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DISTRIBUTION, GROWTH, AND DISTURBANCE OF CATALINA ISLAND RHODOLITHS

A Thesis

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of the Requirements for the Degree

Master of Science

by

Paul Anthony Tompkins

August 2011

The Designated Thesis Committee Approves the Thesis Titled

DISTRIBUTION, GROWTH, AND DISTURBANCE OF CATALINA ISLAND RHODOLITHS

By

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ABSTRACT

DISTRIBUTION, GROWTH, AND DISTURBANCE OF CATALINA ISLAND RHODOLITHS

By Paul A. Tompkins

Rhodoliths are free-living coralline algae (Rhodophyta) that form large beds on the seafloor. Rhodolith beds are globally widespread and biologically diverse shallow marine habitats. Beds are ecologically sensitive, disturbed by humans, and in Europe are protected by law. While rhodolith beds have been found in California waters at Catalina Island, no literature exists regarding their distribution or ecological significance. This study sought to (1) map the distribution and characterize the rhodolith beds around Catalina, (2) determine the seasonal growth rates, and (3) investigate the effect of common sources of disturbance. A systematic search of shallow subtidal (0-40 meters) areas revealed seven beds. These were mapped by divers using SCUBA. Living and dead rhodolilths and rhodalgal sediments covered approximately 22,900 and 42,696 square meters of seafloor, respectively. Percentage cover, and mean size of living rhodoliths varied across beds. Growth rates varied seasonally but were consistent with global averages; branches grew just over a millimeter a year. Vessel mooring chains were a common source of disturbance, and decreased 3-dimensional rhodolith habitat and living rhodolith cover. More benthic fauna were seen in living beds compared to dead, impacted rhodolith sediments or adjacent sandy benthos. Highly disturbed and slow to recover, this novel habitat should be considered a high priority for future protection, monitoring, and restoration efforts.

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Background

Rhodoliths are free-living, non-geniculate coralline red algae (Figure 1).

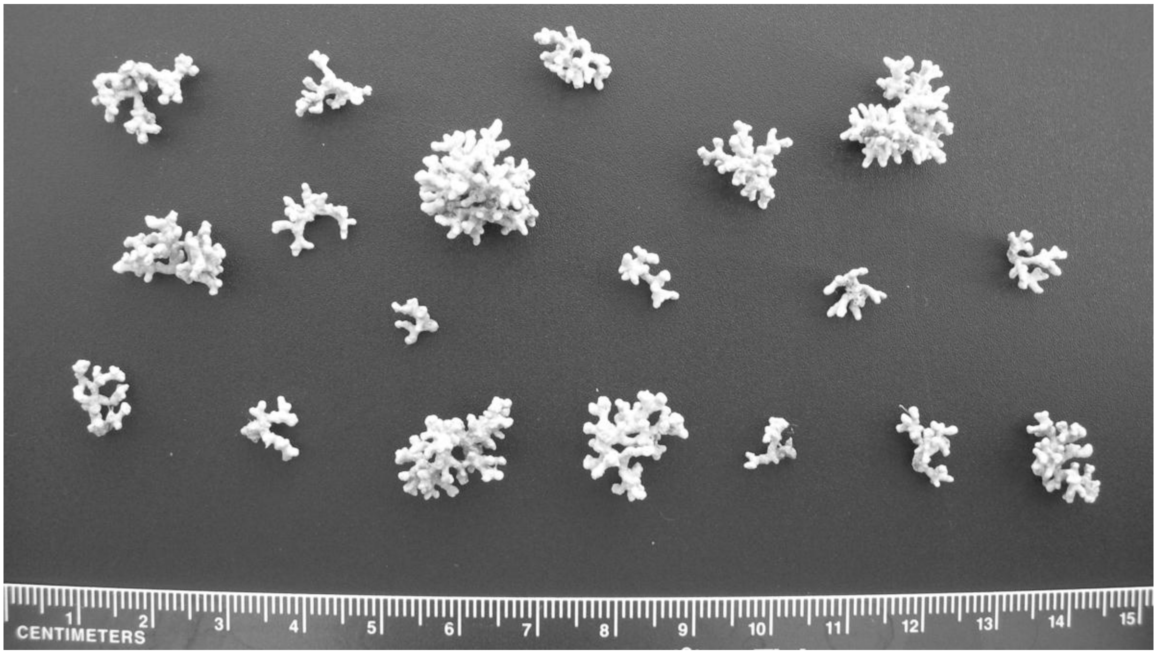


Figure 1. Representative sample of Catalina Island rhodoliths *Sporolithon australe* per R. Riosmena-Rodriguez) from Cherry Cove.

They have been documented in every ocean worldwide, from polar seas to the tropics (Bosence 1983b; Foster 2001). In Europe, rhodoliths are often referred to as “Maerl,” a Breton term. Individual rhodoliths, or “nodules,” can be intricately branched, and large aggregations of nodules, or “beds,” create a complex living matrix of branches and interstitial spaces on the seafloor. This structure creates an attractive benthic marine habitat, and relative to adjacent soft-sediment benthos, beds support highly diverse and often unique assemblages of associated species (Cabioch 1969; Keegan 1974; Foster 2001). Valued as a source of carbonate and as productive fishing grounds, rhodolith beds have been exploited for centuries (Blunden 1975). Rhodolith beds have been reported in

California waters, yet no information exists regarding their extent or ecological significance.

Given their importance as a biological resource, recent work has focused on characterizing rhodolith bed habitats in terms of location, extent, and population-level characteristics (Foster et al. 1997; Konar et al. 2006; Amado-Filho et al. 2007; Sciberras 2009). Mapping efforts have been encouraged by conservation and management interests (De Grave 1999; De Grave 2000; Hetzinger 2006; Ryan et al. 2007; Hall-Spencer et al. 2008; Halfar et al. 2009), and methodologies for identifying and mapping beds have included the use of aerial surveys, benthic grab and dredge samples, drop still and video cameras, SCUBA surveys, and several different acoustic mapping techniques (Steller and Foster 1995; Ehrhold 2006; Ryan et al. 2007). Using these methods studies have described rhodolith beds ranging in size from a few hundred square meters to tens of square kilometers (Pena and Barbara 2009; Sciberras 2009). Beds are common in the Mediterranean, Northeast Atlantic, and Gulf of California and along the Brazilian Atlantic shelf from 2º North to 25º South (Kemph 1970; Testa and Bosence 1999; De Grave 2000; Foster 2001; Gherardi 2004; Tews et al. 2004).

Though globally widespread, distributions of living beds appear spatially limited by a combination of physical processes including variability in light, wave energy, and seafloor slope (Bosence 1983b). Red algae, and corallines in particular, are some of the deepest-growing of all macroalgae (Littler et al. 1985) and are abundant in shallow water (Adey and Macintyre 1973; Steneck 1986). Living rhodoliths have been reported at depths exceeding 200 meters (Littler et al. 1991). These are rare; the majority of reported beds range from the intertidal to ~30 meters (Lemoine 1910; Steller and Foster 1995; Konar et al. 2006; Pena and Barbara 2009). Being unattached, rhodoliths both require and are susceptible to movement by hydraulic energy (Marrack 1997), which can limit the upper boundaries of wave-exposed beds (Steller and Foster 1995). A combination of extreme water motion and a steep seafloor can cause rhodoliths to be moved down slope, beyond photic depth limits (Steller and Foster 1995). However, water motion must be sufficient to prevent sedimentation; rhodoliths are highly susceptible to smothering in silt and mud (Wilson et al. 2004), and sedimentation may set deeper bed boundaries in calmer waters (Steller and Foster 1995).

Rhodoliths typically live in relatively flat, shallow areas of low to intermediate water motion, making the relationship between coastal morphology and hydraulic energy a major deterministic factor for widespread rhodolith distribution. This pattern was modeled by (Bosence 1980) who proposed that rhodoliths in the British Isles and Brittany were likely to colonize deeply indented coastlines, and be found in shallow bays with headlands situated at oblique angles to the prevailing wind and swell directions. Beds exist in conditions like these worldwide (Scoffin et al. 1985; Steller and Foster 1995; Fazakerley and Guiry 1998; Friewald 1998; Wehrmann 1998; De Grave 2000), and where they are found, population-scale variables such as size, sphericity, and branch density of nodules are known to vary with environmental conditions (Bosellini and Ginsburg 1971; Bosence 1976; Steller and Foster 1995; Amado-Filho et al. 2007; Pena and Barbara 2009). For example, rhodoliths living in highly exposed areas tend to be more spherical and densely branched; frequent turning encourages uniformity in growth throughout the thallus, and dense lateral branching results from abraded apical meristems (Bosence 1976; Bosence 1983a; Bosence 1983b). This relationship has lead to the use of living bed characteristics to estimate the environmental conditions present during the formation of fossil beds (Manker 1987; Nalin et al. 2008; Johnson et al. 2009).

Rhodoliths are excellent paleoclimatic recorders as they grow slowly and fossilize well (Kamenos et al. 2008; Titschack et al. 2008). Coralline algae grow by precipitating calcium carbonate (high Mg-Calcite) between cell walls (Cabioch and Giraud 1986). This growth is a slow process; rhodolith branches typically grow no more than a millimeter a year (Cabioch 1969; Konishi 1975; Bosence 1980; Fazakerley and Guiry 1998; Frantz et al. 2000; Rivera 2004; Kamenos et al. 2008). Large rhodoliths may be 30 cm in diameter, and hundreds of years old (Frantz et al. 2000).

Crustose coralline algae typically create rows of thick and thin walled cells as they grow, producing alternating dark and light cell “bands”, much like rings on a tree (Cabioch 1966; Adey and McKibbin 1970; Bosence 1983a). Studies to determine the periodicity and causes of this internal banding pattern have produced conflicting conclusions. The majority of results show annual or semi-annual banding, with thick/thin cell walls supposedly produced in the winter/summer, respectively, creating one complete band/year (Cabioch 1966; Adey and McKibbin 1970; Halfar et al. 2000). Other studies have shown a higher-frequency periodicity, on a monthly scale, which may relate to tidal or lunar cycles (Freiwald and Henrich 1994; Blake and Maggs 2003). Slow growth rates, banding patterns, and isotopic signatures of the carbonate lattice are rhodolith characteristics that have made them useful as paleoclimactic indicators (Halfar et al. 2000; Kamenos et al. 2008; Kamenos 2010).

The slow growth rate and inherent fragility of rhodoliths also contribute to their ecological sensitivity; rhodolith beds are slow to recover from catastrophic disturbances (Hall-Spencer and Moore 2000). The density of branching can reach as much as twenty branches per square centimeter, and because the larger scale complexity of mature individuals offers more habitat for other species, larger rhodoliths often harbor more diverse cryptofauna (Adey and Macintyre 1973; Steller and Foster 1995; Frantz et al. 2000; Steller et al. 2003; Amado-Filho et al. 2007). These large rhodoliths are rare in disturbed beds, where branches are frequently broken and live individuals are typically smaller (Bordehore et al. 2003).

Worldwide, biodiversity is linked to habitat heterogeneity. As a general rule, more complex habitats offer a wider range of niches and environmental resources, supporting more diverse and trophically complex communities (MacArthur and Wilson 1967; Lack 1969; Lawton 1983; McCoy and Bell 1991; Tews et al. 2004; Alison et al. 2006). Much like trees and corals, rhodoliths act as autogenic ecosystem engineers, creating biologically derived physical structures, which modify the environment and create refuge (Jones 1994). Surveys of beds in Scotland revealed a community of over 460 floral and faunal species (BIOMAERL 1998), while communities in the Iberian peninsula consisted of over 450 species (Bordehore et al. 2003). In the Gulf of California, faunal species richness and abundances increased with rhodolith branching density and the overall density of nodules (Steller et al. 2003), showing a direct relationship between habitat complexity and biodiversity. This study also found species richness 1.7 times higher and abundance approximately 900 times higher in a rhodolith bed compared to adjacent sand flats. Robust rhodolith beds are important to marine biodiversity, but beds are a highly sensitive habitat, easily disturbed and, due to slow growth rates, likely slow to recover.

Anthropogenic disturbances can have dramatic impacts on the seafloor (Watling and Norse 1998) and can turn living rhodolith beds into relatively homogenous sand flats (Grall and Hall-Spencer 2003). Rhodolith beds worldwide are threatened by a variety of anthropogenic disturbances including direct extraction (as a source of carbonate), dredging, trawling, aquaculture, and anchoring. Extraction removes the habitat completely and has eradicated large beds in Brittany (Grall and Hall-Spencer 2003). Dredging smothers rhodoliths in silt and mud, and trawling-related impaction crushes the branching matrix, homogenizing the seafloor (Bordehore et al. 2003; Hauton 2003; Kamenos 2003). These disturbances can create long-lasting, if not permanent, effects. Beds act as nursery grounds for commercially important species of bivalves (Kamenos et al. 2004), and scallop dredging has been found to greatly reduce cover of live rhodoliths, with no discernable recovery over four years (Hall-Spencer and Moore 2000). Determined to be a non-renewable resource crucial to overall marine biodiversity in the North-East Atlantic, rhodolith beds are now afforded special protections under the United Nations Environment Programme's Mediterranean Action Plan (Agnesi 2009).

Despite worldwide distribution and interest in rhodoliths, there is currently a gap in the published distribution of rhodoliths in the northeast Pacific. Beds have not been described between Prince William Sound, Alaska (USA), and Bahia Magdelena, Baja Sur (Mex.). Considering the environmental tolerances of rhodoliths (Bosence 1983b), and the range of oceanographic conditions along this stretch of coastline, rhodolith beds are likely to exist in protected marine embayments, and this distributional gap may be due to a lack of research.

Rhodolith-forming species have been described from California waters (Foslie 1906; Dawson 1949; Mason 1953) and include species of *Lithothamnion*. Rhodolith beds have only recently been reported from around the Channel Islands (K. Miller, J. Alstatt, D. Divins, pers comm), and their distributional extent and ecological significance are unknown. Around Catalina Island, rhodoliths have been reported in four shallow (<20 m) and protected coves (Parnell et al. 2006). Considering the ecological value and sensitivity of this habitat worldwide and the reported presence of Catalina Island rhodolith beds, this investigation seeks to (1) define the distribution and characterize the rhodolith beds around Catalina, (2) determine seasonal rhodolith growth rates, and (3) examine the effects of common sources of disturbance on rhodolith habitat quality.

Methods

Study Site and Species

Catalina Island (33.40ºN, 118.40ºW) is located approximately 32 km (20 mi) south of Los Angeles, California, in the warm-temperate waters of the Southern California Bight. Oceanic swells approach the California coastline primarily from the Northwest in the winter and from the Southwest in the summer. Predominant winds are westerly; high pressure systems generate winds from the Northwest, and low pressure systems generate winds from the Southwest. Therefore, Catalina Island's NW-SE orientation creates a range of conditions in wind and wave exposure between the windward (SW facing, or "backside") and leeward (NE facing, or "frontside") coasts. This feature, combined with 87 km (54 mi) of highly indented coastline with numerous embayments, creates marine microclimates experiencing a range of hydraulic energies.

The morphologic features of Catalina Island rhodoliths appear to be consistent with the species *Sporolithon australe* (sensu R. Riosmena-Rodriguez 2002). However, this taxonomic determination has yet to be verified due to a paucity of reproductive material.

Distribution and Characteristics

To assess the distribution of live and dead rhodolith material around Catalina Island, a systematic survey of offshore waters from 0 to 30 m in depth was combined with underwater mapping techniques. Survey efforts were initially stratified to focus effort in areas thought likely to support rhodoliths. Anecdotal reports of rhodoliths were produced from a variety of sources, including Dr. Kathy-Ann Miller, Deidre Sullivan, Dr. Steve Lonhart, and Lorraine Sadler (pers comm) Search efforts were initially focused in areas where rhodoliths had been reported: Emerald Bay, Cherry Cove, Fourth of July Cove, and Big Fisherman's Cove (Parnell et al. 2006). After these areas had been searched, effort was directed to other areas likely to support beds; these were identified based on the general physical setting of beds worldwide, i.e., shallow, protected, gently sloping embayments. A variety of methods were used in combination to survey these locations. SCUBA, snorkel, and manta tow (Moran and De'ath 1992) surveys were used to visually scan the seafloor to depths of ~20 m. Random points were distributed within these zones and sampled with a drop camera lowered from a skiff. Any questionable images were verified by free diving or by divers using SCUBA. As logistics permitted, these surveys were extended to other areas of the island, thought to be less likely to support rhodolith beds.

Once rhodoliths were located, divers on SCUBA surveyed and mapped areas of both live and dead rhodolith material. The approximate center of each live bed was marked with a sand anchor and surface float, and location recorded with a GPS. Divers swam eight linear transects radiating from this point (45º between each). To map the distribution of live and dead rhodoliths, the distance to the end of live (>10% cover of pigmented rhodoliths, as per Steller et al. 2003) and dead (<10% cover of cover of pigmented rhodoliths, and covered by >10% dead, unpigmented rhodolith nodules or fragments) rhodolith material was recorded along each transect and these data were entered in to a GIS to create a map of bed distributions. Average percent cover of live rhodoliths per bed was determined within gridded, 0.25m^2 quadrats. One quadrat was placed randomly in each 10 m increment of distance along transects. Live cover data were statistically compared across beds using a one-way ANOVA. A Fisher's LSD test was applied to the data to examine sources of any significant differences.

To compare characteristics of live rhodoliths among beds, divers collected three 10-cm deep by 10-cm diameter cores from within each bed. Cores were taken within areas of >75% live cover, and were separated from each other by at least 5 meters. After transport to shore, non-rhodolith material was removed from all cores, and live and dead material separated, blotted dry, and weighed. To determine size frequency, all live material from each core was placed on a transparent sorting tray, and those individuals above or closest to each of 50 randomly placed points were removed. Individuals were then separated into size bins (0-5, 5-15, and 15-25 mm) and enumerated. Ten randomly selected individuals from each core were set aside to collect long axis, sphericity, and branch density data. The longest, shortest, and intermediate axes were measured to the nearest millimeter using calipers, and all branch tips were counted and marked. Maximum projection sphericity values were determined by using the formula $\sqrt{(Short^2 \div (Long \times Intermediate))}$ (Sneed and Folk 1958). Reported branch densities for rhodoliths are commonly determined by averaging branch counts from multiple randomly placed 1 cm^2 quadrats (Steller and Foster 1995). However, this method was not valid for Catalina Island rhodoliths, given their smaller size distribution. Instead, branch density for each nodule was calculated by dividing the branch counts by the ellipsoidal volume ($\sqrt{(Long \times Intermediate \times short) \div 4\pi}$) of each nodule (Bosence 1976). Rhodolith characteristics data were averaged for each core (n=3 per bed), and statistically compared among beds using an ANOVA. A post-hoc Fisher's LSD test was applied to the data to identify sources of any significant differences.

To estimate population sizes for Cherry Cove, Fourth of July Cove, and Isthmus Harbor rhodolith beds, the total number of live individuals in one core from each bed was enumerated, scaled up to estimate the number of individuals $meter^{-2}$, and multiplied by the live area and average percent live cover of each bed.

Growth Estimation

In situ seasonal growth rates were estimated for the Catalina Island *Sporolithon australe* rhodoliths. Alizarin Red stain (Fisher Scientific), a marker for calcium carbonate deposition, has been used reliably on corals, and geniculate coralline algae (Lamberts 1978; Andrake and Johansen 1980). It has been used with varying success on rhodoliths (Blake and Maggs 2003; Steller et al. 2007). Rhodoliths were collected from Big Fisherman's Cove in both July 2008 and January 2010. For each period, 50 individuals were stained in ambient light conditions for 24 hours in an aerated alizarin bath at a concentration of 0.25 g/liter of seawater. Post-staining, rhodoliths were outplanted into three plastic mesh corrals in Big Fisherman's Cove at 16 meters depth (average depth of live cover), and collected after approximately 200 days.

Upon recovery of samples, individuals were air dried, and a minimum of six branch tips from each nodule was mounted on glass microscope slides with a drop of epoxy resin (Aluzine epoxy system, Fiberglass Hawaii). A polishing wheel (Buehler LTD Ecomet III grinder) with 1200 grit sandpaper was used to grind the embedded tips in half lengthwise, exposing the alizarin stain. To differentiate between stain and similarly colored photosynthetic pigments post-grinding, slides were placed in a fresh water bath for ~2hrs to bleach photosynthetic pigments (as per Blake and Maggs 2003). The sections were examined with a digital camera (Diagnostic Instruments Inc. model 2.3.1) mounted on a microscope (Leica MZ 125), and where stain was obvious, images captured and adjusted using Spot Basic. A digital image analysis program (Image Pro-plus) was then used to measure the distance (in mm) along the main growth axis between stain and branch tip. An average growth rate was determined for each individual rhodolith by averaging growth between all branch tips and dividing by time outplanted (days). Growth rate was standardized by converting growth per days outplanted to an annual growth rate in mm yr^{-1}. Growth rates were determined for both Fall 2008 (July 2008-January 2009) and Spring 2010 (January 2010-August 2010) by averaging rates of all individuals per time period, and these were compared with a t-test.

Distinct growth bands within the new growth were measured and counted (one dark/light cycle = one band), and a band production rate generated by dividing the average # of bands by the time outplanted.

Disturbance

During the course of mapping and characterizing Catalina rhodolith beds, several sources of disturbance were identified. These included, but were not limited to: bioturbation (e.g., bat ray and sheephead feeding, movement of large gastropods), propeller wash (particularly in shallower portions of beds), wave and current energy (ripples and sand waves), smothering beneath debris and rubbish dropped from vessels, sedimentation, diver-induced disturbance, and, the most widespread, mooring chain impaction.

Recreational vessel moorings were a ubiquitous feature of almost every rhodolith bed mapped at Catalina Island, with the exception of Big Fisherman’s Cove West. At the base of each floating mooring ball, a large, heavy chain drops to the seafloor and extends horizontally along the seafloor for approximately ten meters to a mooring block. The chains bounce vertically on the seafloor with wind chop and swell, and drag horizontally as attached vessels manipulate the surface line or are moved sideways by winds (pers obs).

Mooring chain impaction was a major source of disturbance; swaths of crushed, dead rhodolith material lay beneath and around each chain located in a bed. Due to the widespread mooring disturbance at Catalina, the effect of this common disturbance on rhodolith habitat quality was assessed. As rhodoliths fracture and crumble, the volume of interstitial space diminishes, though the total mass of the material is unchanged. Hence, a weight to volume ratio (wt vol^{-1} or overall density of the material) was used in this study to measure 3-dimensional complexity differences between larger, branching nodules (natural, undisturbed material) and smaller, fragmented pieces of rhodoliths (impacted material).

The following experiment was designed to test the hypothesis that mooring chains have a negative (reducing) effect on the complexity of the rhodolith habitat. Live, branching rhodoliths (ranging in longest axis from 5-25 mm) were carefully collected from areas of >75% live cover at similar depths in Cherry Cove, air dried, tagged with fluorescent green paint, and separated into fifteen samples of similar weights. The dry weight per unit volume ratio (wt vol^{-1}) for each sample was determined by first weighing the sample, then estimating the level of the uppermost rhodolith protrusions in a 1000 ml graduated cylinder filled with water. Samples were then assigned to one of three treatments (n = 5 replicates/treatment): (1) Chain - material placed directly beneath the point of impact of chains; (2) Live - material placed back into the Cherry Cove rhodolith bed, in areas of >75% live cover; (3) Chain Removal - material placed at the original point of impact of shortened chains, thus removing the direct chain disturbance (the chain removal treatment level was designed to test for any influential local factors independent of the effect of the chains). Within Cherry Cove, all ten mooring chains used in the experiment were within 3 meters of live rhodoliths, and shared similar depths (6-7 m). Disturbance treatments were randomly assigned to mooring chains, and the ‘Live’ treatments distributed between them. The experiment ran in Cherry Cove for five days.

At the end of the experiment, painted material from all treatments was carefully collected by hand (ten minute collection time per replicate), placed in plastic buckets, and transported to shore. Samples were air-dried, and the new wt vol^{-1} calculated by repeating the methods outlined above. To test for any treatment effect, the initial wt vol^{-1} of each replicate was subtracted from the final wt vol^{-1}, these values averaged for each treatment, and significant differences between means of treatments were tested using a one-way ANOVA across treatment levels ($N=5$, $\alpha=0.05$). Significant differences were identified by a post-hoc Tukey’s test.

To examine the effects of the drying and painting on the fragility of the treatments, the wt vol^{-1} of (1) dried, painted rhodoliths and (2) freshly collected rhodoliths ($N=3$ for each) was measured before and after crushing treatments for equal amounts of time (~1 min) with a chain in a 5 gallon bucket. A t-test was used to test for a significant difference in wt vol^{-1} between the two treatments.

To test for existing sedimentological differences with between chain-impacted and live rhodoliths, six cores were taken from similar depths (6 meters at time of sampling) in the mooring field at Cherry Cove. Three replicate cores (5.5 cm diameter x

16 cm height) were taken in ‘Chain’ and ‘Live’ areas. ‘Chain’ cores were taken directly beneath the impact point of mooring chains located within the rhodolith bed and ‘Live’ cores were taken from the undisturbed portions of the bed adjacent to the chains, in areas of >75% live rhodolith cover, and spaced at least 5 meters apart. Cores were then brought to the surface and carefully transported back to shore for processing.

To determine if sediment characteristics changed with core depth, sediment cores were cut into 2 cm horizons as they were manually extruded from core sleeves. These sub-sample horizons were dried in an oven for 14 hours at 50ºC, after which visual observations on sedimentological characters and digital photographs were recorded. Samples were manually sieved into the following millimeter fractions which correspond to the divisions in the Wentworth scale: <0.063, 0.063-0.125, 0.125-0.25, 0.25-0.5, 0.5-1, 1-2, and >2 millimeters (Wentworth 1922). These fractions were weighed on a digital scale (Ohaus ScoutPro), converted to percentage data for each horizon, averaged (N=3 per location), and statistically compared to with a 3 factor ANOVA testing for differences across locations, depth horizons, and size fractions.

To investigate a possible relationship between mooring chain density (chains m^{-2}) and live rhodolith cover, the number of chains present within each live bed were counted and plotted against mean live cover values (N=6) generated during bed mapping. Linear regression analysis was applied to the data to test for any significant relationship.

To quantify community-level differences at Cherry Cove and Isthmus Harbor between non-impacted portions of the living rhodolith bed, chain impacted areas of the living bed, and adjacent sand flats, divers identified and counted macro organisms (flora and fauna) within four replicate 1m^2 quadrats placed in (1) ‘Live” areas of >75% live rhodolith cover, (2) ‘Chain’ areas within one meter of the impact point of mooring chains, and (3) ‘Sand’ areas of 0% rhodolith material (living or dead) on the adjacent sand flat. All quadrats were placed at similar depths (6-7 m). Both the total number of genera, and abundance (number of individuals per genera) were averaged per habitat per site and statistically compared with a two-way fixed-factor ANOVA across sites and habitat types.

Data Analysis

All statistical analyses were performed using Systat 12. Normality of all data was examined prior to analysis using a Kolmogorov-Smirnov test and data transformed if necessary.

Results

Over the course of this study, approximately half of the Catalina coastline was surveyed, including all of the areas considered most likely to contain rhodolith beds (Figure 2).

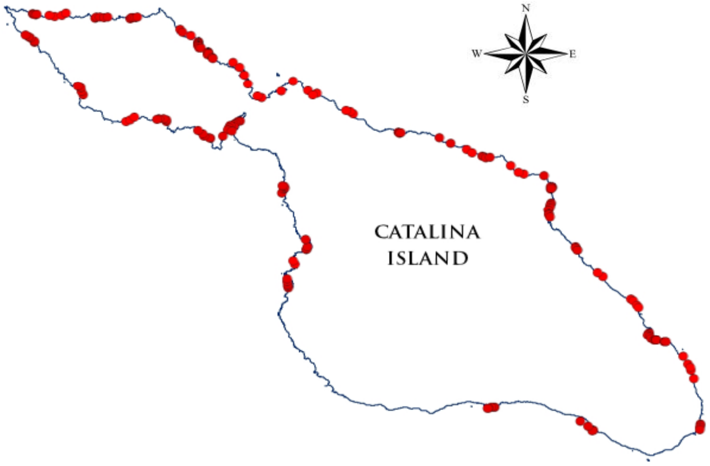


Figure 2. Map of areas searched for rhodolith beds around Catalina Island. Each mark (n= 205) represents a location where a combination of drop camera, snorkel/scuba surveys, and manta tows were performed.

Surveys revealed seven distinct rhodolith beds around Catalina Island. These were all mapped and characterized, including two new beds. Beds were all located on the leeward side of the island (Figure 3). Two beds, separated by a fan-shaped swath of non-biogenic sediment, were mapped in Big Fisherman Cove.

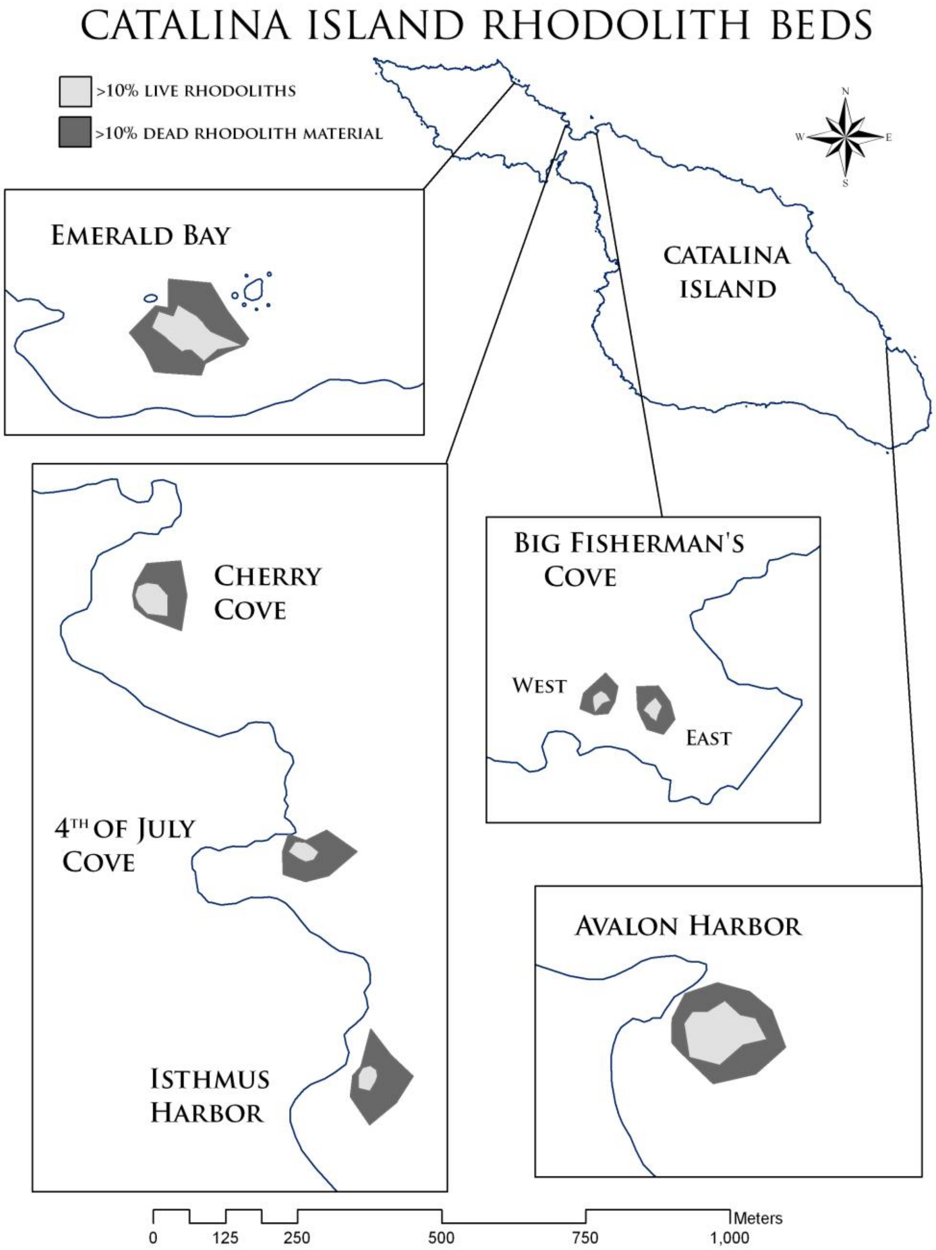


Figure 3. Locations of the seven Catalina Island rhodolith beds detected and surveyed in this study. Boundaries were determined by extent of live (>10% live) and dead (>10% dead) rhodolith material.

The area of live rhodolith cover of the seven Catalina Island beds ranged from 671 to 9,765 m^2, and dead rhodoliths from 2,268 to 13,718 m^2. Depth of live cover varied among beds, and ranged from 4.2 to 20.7 m (Table 1). While two beds were within Blue Cavern State Marine Reserve, and one within a State Marine Conservation area, rhodolith beds are not listed as a recognized habitat in current or proposed management (CADGF 2009). Four beds currently have no protection status (Table 1).

Table 1. Coordinates in decimal degrees, cover, depth, and protection status of seven rhodolith beds at Catalina Island.

Bed	Latitude (N)	Longitude (W)	Live Cover (m^2)	Dead Cover (m^2)	Depth Range Live Material (m)		Protection Status
					Min	Max	
Avalon Harbor	33.3477	118.3246	9,765	4,093	7.8	21	No protection
Big Fisherman's Cove East	33.4448	118.4861	779	3,059	12.5	20.7	Within Blue Cavern SMR
Big Fisherman's Cove West	33.4451	118.4871	671	2,268	7.9	18.6	Within Blue Cavern SMR
Cherry Cove	33.4515	118.5022	2,627	5,543	5.8	7.3	No protection
Emerald Bay	33.4681	118.5281	6,673	13,718	4.2	6.1	Within Arrow Point to Lion Head Point SMCA
4th of July Cove	33.4478	118.4993	1,247	6,076	8.2	15.1	No protection
Isthmus Harbor	33.4441	118.4982	1,148	7,939	4.3	6.1	No protection

The average live rhodolith cover ranged from 21 to 51 percent, and varied significantly across beds ($F_{(6,223)} = 3.76$, $P = 0.001$). The beds in Avalon Harbor and Isthmus Harbor had significantly greater live cover than beds in Big Fisherman's Cove (East and West) and Fourth of July Cove (Figure 4).

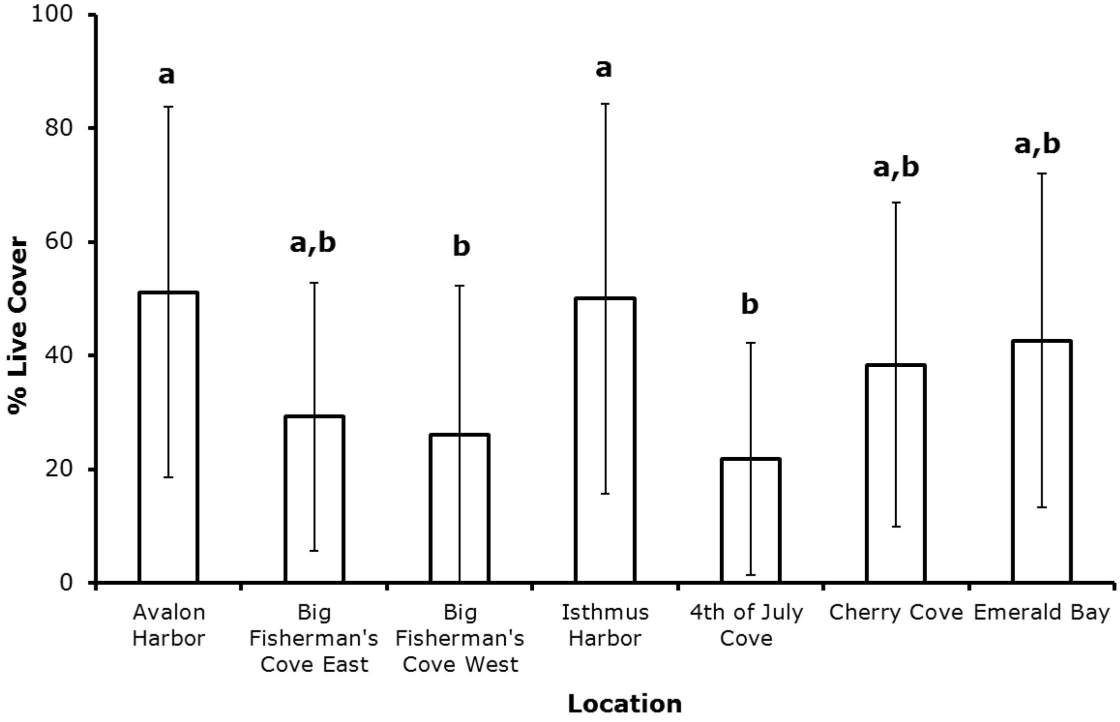


Figure 4. Mean percent cover of living rhodolith material within live portions of each bed (mean ± SD). Letters represent significant differences (α=0.05).

In general Catalina rhodoliths had sparse branching morphology (Figure 1), and ranged in size from 3 to 25 mm in diameter (Figure 5). All beds were dominated by intermediate size class rhodoliths with the majority (76-86%) of measured rhodoliths in the 5-15 mm size class. Very few (0-12%) individuals were in the largest 15-25 mm size class. The remainder (7-17%) were 0-5 mm in length. Five beds showed this pattern distinctly. However, in Isthmus Harbor, the proportion of individuals in the largest and smallest size classes were approximately equal, and in Big Fisherman's Cove West, there were more individuals in the largest size class than in the smallest (Figure 5).

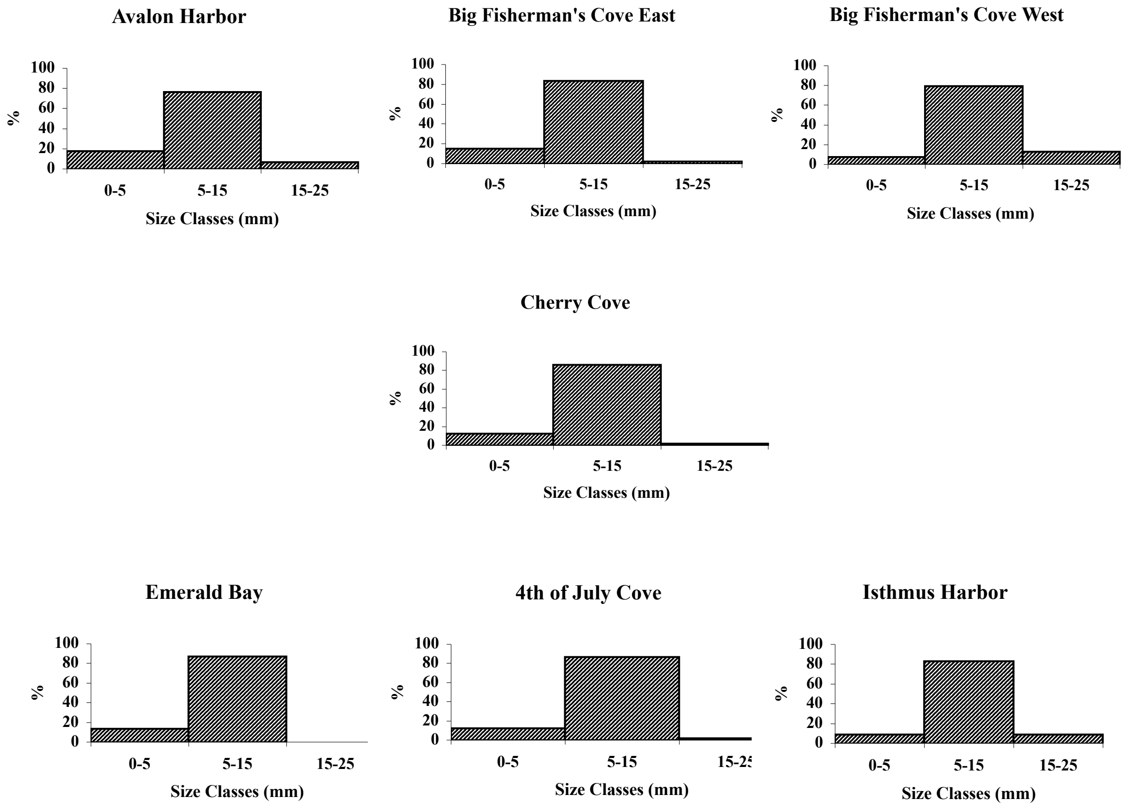

Avalon Harbor
Big Fisherman's Cove East
Big Fisherman's Cove West
Cherry Cove
Emerald Bay
4th of July Cove
Isthmus Harbor

Figure 5. Size frequency distribution of rhodolith populations from Catalina Island rhodolith beds.

Mean long axis measurements varied significantly across beds ($F_{(6.14)} = 3.10$, $P = 0.038$). Individuals from Big Fisherman's Cove West, Cherry Cove, Fourth of July Cove, and Isthmus Harbor (11.97 ± 1.10, 11.52 ± 1.02, 11.50 ± 1.21, 11.47 ± 1.82, respectively, means in mm ± SD) were significantly larger than those from Big Fisherman's Cove East and Emerald Bay (8.73 ± 1.12, 8.47 ± 1.55, respectively, means in mm ± SD). Branch densities ($F_{(6.14)} = 1.77$, $P = 0.117$) and sphericity values ($F_{(6.14)} = 2.14$, $P = 0.112$) did not vary significantly across beds (Figure 6). Population estimates of live rhodoliths were as follows: Cherry Cove = 137,000,000; Fourth of July Cove = 33,500,000; Isthmus Harbor = 75,000,000.

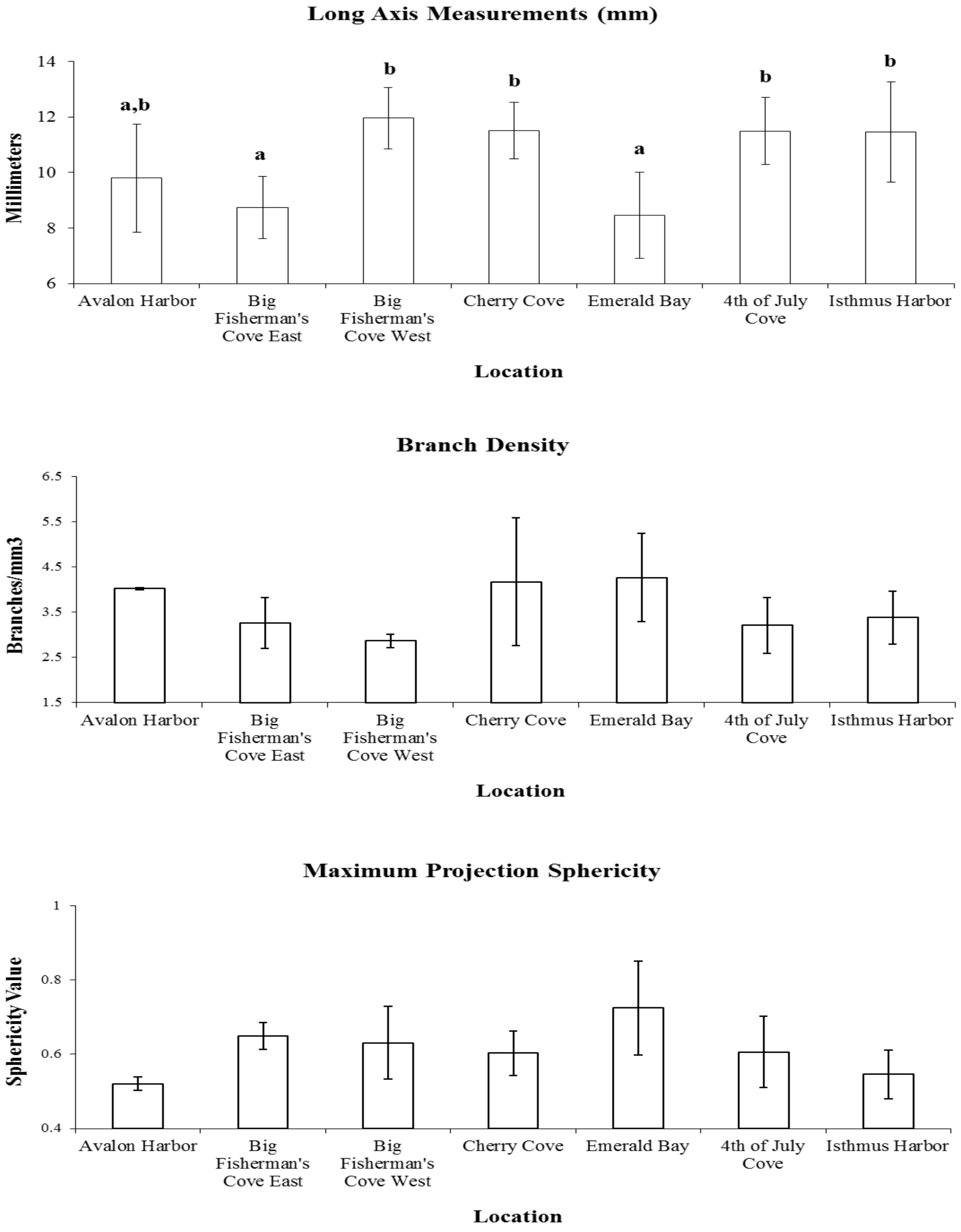


Figure 6. Mean rhodolith size, branch density, and sphericity relative to location at Catalina (mean ± S.D., n=3 per bed). Letters represent statistically significant groupings, differences (α=0.05), lack of letters reflects statistical insignificance.

Growth and Banding

Stain was only clearly detected in 18% of stained individuals (8% in Fall 2008 and 10% in Spring 2010). Seasonal growth rates of *Sporolithon australe* at Catalina Island (mm yr^{-1} ± SE) varied significantly ($t_{32} = 6.46$, $P < 0.001$) between the two seasons and were greater in Fall 2008 = 1.56 ± 0.42 (n= 4 individuals, 32 branch tips) relative to Spring 2010 = 0.93 ± 0.21 (n= 5 individuals, 34 branch tips).

Reproductive material was never observed. Well-defined conceptacles were not seen in microscopic analysis of the surfaces of living rhodoliths, in samples sent to K Miller or R Riosmena-Rodriguez for species identification, nor in over 200 sectioned branch tips examined in the growth study. Internal cell bands were clearly discernable in most sectioned material, and averaged 0.17 mm in thickness. An average of 3.84 new bands per branch gave a band production rate of approximately one band every 51 days.

Disturbance

In the in situ mooring chain disturbance experiment, the mean difference in wt vol^{-1} of Chain treatments was significantly higher ($F_{(2,12)} = 7.48$, $P = 0.009$) than those of the Live or Chain Removal treatments (Figure 7). In the fragility bucket experiment no significant difference was detected between the mean wt vol^{-1} of live and dried/painted rhodoliths ($t_3 = 0.31$, $P = 0.77$).

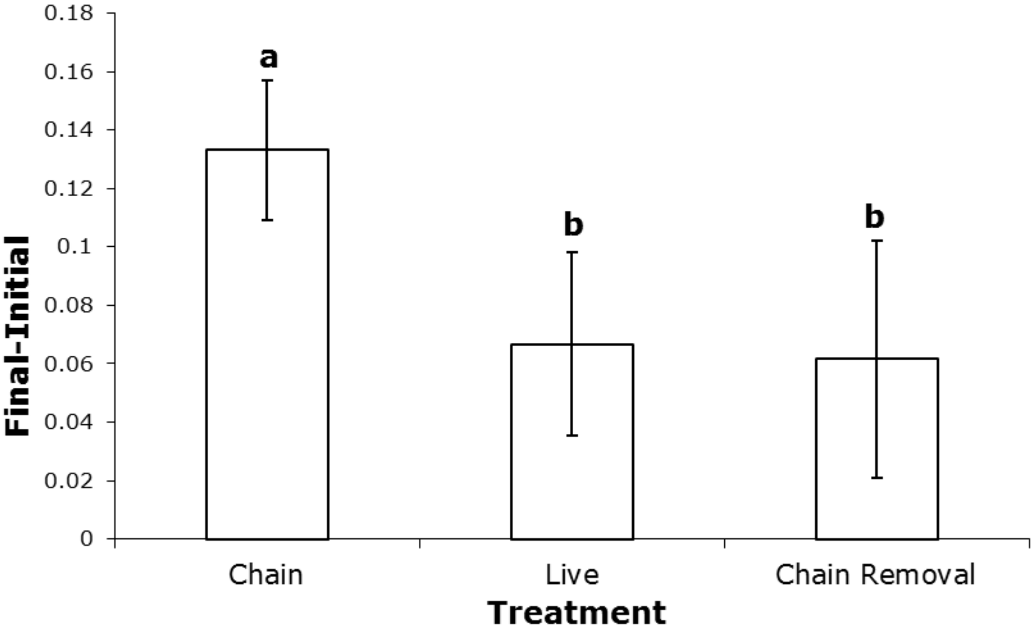


Figure 7. Results of mooring chain disturbance on rhodoliths at Catalina Island (mean ± S.D., n=5 replicates per treatment for each time period). Letters represent significant differences (α=0.05).

When comparing sedimentological differences between core material from chain impacted and live rhodolith locations, there was a significant statistical interaction between all factors (location, horizon depth, and size fraction). These interactions were driven by two main differences in percent weight of sediment within specific horizon depths between locations. In the 0-2 and 2-4 cm horizons, there was more >2 mm sediment in live cores than in chain cores (Figure 8). Below this depth (deeper than 4 cm) there was more >0.125 mm sediment in the live cores than in the chain. While the percentage of different fractions varied across depths in live cores, chain cores were relatively similar across depths, and dominated by the 1-2 mm size fraction (Figure 8).

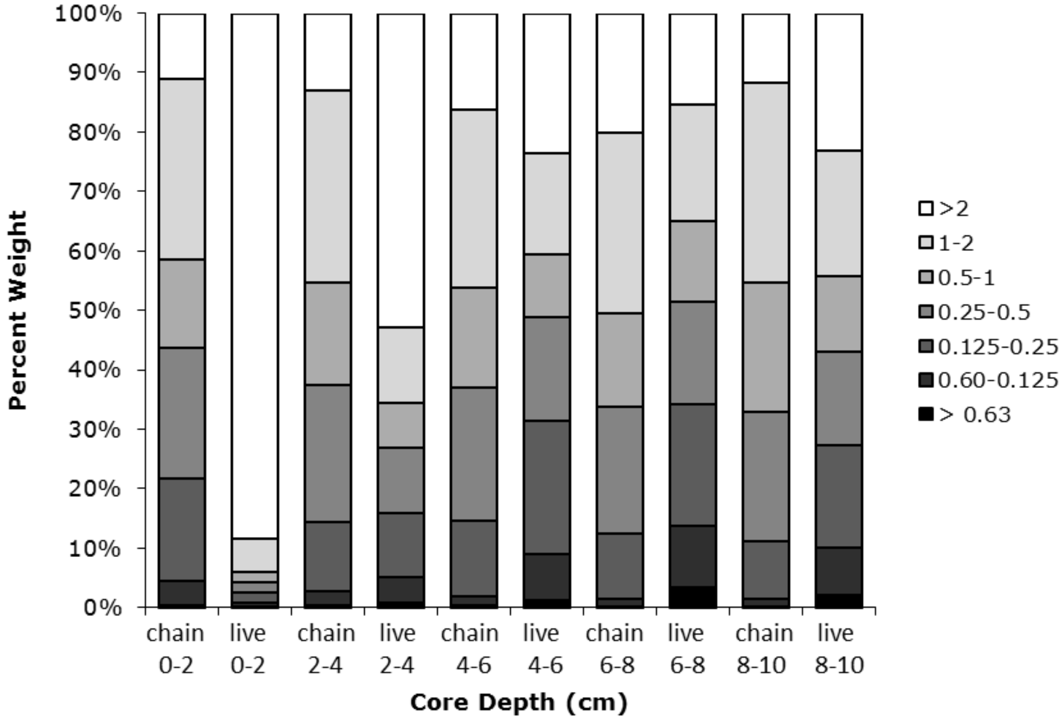


Figure 8. Results of sediment core fractionation analysis.

In the examination of the relationship between mooring density and percent of live cover across beds, there was a significant negative relationship ($r^2 = 0.57$, $F_{1,4} = 5.31$, $P = 0.083$, Figure 9).

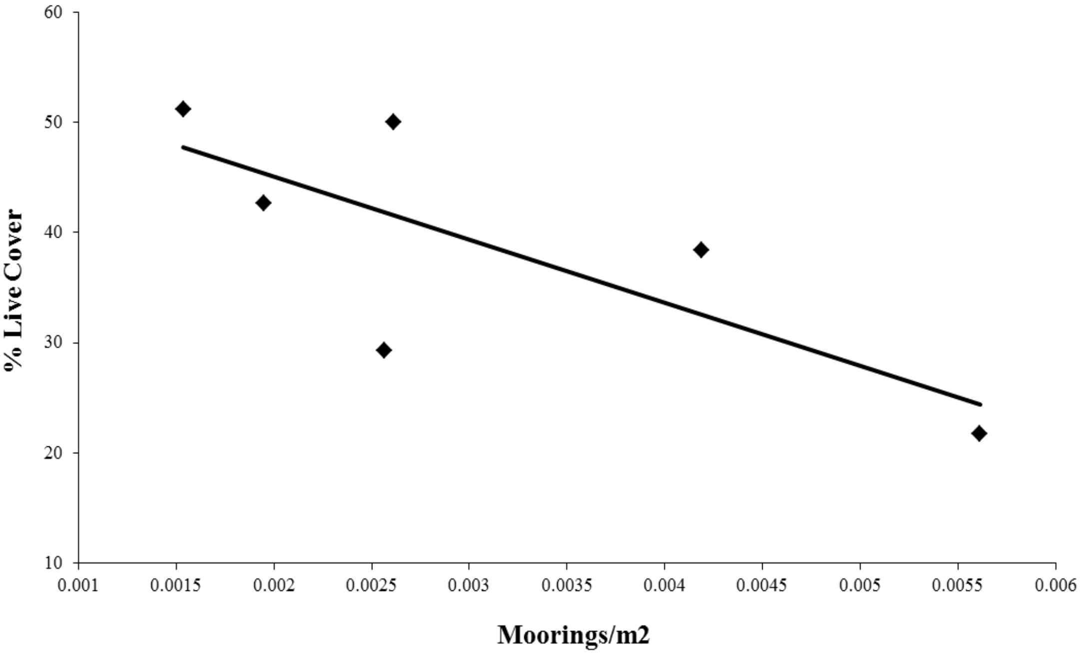
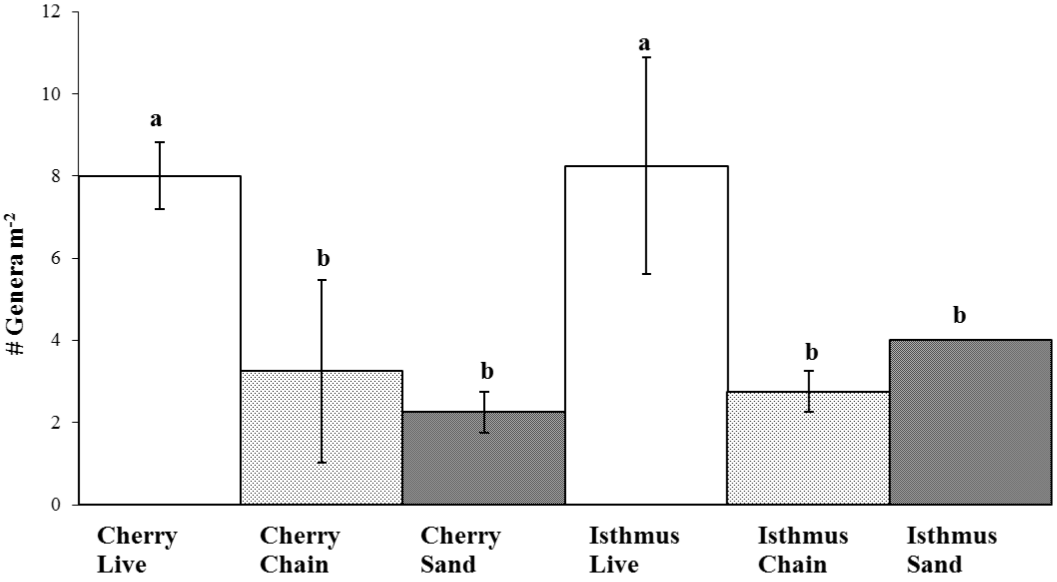


Figure 9. Relationship between live rhodolith cover and mooring density.

Fourth of July Cove had the most chains per bed area, and the lowest average percent cover of live rhodoliths. Approximately seven chains lay within the live rhodolith bed at Fourth of July Cove. Mooring chains were typically 10 meters in length (distance from the mooring block to the "impact point," where the chain left the bottom and angled to the surface). Chains were seen moving vertically and horizontally (as much as 2.5 meters in either direction), creating fan-shaped "footprints" of crushed rhodolith sand on the seafloor. Given the ~25 m^2 footprint of these chains, as much as 175 m^2, or 14% of the Fourth of July Cove rhodolith bed was within the potential swing radius of these chains.

Diversity of associated macro-organisms did not vary between Cherry Cove and Isthmus Harbor ($F_{(1,20)} = 0.678$, $P = 0.420$), however diversity varied significantly among habitats within these sites ($F_{(2,20)} = 30.904$, $P = 0.000$). In both sites, there were significantly more genera in the Live quadrats than in either Chain or Sand (Figure 10A). Abundances of these organisms varied both across sites ($F_{(1,18)} = 4.77$, $P = 0.042$) and across habitats ($F_{(2,18)} = 7.184$, $P = 0.005$), with a significant interaction between site and habitat ($F_{(2,18)} = 4.375$, $P = 0.028$). Abundances were higher in Cherry Cove than in Isthmus Harbor. Across habitats, abundances were greatest in Live, intermediate in Sand, and lowest in Chain. The interaction was driven by Cherry Cove having higher overall abundances of benthic organisms in Live and Sand habitats than in the Chain, while abundances did not vary across habitats in Isthmus Harbor (Figure 10B).

A.



B.

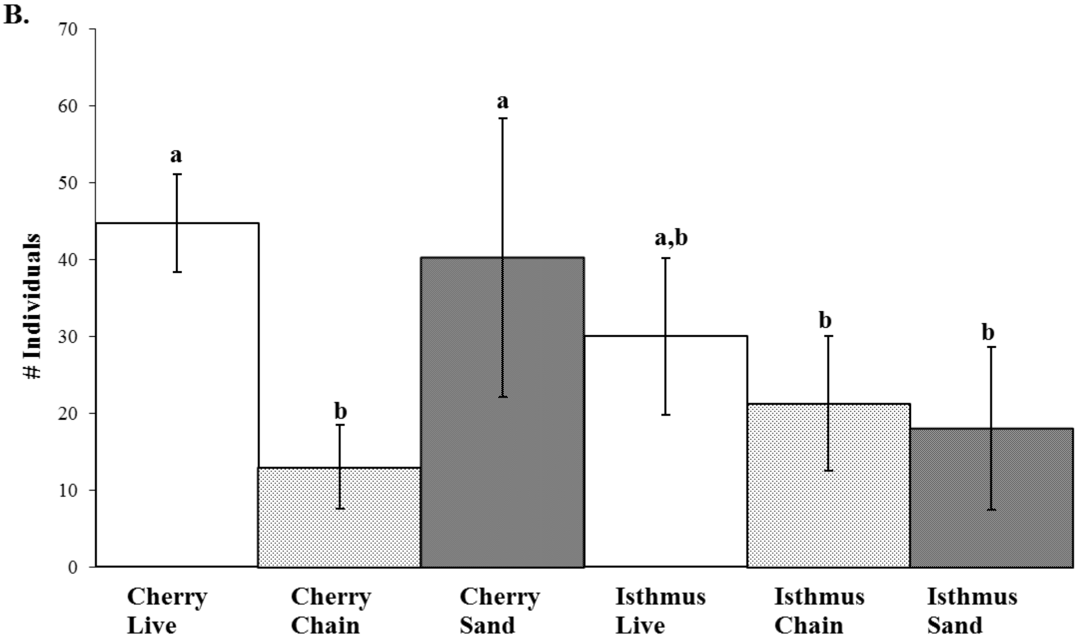


Figure 10. Result of benthic 1 m^{-2} quadrat counts from live, chain disturbed, and adjacent sand flat habitats of Cherry Cove and Isthmus Harbor rhodolith beds (mean ± S.D., n=4 habitat). A. Mean # of genera m^{-2} per habitat per site. B. Mean # of individuals m^{-2} per habitat per site.

Discussion

The physical settings of Catalina rhodolith beds were similar to beds described worldwide: rhodoliths were found in shallow embayments protected from predominant swell direction (Bosence 1980; Scoffin et al. 1985; Pena and Barbara 2009; Rosas-Alquicira et al. 2009). The aspect of the seafloor beneath beds was typically easterly, opposite the direction of predominant wind and swell, with two notable exceptions. While the slope of beds in Big Fisherman's Cove and Emerald Bay faced north, and were more exposed to dominant swell direction, they were in the relative protection of surrounding kelp forests (Habitat Reef and Indian Rocks, respectively), which may buffer incoming hydraulic energy (Jackson and Winant 1983; Eckman et al. 1989).

The areal extent of live rhodolith cover at Catalina was low relative to most other beds worldwide. For example, mapping exercises and visual estimations elsewhere have revealed beds ranging in size from a few hundred square meters to over 50 square kilometers (Bosence 1983b; Littler et al. 1991; Rosas-Alquicira et al. 2009). Many live beds are square kilometers in scale (De Grave 2000; Ehrhold 2006; Konar et al. 2006; Harvey and Bird 2008; Pena and Barbara 2009; Sciberras 2009). At Catalina, live rhodoliths only covered a small percentage of the available soft sediment area of the embayments in which they were found. The cover of dead material (<10% live) surrounding the living Catalina beds was high relative to studies such as that by Pena and Barbara (2009) who reported only 1.4% total cover of Galician maerl beds completely dead. The limited extent of live cover relative to high dead cover may be a result of high levels of disturbance from anchoring and moorings, practices that can locally eliminate marine vegetation (Walker et al. 1989). More work is needed to determine if disturbance currently limits the extent of beds, and to determine the historical cover of rhodoliths at Catalina.

The depth range of live rhodolith beds at Catalina (4->20 m) was shallow compared to the reported 0-40 m range of temperate water beds (Lemoine 1910; Konar et al. 2006; Pena and Barbara 2009), and much shallower than depths of 30->100 m reported from clear, temperate to tropical waters (Kemph 1970; Littler et al. 1991; Amado-Filho et al. 2007; Sciberras 2009). While light limitation may restrict the lower limits of beds at Catalina, geomorphology likely plays a larger role. Seafloor slopes typically increased at the deeper limits of these beds, as live cover declined (pers obs), a process noted in other beds (Littler et al. 1991). The shallow limit of the beds at Catalina did not extend into the intertidal, as has been seen elsewhere (Bosence 1976; Scoffin et al. 1985; Sciberras 2009; Riosmena-Rodriguez et al. 2010), but appeared limited by a combination of fringing rocky reefs, wave motion, and terrestrial runoff (pers obs). More work is needed to examine the factors limiting both the deep and shallow extent of these beds, and to investigate the existence of deeper beds beyond 30 m.

While the average live cover of rhodoliths in Catalina beds (30-50%) was consistent with results elsewhere (Konar et al. 2006; Harvey and Bird 2008; Pena and Barbara 2009), at Catalina variability in live cover was high. This variability was likely the result of a combination of the patchy nature of the live beds (possibly created by hydraulic energy, M. Foster, pers comm) and high disturbance levels. The uniformly dichromatic bed maps in Figure 2 are misleading; live portions of beds are discontinuous, characterized by large swaths of small-grain (2-5 mm) dead rhodolith material punctuated by networks of larger (5-30 mm) live nodules. During mapping exercises, randomly placed quadrats sometimes landed within high-density live patches (up to 100% live cover), but often they fell on patch edges, or between patches where only a few live individuals lay atop dead rhodolith sand (0-20% live). Quadrats placed near mooring chains were likely to have no live rhodoliths at all (pers obs). Sparse, patchy cover of live rhodoliths is consistent with high levels of disturbance.

The population estimates showed an interesting pattern. Though the live rhodolith bed in Isthmus Harbor was ~100 square meters smaller than that of Fourth of July Cove, the population estimate in the former (75,000,000) was more than double that of the latter (33,500,000). This disparity in population sizes was likely due to a difference in the disturbance regime between these two areas. The mooring density in Isthmus Harbor was less than half (0.0026 moorings m^{-1}) that of Fourth of July Cove (0.0056 moorings m^{-1}). These results are consistent with a negative effect of mooring chains on rhodolith populations. Existing mooring densities are likely inhibiting any population recovery, and increasing mooring densities may eventually lead to local extirpations of rhodoliths at Catalina.

Globally, reported sizes (longest axes) of live rhodoliths range from 1 to over 30 cm, with averages most commonly in the 4-8 cm range (Bosellini and Ginsburg 1971; Scoffin et al. 1985; Littler et al. 1991; Konar et al. 2006; Pena and Barbara 2009; Rosas-Alquicira et al. 2009; Sciberras 2009). Catalina rhodoliths, by comparison, were very small. No live individuals from core samples were greater than 2.5 cm, and larger live specimens were rarely found during surveys and observations. Average rhodolith sizes can be reduced over time due to high levels of disturbance (Bordehore et al. 2003), and the lack of large live rhodoliths at Catalina is further evidence of the high levels of disturbance within these beds.

The significant difference in mean rhodolith size between the two beds in Big Fisherman's cove was particularly interesting, as it highlights the non-uniform effects of disturbance in this system. The separation of these two beds could be the result of a landslide from "Chalk Cliffs" above, which may have created the two smaller beds by smothering part of a larger one. Rhodoliths in the East bed (average diameter = 8.73 mm) are impacted by moorings, and were significantly smaller than those from the West bed (average diameter = 11.97 mm). The West bed is the only area at Catalina where rhodoliths were found in the absence of moorings, and the only bed where the size frequency was shifted toward larger individuals. This is also one of the most exposed beds on the island, and was highly disturbed by a large storm event in January of 2009. Observations indicated that while this storm caused the overall cover of live rhodoliths in the bed to decrease, the largest rhodoliths were left intact. Larger rhodoliths are less susceptible to movement by hydraulic energy (Bosellini and Ginsburg 1971). From this example, it appears that mooring disturbance has a much different effect on population characteristics than natural events.

Though branch densities and sphericities did not vary significantly among beds, an interesting pattern was apparent. During the course of this study, water motion at Emerald Bay was consistently higher than at other sites (pers obs), and was the result of both laminar currents and oscillatory wave motion. Globally, rhodoliths in higher-energy environments are thought to have characteristic morphologies: smaller, more spherical, and more densely branched (Bosence 1983b; Steller and Foster 1995; Amado-Filho et al. 2007). Consistent with these trends, Emerald Bay rhodoliths were on average the smallest, most densely branched, and most spherical rhodoliths at Catalina.

Published average growth estimates (one-dimensional branch extension in mm yr^{-1}) of free-living corallines (maerl and rhodoliths) range from 0.105 to 2.56 (*Lithothamnium corallioides,* Adey and McKibbin 1970, and *Lithophyllum margaritae,* Steller et al. 2007, respectively). Most studies report rates of less than a millimeter per year (Bosence 1980; Fazakerley and Guiry 1998; Frantz et al. 2000; Rivera 2004; Kamenos et al. 2008). The results of this study show relatively rapid growth for *Sporolithon australe*, and are most similar to the branch extension rates of 1.2-1.8 mm yr^{-1} for *Phymatolython calcareum* in the northeast Atlantic (Blake and Maggs 2003).

The seasonal difference in growth measured in this study revealed a pattern similar to most reported estimates of growth in temperate articulated and crustose corallines. The few studies that have examined seasonal growth, both from the subtropical Gulf of California, have produced conflicting results. Steller et al (2007) measured faster summer growth (5.02 ± 1.16) relative to winter (0.83 ± 0.16), results supporting the predicted physiological response to variation in water temperature. Rivera et al (2004), however, measured faster rates of growth in *Lithothamnion muelleri* in winter and spring, relative to summer and fall. This unexpected result was attributed to inhibition of calcification due to anomalously high water temperatures during an El Nino year. The seasonal growth measured by Steller et al (2007) was consistent with physiological studies conducted in the lab across a range of temperatures.

The estimated banding frequency measured in this study of one band every ~50 days is inconsistent with most studies which have identified annual or semi-annual banding frequencies (Wehrmann 1998; Georgina-Rivera 1999; Halfar et al. 2000; Rivera 2004; Kamenos et al. 2008). However, other investigators have described monthly banding periodicities, or second-order banding patterns, consistent with lunar or tidal cycles, within first-order, seasonal banding (Freiwald and Henrich 1994; Blake and Maggs 2003). Kamenos (2010) found density of calcitic areas (cell walls) is controlled by temperature. Generally, colder temperatures result in thicker, denser cell walls (dark bands). Given this, the banding pattern of Catalina rhodoliths could be the result of variations in the depth of the thermocline over the course of a lunar cycle, however, more work is needed to correlate these factors.

The primary effect of the mooring chains on the rhodolith habitat was loss of three-dimensional structure. In the experiment, this loss was rapid and dramatic; after only five days the chains had smashed treatments, creating smaller rhodolith fragments. The typically high biodiversity found in rhodolith beds is thought to be a function of their small-scale habitat complexity (Steller et al. 2003). The matrix of interstitial spaces provides predation refuge for small invertebrates, a settlement substrate for epiphytes and epifauna, and can act as a nursery habitat (Barbara et al. 2004; Kamenos et al. 2004; Leliaert et al. 2009; Steller and Caceres-Martinez 2009). The complexity, and therefore the inherent benefit of this habitat, is compromised by physical impacts that break branches and fill and reduce the spaces between (Kamenos 2003).

In addition to reducing structure, the homogenization of rhodolith sediment beneath the Catalina mooring chains could directly alter rhodolith habitat community structure through influencing the passive and active recruitment of planktonic larvae and spores. Passive settlement is influenced by the relationship between hydrodynamics and physical aspects of the seafloor. Swimming larvae preferentially settle based on biological factors, including those associated with coralline algal surfaces (Daume et al. 1999; Steller and Caceres-Martinez 2009). Physical structures can alter fluid flow by creating downstream turbulence creating regions of weak circulation and low shear. Fluid currents ultimately slow as they pass though vegetation (Burrell and Schubel 1977; Jackson and Winant 1983; Duggins 1987). Flow velocities influence planktonic propagule settlement; slower flows mean more settlement (Orth 1992). As such, particle settlement is exacerbated beneath and downstream of seagrasses and kelps (Jackson and Winant 1983; Eckman et al. 1989). The branch matrix of the 4-cm thick layer of live rhodoliths at Catalina and rhodoliths may have the same effect, explaining the higher percentages of fine-grained material beneath living rhodoliths. More work is needed to determine if biological settlement is similarly influenced.

As mooring chains crush rhodoliths, they dramatically decrease the quality of rhodolith bed habitat. The high frequency of this disturbance has the potential to reduce habitat recovery close to the chains, as is evident from the “halo” of crushed, dead, rhodolith material around the impact point. Typically, this impact is discreet in space:

When no vessel is attached to the mooring, the chain mostly moves vertically as the mooring ball above bounces in the waves, continually impacting ~one square meter of seafloor. Further from the chains, the impact is less frequent, but can occur periodically as vessels drag chains sideways. As one end of each chain is attached to a heavy mooring block, this horizontal movement results in a fan-shaped impact footprint, which can be 25 square meters in size, and undoubtedly contributes to the high variability in live cover measured in the Catalina rhodolith beds. High-density patches of live material were only found well away from the impact point of the chains, and outside of the potential swing radius. Large, episodic storm events have the potential to create enough surge to transport rhodoliths (Bosellini and Ginsburg 1971; Marrack 1997), possibly shifting them beneath the moorings, and further exacerbating the overall impact of the chains.

The locations of these chains have not been fixed over time. Whenever more moorings are added to bays or harbors, the others are moved to ensure even spacing between vessels. This movement creates a massive disturbance of high sedimentation, reduced water clarity, and widespread crushing of the seafloor, large in space but short in time (pers obs). Combined with the constant impacts of mooring chains, these periodic larger-scale events have likely contributed to the overall small size and patchy coverage of rhodoliths at Catalina, possibly mirroring the effects of benthic trawling in Europe (Bordehore et al. 2003). Over time, this high level of disturbance could have drastically decreased the areal extent of these beds, along with shifting the size distribution. Hundreds of years ago, before vessels began anchoring at Catalina, beds may have been much more expansive, the live material denser, and composed of much larger individuals.

The extensive banks of dead rhodolith sediment combined with the large, dead rhodoliths found at the surface and exhumed from the sediment are evidence of this. However, further research is needed to determine historical rhodolith distributions, and the ages of these large nodules.

While the effect of natural disturbances can be subtle and variable (Hinojosa-Arango et al. 2009), the effects of human-caused disturbances can be clear and catastrophic. Anthropogenic alterations of habitats typically result in decreased habitat complexity, both physical and biological (Airoldi et al. 2008). Destruction and loss of marine biogenic reefs is an ongoing process, and a major threat to marine biodiversity (Beatley 1991; Gray 1997; Barbera et al. 2003; Roberts and Hirshfield 2004; Airoldi and Beck 2007). The degradation or loss of autogenic ecosystem engineers like rhodoliths can lead to local scale trophic simplification, an process seen as forests are converted to grasslands, or kelp forests to urchin barrens (Graham 2004). Shrinking rhodolith beds would support fewer species, as diversity and habitat size are directly linked (MacArthur and Wilson 1967; Kohn and Walsh 1994). Even at small scales, this “biologic homogenization” of communities can have unknown, or unintended, ecosystem-level effects (Airoldi et al. 2008).

Overall the communities supported by biogenic reefs, and vegetated marine habitats in particular, are productive systems compared to their less structurally complex, or unvegetated counterparts (Edgar 1990; Ferrell and Bell 1991; Bustamante et al. 1995; Graham 2004; Hosack et al. 2006; Thrush et al. 2006). Rhodolith beds are productive systems (Martin et al. 2007a; Martin et al. 2007b), and the degradation or loss of rhodoliths beds at Catalina could mean a decrease in local carbon sequestration and oxygen production, as rhodoliths and their epiphytes are lost. In this study, the fewer bioturbators in disturbed and sandy areas relative to rhodoliths suggests that the supply of organic material and oxygen to the sediments would therefore decline with live rhodolith cover (Rhoads 1974; Aller 1983; Hansen and Kristensen 1998). This loss of both local productivity and biodiversity may propagate across larger-scale food webs (Edgar and Shaw 1995; Jackson et al. 2001; Dobson et al. 2006)

During this study, rhodolith core samples were collected to support future community-level research. Subsequent processing revealed that most of the cryptic invertebrates living in the matrix were juvenile stages, underscoring the potential for Catalina rhodolith beds to serve a nursery-habitat function (K Meagher, pers comm). Some of these species may be settling and growing in the beds, and later recruiting to adjacent kelp forests. Fish seen feeding in rhodolith habitats were mostly kelp-forest species, and could be subsidizing their diets by foraging in the beds. If these beds are lost, species requiring or benefiting from the refuge of rhodoliths, and those foraging in the beds may be negatively impacted.

There is potential for recovery of these habitats, though this process would require drastic change in the current disturbance regime. Given the average branch tip extension growth rate of 1.2 mm yr^{-1}, and average rhodolith size of 1.2 cm, it would take at minimum ~5 years for the average Catalina rhodolith to reach the maximum measured size of 2.5 cm. An excess of 30 years would be required for these rhodoliths to attain sizes akin to those of the dead, buried rhodoliths assumed to be relics from preanthropogenic ages. These estimates assume both a constant growth rate with size, the complete cessation of further disturbances (including natural disturbances such as bioturbation, grazing, and storm events), and do not consider population-level recovery estimates.

While natural disturbances cannot be halted, minimizing human disturbance to rhodolith beds at Catalina Island would be a matter of modifying the mooring chains. Chains within live beds could be lifted from the seafloor by a series of floats, without jeopardizing their functionality. Ideally, annual monitoring using methods similar to those initially used to map the beds would follow modifications. To minimize impact, morphological measurements could be done in situ at random points along transects, so that live nodules could be replaced alive and undamaged. Digital imaging and subsequent analysis could produce more quantitative and comparable measurements of percent cover.

This study represents a preliminary ecological study of Catalina rhodolith beds, and many questions remain. Being a novel and unique system in California waters, there is vast potential for future research. Future efforts should explore: the presence of deeper rhodolith beds (>30 meters); taxonomy, phylogeny, and population-level relationships (i.e., the level of clonality within and among beds, and the relationship between free-living nodules and adjacent epilithic crusts) using molecular techniques; the historical extent and characteristics of these beds, and the overall effect of human impacts over time; the role of these beds in the marine carbon cycle, and their susceptibility to ocean acidification; the floral, faunal, and microbial community in these habitats, and the effect of seasons and disturbance on the structure community; trophic relationships both within beds and across adjacent habitats (i.e., foraging of mobile macrofauna); the potential nursery function of this habitat, and mechanisms of larval substrate selection and settlement.

Rhodolith beds at Catalina are novel and unique habitats, offering a multitude of opportunities for further research. With the combined effects of direct impaction, marine pollution, and ocean acidification, the longevity of these habitats is uncertain. Clearly sensitive and highly disturbed, rhodolith beds at Catalina Island would greatly benefit from special protections and future restoration/monitoring efforts.

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