has been utilized for centuries by indigenous people to contend with habitat degradation (Stevens 1997). Yet, this practice has only recently been developed as a scientific discipline (Young et al. 2005). As such, science-based restorations combine ecological theory and scientific experimentation rather than trial and error (Falk et al. 2006). This study was designed from a scientific perspective whereby factors believed to critically affect the re-establishment of *Silvetia*, an important canopy-forming rockweed, were experimentally evaluated in two separate Phases. Two of the factors, canopy and grazer presence/absence, along with two out-planting methods, transplantation and relocation of reproductive material, were tested in Phase I of the study. The results were then used to guide the design and application of Phase II in which size class and orientation, two other factors considered to be potentially crucial to successful rockweed re-establishment, were examined.

Based largely on Phase II, the results of this study suggest that *Silvetia* can be re-established for ecological restorative purposes. While the technique that we used involving the relocation of reproductive material was unsuccessful, the transplantation technique applied in this experiment appears to be a feasible method for reintroducing *Silvetia*, and likely other seaweeds species as well. Successful re-establishment was increased when large or adult stages of the rockweed were transplanted onto vertical surfaces. Although monitoring needs to be continued, given the survival rates of transplanted materials and the high number of transplants placed at CDM, we may have successfully re-established a self-sustaining rockweed population at the site. Furthermore, we have found subsequent natural recruitment of 13 rockweed thalli likely resultant from our *Silvetia* transplants.

The relocation of microscopic early-life stages has been implemented to successfully re-establish targeted algal species such as the kelps *Macrocystis pyrifera* (Devinny and Leventhal 1979, Dayton et al. 1984) and *Nereocystis luetkeana* (Carney et al. 2005), *Sargassum muticum* (Terawaki et al. 2003), and the rockweed *Fucus* (Stekoll and Deysher 1996), as well as seagrass (*Zostera marina*) (Harwell and Orth 1999). In nearly all cases, with the exception of *Fucus*, reproductive structures containing spores or seeds have been placed directly into mesh bags hung above the substratum. In the case of the kelp species and the rockweed, early post-settled Phases have been cultured in the lab and "seeded" onto nylon or coconut-fiber lines laid across the surface of the study site. Regardless of the method or species, the use of early-life stages requires that seeding is timed to coincide with the natural "recruitment window" of the desired species (Deysher and Dean 1986, Schiel and Foster 1992).

Given the high success of re-establishment in other spore out-planting experiments, it is somewhat surprising that our attempt to re-establish *Silvetia* through natural seeding failed. Early life stages of *Silvetia*, like those of most macrophytes, do have extremely high rates of mortality despite having fertilization rates that are ≈100% successful (Brawley 1990, Johnson and Brawley 1998). For example, Moeller (2002) documented mortality of early post-settled Phases to be more than a million-fold. Therefore, it is possible that we simply did not relocate enough receptacles to overcome the inevitable high rates of mortality that normally occur for *Silvetia*. We know that the receptacles used in this study were reproductive since we were able to induce the release of gametes in the lab which subsequently developed into young embryos under laboratory conditions. In addition, we found that recruitment can occur at our experimental site as evidenced by newly established recruits likely from the transplanted adults. Observationally, another possible reason for the poor success of the natural seeding technique may have been the large amount of debris in the form of sediment and shell fragments that regularly accumulated underneath the porous containers used to hold fertile receptacles. The debris may have inhibited gametes from successfully dropping onto the substratum. Likewise, any establishment of embryos may have been negatively impacted at a later period through the subsequent inundation of debris. Similarly, sediment accumulation is considered a primary explanation for the inability of *Silvetia* to recruit in habitats dominated by algal turfs (Vadas et al. 1992), since these environments also provide excellent entrapments.

The second out-planting experiment that we applied in Phase I involving the transplantation of juvenile stages of *Silvetia* was only moderately successful since only

18 thalli remained out of 96 (18%) following the completion of the 12-month study period. However, the transplantation technique itself has proved to be effective. Even though a substantial amount of mortality occurred during the first three months, all transplants were not lost, as would be expected if the technique was unsuccessful. Also, in all cases, the marine epoxy used to attach rock pieces and rockweed thalli remained intact throughout the entire study period; all losses of thalli resulted from the loss of thalli from the transplanted rock surfaces. Rather, the elevated level of attrition for transplanted juvenile stages may have been attributed to the high mortality rates normally encountered by early life stages of *Silvetia* (Gunnill 1980, Moeller 2002) similar to those manipulated in this experiment. For instance, Gunnill's (1980) demographic study of a *Silvetia* population in San Diego revealed that only 50% of all newly-recruited individuals lived 80 days and much less (9%) survived 1.5 years. Based on Gunnill's (1985) observations, the mean age of the transplanted thalli in this study was hypothesized to be 30-60 d. Therefore, the survivorship of our transplants across all treatments is actually comparable to that of similar-aged thalli in nature. Anecdotally, our results for survivorship also mimic those of the controls used in Blanchette et al. (2000) where similar methodology was used to transplant juvenile and adult thalli from two species of rockweeds (including *Silvetia*) for the purposes of examining tidal and wave exposure gradients on the Channel Islands, CA.

Phase I results indicated that the survivorship of juvenile stages of *Silvetia* was enhanced by the presence of simulated canopies. This is expected since the canopies used in this study were believed to provide the beneficial services normally rendered by canopy fronds such as reduced desiccation stress (Hruby and Norton 1979, Hawkins 1983, Brawley and Johnson 1991) and water movement (Brawley and Johnson 1992), without the deleterious effects caused by the sweeping action of fronds (Menge 1976, Deysher and Norton 1982, Jenkins et al. 1999, van Tamlen et al. 1997, Viejo et al. 1999). Additionally, the simulated canopies may have protected out-plants from any trampling that likely occurred as a result of visitor usage or debris moved by water surge. However, the positive influence of the simulated canopies on transplanted juveniles was coupled with the negative effect of severe inhibition of growth, an observed effect that has been documented for rockweeds (Chapman 1989, Dethier et al. 2005). For this reason, the canopies were removed from all remaining transplanted thalli following the completion of the study period. Subsequent observations and measurements suggest that an increase in growth occurred.

The second treatment applied to both experiments involving the exclusion of grazers did not appear to be a significant factor affecting early life stages of *Silvetia* at our study sites. This is possibly because the transplanted juvenile stages had escaped to a safe size (Lubchenco 1983), and the seeded stages failed for other reasons stated above. We did, however, notice a weak pattern of increases in ephemeral algae (*Ulva* spp.) within some of our grazer-exclusion control plots (grazer-exclusion treatment in absence of out-plants). Grazers such as limpets in the genus *Lottia* and chitons (*Nuttalina*, *Cyanoplax*) were successfully excluded with copper-based painted rings applied around selected plots. However, the densities of more mobile invertebrates including shore (*Pachygrapsus*) and hermit (*Pagurus*) crabs as well as littorine (*Littorina*) and turban

(*Chlorostoma*, *Agathistoma*) snails were difficult to reduce, even with frequent removal by hand. Moreover, microherbivores that commonly inhabit *Silvetia* stands such as amphipods (*Hyale, Ampithoe*), isopods, decapods, copepods, rhombognathid mites, and paradoxostomid ostracods (Gunnill 1985) were not excluded. While the effects of many microherbivores on rockweeds have not been well-studied, it is known that the amphipod (*Ampithoe tea*) (Gibb 1957, North 1971, Norton and Benson 1983) and some small gastropods (*Lacuna unfasciata* and *Tricolia rubrilineata*) (Thomas and Page 1983), along with larger gastropods (*Littorina* spp.) (Smith 1973, Dayton 1975, Lubchenco 1982) and various types of crabs (Naylor 1955, Nassichuk 1975, Brusca and Walerstein 1979, Kangas et al. 1982) graze on large brown algae. *Littorina* spp. in particular, have been observed to significantly affect the survivorship of *Silvetia* recruits (Gunnill 1980, 1983), and these were often present in the vicinity of our plots. Therefore, the grazer exclusion treatment may have not been adequately implemented. It is not uncommon for grazer exclusion studies to arrive at contrasting conclusions (e.g. Lubchenco 1980, 1982, 1986, Chapman 1989). According to Chapman (1989), such differences may be due to qualitative discrepancies among grazer guilds.

For Phase II, the same transplant procedure used in Phase I was employed for two size classes of *Silvetia* and two orientations of substrata. We concentrated on transplanting rockweed at only, CDM, because the results of Phase I indicated that *Silvetia* is capable of surviving at the target site as well as at the donor and experimental sites. In Phase II, survivorship improved (36 % among all treatments) with large transplants on vertically-oriented substrata having more than twice the rate of survival (53%) in comparison with the small transplants on horizontal surfaces (23%) over the course of the 12-month study period. These results are comparable to the controls for adult and juvenile transplanted *Silvetia* in Blanchette et al. (2000) as well as the overall survival of juvenile transplants in Phase I. They also agree with the observation made by Gunnill (1980) in which the mortality rate of *Silvetia* decreases with age. Several factors may have converged or acted singularly to differentially reduce survival rates of small transplants in relation to larger individuals. Likely the most influential factor was desiccation (Brawley and Johnson 1991), but water motion (Blanchette et al. 2000) and grazing activity (Lubchenco 1980), have also been shown to cause increased detriment to younger rockweeds.

The transplants located on north-facing vertical substrata during Phase II of the study had a significantly higher rate of survival. Gunnill (1980) indicated that *Silvetia* was not distributed uniformly across the various topographic features and orientations of substrata in his demographic study. Instead, he found the most abundant levels occurring on sloped rock surfaces. It is unclear what why there are greater abundances of *Silvetia* on slopes in comparison with horizontally-oriented surfaces. The desiccation experiment in this study revealed statistical differences between horizontal and vertically-oriented surfaces, whereby the vertical substrata were comparable to canopy-covered microhabitats. This implies that transplanted *Silvetia* occurring on vertical surfaces and under canopy may receive an ecological advantage due to reduced levels of physiological stress (Brawley and Johnson 1991, 1993, Davison et al. 1993). Another plausible explanation for greater survivorship of *Silvetia* on vertical surfaces, at least at a high human use site such as

CDM, may be reduced levels of trampling that likely occur on such surfaces in comparison with horizontal substrata.

Even though survivorship was higher for transplants in Phase II than Phase I transplanted thalli, it was still significantly lower than the natural survival rates of non-manipulated thalli at MOR. As with transplanted thalli, natural survival at MOR was highest for larger thalli on vertical surfaces and lowest for small thalli on horizontal surfaces. One explanation for the disparity between the survival rates of the transplanted population at CDM and the naturally-existing population at MOR may be due, in part, to the intentional spacing of replicates at CDM to eliminate any effects from neighboring thalli. Conversely, marked thalli at MOR tended to be included within aggregations, which have been shown to be ecologically advantageous for rockweeds (Schonbeck and Norton 1979, Gunnill 1980). For example, over half (57%, n=16) of the marked thalli at MOR considered to be exposed (no surrounding frond canopy) (30%, n=28) at the start of the study period did not survive the entire 12 months.

An equally refutable factor may have been unsuitable microhabitat choice for some of the transplants. Long-lived individuals in a natural population likely persist because surrounding conditions involving high levels of stress caused by desiccation, water movement, and grazing are reduced (Gunnill 1980). Canopy presence (McCook and Chapman 1991), and perhaps to a lesser degree, micro-scale features in substrata (e.g. cracks, orientation), can ameliorate the detrimental affects of desiccation, high temperatures, predation, and water movement. However, it is unlikely that we chose proper microhabitats for all transplanted individuals particularly since natural canopy cover did not exist at CDM. Also, as mentioned, deleterious impacts such as trampling are likely greater on horizontal surfaces than on vertically-oriented substrata. This may not only serve as an explanation for disparate survival rates of *Silvetia* on the two substratum orientations, but it could also account for the significantly lower survivorship at CDM since this site experiences the greatest number of visitors relative to its size than any other rocky intertidal site in southern California (Tenera Environmental 2004). Conversely, MOR is one of the least visited sites in the region (Ware, pers. omm..).

In contrast to the significant results for survivorship, the growth measurements obtained in Phase II, for the most part, were relatively similar across all three factors (site, size, and orientation). The only exception was the significantly lower percent change in length measured for transplants at CDM in comparison with naturally-existing thalli at MOR. The explanations mentioned above for differences in survival rates may also have caused discrepancies in overall lengths attained by the two populations of *Silvetia* studied in Phase II. For fucoids such as *Silvetia*, aggregated individuals are typically more elongate than isolated thalli (Gunnill 1985), and it has been suggested that survival (Gunnill 1980) as well as growth rates (Moss 1964, 1967, Chamberlain et al. 1979) increase with plant density. Such differences are likely attributed to local variances in salinity (Jordan and Vadas 1972), desiccation (Mshigeni 1977, Oates and Murray 1983), and water motion (Gunnill 1985, Blanchette et al. 2000). However, biological factors such as competition for light and nutrients (Cousens and Hutchings 1983) as well as grazing (Gibb 1957, Black 1976, Gunnill 1985) may also play a role. This trend towards increased survivorship and growth is strikingly contradictory to the findings of self-thinning, a form of intra-specific competition that has been documented for various other algal species by Adams and Austin (1979), Harger and Neushul (1983), and Neushul and Harger (1985), whereby density is positively correlated with mortality and reduced growth.

For future studies, we recommend the implementation of similar methodology to that used in Phases I and II involving transplantation despite a relatively minor impact on donor populations. And, based on Stekoll and Deysher's (1996) failed attempt to re-introduce a self-sustaining population of *Fucus* on Alaskan rocky shores following the Exxon Valdez oil spill, it is also recommended that a heterogenous size (and presumably age) structure be transplanted to reduce the occurrence of a population dominated by one cohort. Even though we realized moderate success with the relocation of large thalli, most notably onto vertical surfaces, we hypothesize that survival may be equal or better for similar sized individuals placed into aggregates rather than spaced apart. This way, the structure of a naturally-occurring population of *Silvetia* would be more closely mimicked, thereby allowing transplanted individuals to benefit ecologically from neighboring thalli (Schonbeck and Norton 1978, Gunnill 1980, McCook and Chapman 1991).

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Figure 14. Results for the percent change in surface area (sq cm) calculated from quarterly measurements of small transplants at CDM and naturally-existing marked thalli at MOR: (A) combined vertical and horizontally-oriented thalli; (B) S/H, small horizontal; (C) S/V, small vertical. Figured are means (+ 1 SE) for each parameter. Sample sizes for quarterly assessments of surface area at CDM and MOR respectively were: (A) n = 72 and n = 50 (January 2008), n = 42 and n = 40 (May 2008), n = 24 and n = 27 (September 2008), n = 19 and n = 23 (January 2009); (B) n = 35 and n = 25 (January 2008), n = 16 and n = 20 (May 2008), n = 9 and n = 9 (September 2008), n = 8 and n = 9 (January 2009); (C) n = 37 and n = 25 (January 2008), n = 24 and n = 22 (May 2008), n = 15 and n = 18 (September 2008), n = 11 and n = 14 (January 2009). Significant differences in percent change of surface areas were detected by a repeated measures 2-way ANOVA .

Figure 15. Results for the percent change in maximum length (cm) calculated from quarterly measurements of large transplants at CDM and naturally-existing marked thalli at MOR: (A) combined vertical and horizontally-oriented thalli; (B) L/H, large horizontal; (C) L/V, large vertical. Figured are means (+ 1 SE) for each parameter. Sample sizes for quarterly assessments of maximum length at CDM and MOR respectively were: (A) n = 60 and n = 48 (January 2008), n = 49 and n = 48 (May 2008), n = 32 and n = 44 (September 2008), n = 27 and n = 39 (January 2009); (B) n = 30 and n = 24 (January 2008), n = 21 and n = 24 (May 2008), n = 14 and n = 22 (September 2008), n = 10 and n = 19 (January 2009); (C) n = 30 and n = 24 (January 2008), n = 28 and n = 24 (May 2008), n = 18 and n = 22 (September 2008), n = 17 and n = 20 (January 2009). Significant differences in percent change of surface areas were detected by a repeated measures 2-way ANOVA . Asterisks denote significance (P = <0.05)

Figure 16. Results for the percent change in maximum weight (g) calculated from quarterly measurements of large transplants at CDM and naturally-existing marked thalli at MOR: (A) combined vertical and horizontally-oriented thalli; (B) L/H, large horizontal; (C) L/V, large vertical. Figured are means (+ 1 SE) for each parameter. Sample sizes for quarterly assessments of maximum weight at CDM and MOR were same as reported for Fig. 13. Significant differences in percent change of surface areas were detected by a repeated measures 2-way ANOVA.

Figure 17. Percent weight loss (g) of *Silvetia* sampling units as they dehydrated over the course of an afternoon low tide period (3 hrs) in (A) March 2008, and (B) January 2009. Bars indicate means (+ 1 SE). Sample sizes for each treatment were n = 15 (A) and n = 10 (B). Significant differences in weight loss were detected by a two-sample t-test (A) or ANOVA (B). Letters above each bar indicate subsets of means based on results of Tukey's *a-posteriori* multiple comparison test.