

Living carbonate habitats in temperate California (USA) waters: distribution, growth, and disturbance of Santa Catalina Island rhodoliths

Paul A. Tompkins*, Diana L. Steller

Moss Landing Marine Laboratories, 8272 Moss Landing Rd., Moss Landing, California 95039, USA

ABSTRACT: Rhodoliths are globally widespread, free-living coralline red algal nodules (Rhodophyta). Living beds of rhodoliths create carbonate-based biogenic benthic habitats, which are sensitive to human disturbance and slow to recover. Despite their ecological importance, few quantitative assessments of the distribution and anthropogenic impacts on rhodoliths exist for the eastern Pacific Ocean. Following historical reports of beds in the Channel Islands off California, USA, we mapped bed distributions, examined rhodolith habitat sensitivity to human disturbance, and determined seasonal growth rates to assess rhodolith recovery potential at Santa Catalina Island. Rhodolith material from 7 beds covering 23 000 m² of live rhodoliths and 43 000 m² of dead rhodolith sediment were mapped. Beds were patchy, dominated by small *Lithothamnion australe* rhodoliths (mean \pm SD: 10.6 \pm 0.8 mm in diameter), and 6 beds were disturbed by mooring arrays. Surveys of mooring frequency and experimental manipulation of mooring chains showed that the cover of live rhodoliths, their physical structure, and the diversity and abundance of associated benthic species were negatively related to this prevalent anthropogenic disturbance. Axial growth rates of Santa Catalina Island rhodoliths were relatively slow, seasonally variable, and similar to those reported in other rhodolith studies (annual mean: 1.25 \pm 0.62 mm yr⁻¹). Due to their importance as biogenic habitat, sensitivity to disturbance, and slow recovery potential, California rhodolith beds should be considered a priority for monitoring efforts and restoration and should be included within marine protected area planning.

KEY WORDS: Rhodophyta · Disturbance · *Lithothamnion australe* · Coralline algae · Maerl · Channel Islands

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INTRODUCTION

Rhodoliths are free-living, non-geniculate coralline red algae (Rhodophyta) that occur in all oceans (Bosence 1983, Foster 2001). Individual rhodoliths, or 'nodules,' can be intricately branched, and form large aggregations or 'beds,' creating a living matrix of branches and interstitial spaces on the seafloor. These complex structures are considered foundation species that create important marine habitat over otherwise sedimentary bottoms. Relative to non-living soft-sediment benthos, rhodolith beds support highly diverse and often unique biological communities (Cabioch 1969, Keegan 1974, Steller et al. 2003,

Amado-Filho et al. 2007). They act as seed banks for marine life (Fredericq et al. 2014), nursery grounds and adult habitat for commercially important species of bivalves (Steller et al. 2003, Kamenos et al. 2004b), and as habitat for fish (Aburto-Oropeza & Balart 2001, Kamenos et al. 2004a, Pereira-Filho et al. 2015). The role rhodoliths play as an important biogenic habitat is expanding as our understanding of their distribution and ecological role increases.

Rhodolith thalli are highly calcified, easily fragmented, and grow slowly, typically <1 mm yr⁻¹ (reviewed by Foster 2001, Foster et al. 2013). These features make beds susceptible to physical disturbances and slow to recover. Destructive anthropogenic impacts

*Corresponding author: ptompkins25@gmail.com

on rhodolith beds include mechanical destruction from mining and extraction, fishing activity, pollution, anchoring, eutrophication and sedimentation from coastal development, and ocean acidification (BIOMAERL Team 1999, Barbera et al. 2003, Grall & Hall-Spencer 2003, Jokiel et al. 2008, Felder et al. 2014). Degradation of rhodolith beds from physical disturbance reduces live cover and structural complexity, with long-lasting effects on habitat productivity (Hall-Spencer & Moore 2000, Bordehore et al. 2003, Hauton et al. 2003, Kamenos et al. 2003). Diminished habitat quality may result in reduced settlement and survival of species associated with rhodolith habitat (Hauton et al. 2003, Steller & Cáceres-Martínez 2009).

Rhodoliths are increasingly recognized and contrasted with other marine habitats due to their conservation value (Airoldi et al. 2008). Because of their biological significance and susceptibility to disturbance, rhodolith beds in the North-East Atlantic and Mediterranean Sea have been afforded special protection under the European Union Council Directive 92/43/EEC, and the United Nations Environment Programme's Mediterranean Action Plan (Council of the European Commission 1992, UNEP-MAP-RAC/SPA 2008). Similar protections have been recommended for New Zealand (Nelson et al. 2012), Australia (Harvey et al. 2016), and Brazil (Amado-Filho et al. 2012). Despite this increased awareness, protection of beds worldwide is hampered by lack of precise information on both distribution and ecological significance.

Despite their ecological value, sensitivity to disturbance, and potential importance for commercial resources, little information exists on rhodoliths from the northeastern Pacific. Reports of rhodolith forming species exist from the Aleutian Islands, Alaska, USA, to Bahia Magdalena, Mexico (reviewed in Robinson et al. 2016). However, rhodolith beds have only been described in Prince William Sound, Alaska, USA, (Konar et al. 2006), and in Bahia Magdalena (Avila & Riosmena-Rodriguez 2011), with little information on their status in the 5000 km between these regions. Historically, live rhodoliths were reported from California waters (Foslie 1906, Dawson 1949, Mason 1953), yet no systematic information on their distributions, ecological significance, or conservation status has been published. Anecdotal reports exist describing rhodoliths at Santa Catalina Island (hereafter Catalina), California, in 4 shallow (<20 m) and sheltered coves (Parnell et al. 2006). The current investigation sought to (1) describe the distribution and size of Catalina rhodoliths, (2) examine the sensitivity of

rhodolith habitat and the associated community to human disturbance, and (3) determine seasonal growth rates to estimate habitat recovery potential.

MATERIALS AND METHODS

Study site

Catalina (33.40°N, 118.40°W) is located approximately 32 km south of Los Angeles, California, USA, in the Southern California Bight. The island's long axis extends in a NW to SE direction (Fig. 1). The coastline is dominated by rocky reef and numerous sandy bays, many of which form natural harbors. The island is a popular boating destination with mooring arrays in most protected bays.

Rhodolith distribution and population characteristics

The distribution and areal coverage of rhodolith beds between 0 and 30 m depth at Catalina was estimated using multiple methods. Search efforts were initially focused in embayments where rhodoliths had previously been reported (Parnell et al. 2006, K. A. Miller, D. Sullivan, S. Lonhart, & L. Sadler pers. comm.). Available aerial and satellite imagery (e.g. Perry 2008) was used to further identify potential rhodolith bed locations based on seafloor color. Subsequent systematic circum-island searches were done using underwater drop cameras, manta tows (Moran & De'ath 1992), and diver surveys. Search efforts were allocated to areas of higher probability to support beds based on published information on the general physical setting of beds worldwide: shallow, protected, gently sloping embayments (Bosence 1980, Scoffin et al. 1985, Peña & Bárbara 2009, Rosas-Alquicira et al. 2009). To search lower-probability areas (exposed, steep, rocky coastlines), random points were allocated along the coast and sampled by drop camera. Any questionable images were ground-truthed by diver observations.

Upon locating rhodolith beds, preliminary mapping was conducted using acoustic surveys (Reson 8101 multibeam sonar system operating at 240 kHz, measuring relative water depths within a 150° swath consisting of 101 beams of 1.5 × 1.5°). Areal coverage of live and dead rhodolith material (rhodalgal carbonate sand) was then estimated using diver surveys. A central point within the area of live cover was located and recorded with GPS, and 8 radiating transects (45°

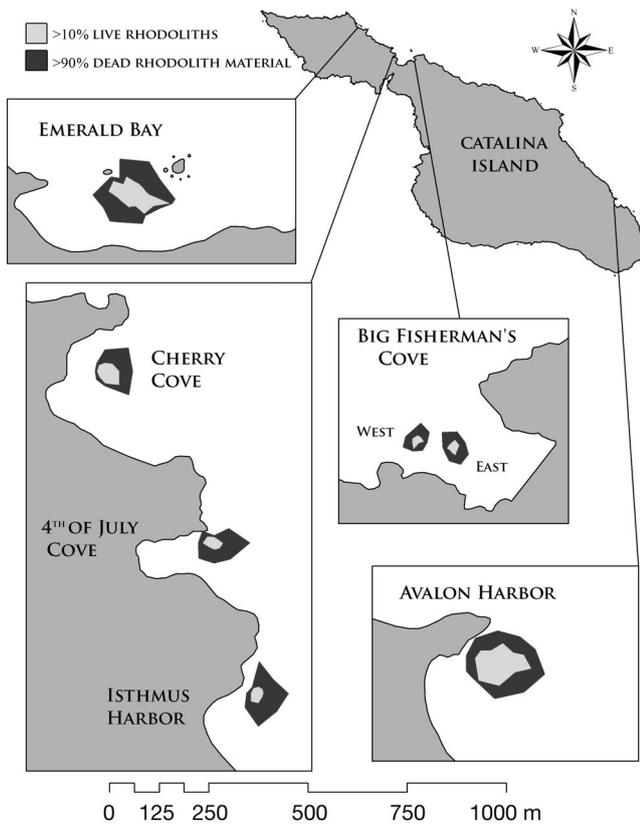


Fig. 1. Locations of 7 Santa Catalina Island (California, USA) rhodolith beds detected and surveyed in this study. Boundaries were determined by extent of live (>10% live) and dead (>90% dead) rhodolith material. Island length is 34 km, scale bar refers to all insets

between each) were extended out to measure distances to the edges of both live and dead rhodolith material. These transects were geo-referenced (ArcGIS® software, ESRI) to map bed distributions and estimate area of both live and dead material.

The Catalina rhodoliths in this study have previously been identified as *Lithothamnion australe* Fossie on the basis of morphology. We are uncertain if this is accurate, and molecular assessment of 4 specimens from 2 sites is underway to confirm their identity. Voucher specimens are archived at the University Herbarium of the University of California, Berkeley (Accession Nos. UC2050593 – UC2050596). To determine if the size of live rhodoliths varied among beds, the mean size was measured for each Catalina bed. Five cores (10 cm diameter × 5 cm height) were taken at haphazard distances along transects (centered in the living portion of the bed, each from within patches of live rhodoliths). From each core, live rhodoliths were separated from other sediments, 25 randomly selected per core, and the longest axes were measured with calipers.

Disturbance assessment

Catalina rhodolith beds are exposed to anthropogenic disturbances including rubbish accumulation, fishing activity, hydraulic disturbance via vessel movements, and mechanical destruction by mooring chains (authors' pers. obs.). Vessel mooring arrays are located within most Catalina rhodolith beds and consist of a surface float connected to a concrete mooring weight by 3 inch (~7.6 cm) linked chain. In the rhodolith beds, fan-shaped swaths of crushed, bleached dead rhodolith material lie around each chain, most conspicuously under the point of impact (POI), where the descending chain first touches the seafloor, before extending horizontally to the mooring block. To measure the impact of these mooring chains on the extent of live rhodolith habitat, we examined: (1) the relationship between mooring density and percent live rhodolith cover, (2) the experimental effect of mechanical disturbance on rhodolith structural complexity using experimental mooring chain removal, and (3) patterns of benthic communities relative to mooring presence.

The percent live rhodolith cover within the live portions of all beds was estimated using 0.25 m² gridded quadrats (16 intersections per quadrat, n = 20 quadrats per bed) randomly placed along mapping transects. Where moorings were present, the relationship between mooring density and live rhodolith cover was determined by counting mooring density within the perimeter of live bed area to determine moorings m⁻², which was regressed with mean percent live rhodolith cover by bed.

To estimate the mechanical disturbance impact of mooring chains on rhodolith structure, a manipulative experiment was conducted within the mooring field in 1 Catalina rhodolith bed at Cherry Cove in January 2009. Live, branching rhodoliths (5–25 mm in diameter) were randomly collected, air-dried, colored with fluorescent green paint, and separated into 15 replicate samples (each ~100 g). The initial structural complexity, estimated as the ratio of dry weight per unit volume (wt vol⁻¹), was determined using nodule weight relative to volume occupied in a graduated cylinder (Tompkins 2011). Samples were randomly assigned to 1 of 3 treatments (n = 5 replicates per treatment): (1) 'Chain Disturbed'. Material placed directly on sand beneath the mooring chain POI; (2) 'Live Rhodolith'. Material placed back into the rhodolith bed in areas of >75% live cover; (3) 'Chain Removal'. Material placed on sand at the original POI of chains but with shortened chains, thus experimentally removing direct chain

disturbance. The 'Chain Removal' treatment tested for influence of local factors independent of chain effects. Within Cherry Cove, all 10 mooring chains used in the experiment were within 3 m of live rhodoliths and shared similar depths (6–7 m). 'Live Rhodolith' treatments were distributed between the mooring chains. All treatments were left *in situ* for 5 d.

At the end of the experiment, all green-painted rhodolith material was carefully collected by hand (10 min collection time per replicate). Samples were air-dried, and the final wt vol⁻¹ ratios were measured. To test for treatment effects, differences (final wt vol⁻¹ – initial wt vol⁻¹) were calculated for each replicate and treatments were compared using a 1-way ANOVA ($n = 5$, $\alpha = 0.05$). Significant differences were examined with a post hoc Tukey's test.

To estimate the direct impact of mooring chains on benthic communities, we surveyed 2 dominant rhodolith substrate conditions reflecting different disturbance levels (conditions) at 2 Catalina rhodolith bed sites (Cherry Cove and Isthmus Harbor) in December 2011 at 6–7 m depth. The high disturbance or 'Chain Disturbed' condition was surveyed directly beneath 4 randomly chosen mooring chains (within 1 m of the POI) at each site. These were contrasted to the low disturbance condition of 'Live Rhodolith' in randomly chosen patches of live, intact rhodoliths between moorings. At each site, divers identified and counted macroscopic organisms (flora and fauna >1 cm) within replicate 1 m² quadrats randomly placed in each condition ($n = 4$ site⁻¹). Total taxa (macroalgae and macroinvertebrate) and invertebrate abundance (no. m⁻²) were analyzed using a 2-way mixed-model ANOVA with the fixed factor 'Condition' and the random factor 'Site'. Significant differences were identified with a post hoc Tukey's test.

Coralline growth rates

Annual and seasonal growth rates were estimated *in situ* for *L. australe* rhodoliths. Alizarin red stain (Fisher Scientific), a marker for calcium carbonate deposition, has been used to estimate growth of corals, geniculate coralline algae, and rhodoliths (Lamberts 1978, Andrade & Johansen 1980, Blake & Maggs 2003, Steller et al. 2007). Rhodoliths were collected from Big Fisherman's Cove in both July 2008 (fall) and January 2010 (spring). In each time period, 50 individuals were stained under ambient light conditions for 24 h in an aerated alizarin bath in the lab at

a concentration of 0.25 g l⁻¹ of seawater. Rhodoliths were then randomly placed into 1 of 3 plastic mesh corrals (20 × 20 cm) in Big Fisherman's Cove at 15 m depth (mid-depth of live cover). This site and depth were chosen to minimize boat traffic and mooring disturbance. Each set was collected after approximately 200 d during 2 seasons: Fall (July 2008 to January 2009) and Spring (January 2010 to August 2010).

Upon recovery, individuals were air-dried, and a minimum of 6 randomly chosen branch tips per rhodolith were removed from all individuals, mounted horizontally on glass microscope slides, and embedded in epoxy resin (Aluzine epoxy system, Fiberglass Hawaii). Tips were ground in half lengthwise along the growth axis to expose the alizarin stain using a polishing wheel (Buehler LTD Ecomet III grinder) with 1200-grit sandpaper. To differentiate between stain and pink photosynthetic pigments, slides were placed post-grinding in fresh water for ~2 h to bleach photosynthetic pigments (as per Blake & Maggs 2003). The sections were photographed under a microscope (Diagnostic Instruments model 2.3.1 mounted on a Leica MZ 125). The distance (mm) along the main growth axis, between stain and branch tip was measured using image analysis (Image Pro-plus) and used to estimate annual growth rates (mm yr⁻¹) per individual rhodolith by averaging tip growth. Mean seasonal and annual growth rates (mm) were calculated by averaging across individuals. Seasonal growth differences were assessed with a *t*-test.

Data analysis

All statistical analyses were performed using Systat 12. Normality of all data was examined prior to analysis and data were transformed if necessary. Unless otherwise noted, data are presented as means ± SD.

RESULTS

Distribution and rhodolith size

We surveyed approximately 50% of the Catalina coastline to 30 m depth, including all bays, coves, harbors, and coastal areas considered most likely to contain rhodoliths. The combination of aerial photographs, drop cameras, and diver surveys was successful at achieving the aim of the study, and 7 dis-

Table 1. Rhodolith bed location (coordinates in decimal degrees), aerial coverage of live and dead rhodolith material, percent live rhodolith cover within live bed area, depth range of live rhodoliths, and protection status of 7 Santa Catalina Island rhodolith beds. BFC: Big Fisherman's Cove; SMR: State Marine Reserve, SMCA: State Marine Conservation Area

| Rhodolith bed | Lat. (N), long. (W) | Area cover (m ²) | | % Live cover (mean ± SD) | Depth range of live material (m) | | Protection status of bed |
|---------------------|---------------------|------------------------------|-------|--------------------------|----------------------------------|------|--|
| | | Live | Dead | | Min | Max | |
| Avalon Harbor | 33.3477, 118.3246 | 9765 | 4093 | 51 ± 31 | 7.8 | 21 | No protection |
| BFC East | 33.4448, 118.4861 | 779 | 3059 | 30 ± 22 | 12.5 | 20.7 | In Blue Cavern SMR |
| BFC West | 33.4451, 118.4871 | 671 | 2268 | 27 ± 28 | 7.9 | 18.6 | In Blue Cavern SMR |
| Cherry Cove | 33.4515, 118.5022 | 2627 | 5543 | 40 ± 31 | 5.8 | 7.3 | No protection |
| Emerald Bay | 33.4681, 118.5281 | 6673 | 13718 | 43 ± 31 | 4.2 | 6.1 | In Arrow Point to Lion Head Point SMCA |
| Fourth of July Cove | 33.4478, 118.4993 | 1247 | 6076 | 21 ± 20 | 8.2 | 15.1 | No protection |
| Isthmus Harbor | 33.4441, 118.4982 | 1148 | 7939 | 50 ± 34 | 4.3 | 6.1 | No protection |

tinct carbonate or rhodolith beds were located around the island (Fig. 1). All beds were on the leeward (NE-facing) side. Most beds were distinct and named after the embayment within which they were found. Two beds located in Big Fisherman's Cove (BFC), separated by a large fan-shaped swath of non-biogenic sediment, were named BFC East and BFC West. Rhodolith material was not detected in Cat Harbor, the only shallow, relatively protected embayment on the SW-facing coast, where rhodoliths were expected, and was therefore extensively surveyed using manta tow, drop camera, and snorkeling. Multi-beam sonar mapping techniques were unable to delineate bed boundaries or conclusively determine textural differences between live rhodoliths and surrounding substrates. This was primarily due to the small rhodolith sizes and patchy nature of the beds. However, the combination of aerial photographs, drop cameras, and diver surveys was successful at locating both previously reported and newly discovered beds.

The mapped rhodolith material cumulatively covered approximately 0.066 km² of the seafloor surrounding Catalina. The location, areal extent of live and dead rhodolith material, live cover, depth range, and protection status of the beds varied by site (Table 1). Areal estimates of live rhodolith cover ranged from 671 (BFC West) to 9765 m² (Avalon Harbor), and dead rhodoliths covered areas ranging from 2268 to 13 718 m². The largest combined area of live and dead material was at Emerald Cove (20 391 m²). The Avalon Harbor bed had the highest percent cover of live material (51%). The depth distribution of live rhodoliths in the beds ranged from 4.2 to 20.7 m and varied by bed. Three of the 7 beds fall within areas designated as California marine protected areas.

Long axis measurements across live rhodoliths from all beds ranged from 3 to 25 mm, with a mean size of 10.6 ± 0.8 mm. Mean size varied significantly across beds ($F_{6,868} = 3.10$, $p = 0.038$). Individual rhodoliths from BFC West, Cherry Cove, Fourth of July Cove, and Isthmus Harbor were larger (11.9 ± 1.1, 11.5 ± 1.0, 11.5 ± 1.2, 11.5 ± 1.8 mm, respectively) than those from BFC East and Emerald Bay (8.7 ± 1.1, 8.5 ± 1.6 mm, respectively). Avalon Harbor rhodoliths were of intermediate size (10.2 ± 1.7 mm). Periodically, while surveying beds, large, dead individuals, including fossil rhodoliths, were discovered and ranged in size up to 40 mm in diameter. More details on size distribution and morphology information is available in Tompkins (2011).

Mooring chain disturbance

The Catalina beds are highly patchy and the percent cover of live rhodolith material within bed areas was variable, ranging from 21 to 51%, with significant differences across beds ($F_{6,133} = 3.76$, $p = 0.001$, Table 1). The beds in Avalon and Isthmus Harbors supported the greatest mean percent live cover (51 ± 31 and 50 ± 34%, respectively) and the bed at Fourth of July Cove had the lowest (21 ± 20%). The percent cover of live rhodoliths within Catalina rhodolith beds, while not significantly different, was negatively related to mooring density ($r^2 = 0.57$, $F_{1,4} = 5.31$, $p = 0.083$, Fig. 2). Fourth of July Cove had the greatest mooring chain density and the lowest average percent cover of live rhodoliths, while Isthmus Harbor showed the inverse.

Results from the mechanical disturbance experiment revealed that rhodoliths under the mooring chains lost the greatest volume of material relative to

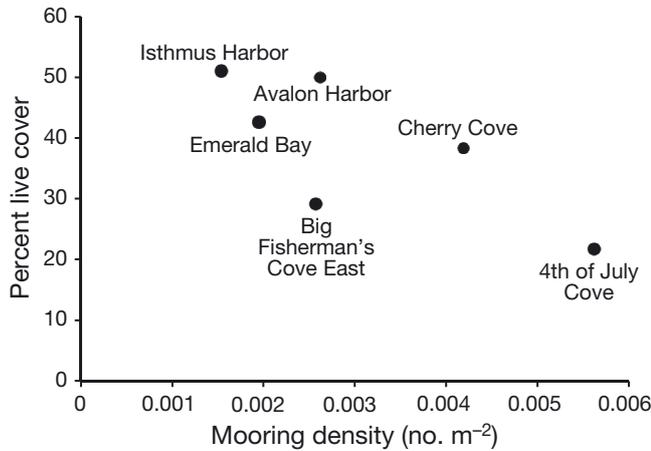


Fig. 2. Percent live rhodolith cover relative to mooring density within Santa Catalina Island rhodolith beds ($r^2 = 0.57$, $p = 0.083$)

other treatments (Fig. 3). This proxy for reduction of structural complexity, the mean change between the initial vs. final wt vol^{-1} , was greater for the 'Chain Disturbed' treatment than for the 'Live Rhodolith' or 'Chain Removal' treatments ($F_{2,12} = 7.48$, $p = 0.009$). The latter treatments did not differ from each other with the post hoc test.

Benthic surveys revealed a significant negative impact of mooring chains on the number of algal and invertebrate taxa. At both the Cherry Cove and Isthmus Harbor sites, significantly more taxa were enumerated in the 'Live Rhodolith' relative to 'Chain Disturbed' condition ($F_{1,6}$, $p = 0.046$, Fig. 4a). There was no significant effect of site on the number of taxa ($p = 0.891$) or any interaction between site and condition ($p = 0.682$). Abundant invertebrate taxa in 'Live Rhodolith' included the Echinoidea *Lytechinus pictus*, the Gastropoda *Conus californicus* and *Megastraea undosa*, the Anthozoa *Pachycerianthus fimbriatus*, and a common spionid tube worm (Family Spionidae). The dominant fleshy macroalgal taxa in 'Live Rhodolith' included *Dictyota binghamiae* and *Zonaria farlowii*.

Macroinvertebrate abundance was greater in the 'Live Rhodolith' condition than that measured in 'Chain Disturbed' in both beds (Fig. 4b). The effect varied with site and a significant interaction between condition and site was detected ($F_{1,6}$, $p = 0.020$). The post hoc test revealed a difference in invertebrate abundance at Cherry Cove ($p < 0.001$), where the mean abundance in 'Live Rhodolith' was almost tripled relative to 'Chain Disturbed' (Fig. 4). This condition-related difference was not detected at Isthmus Harbor ($p = 0.460$), possibly due to high abundances of spionid tube worms in the 'Chain Disturbed' condition.

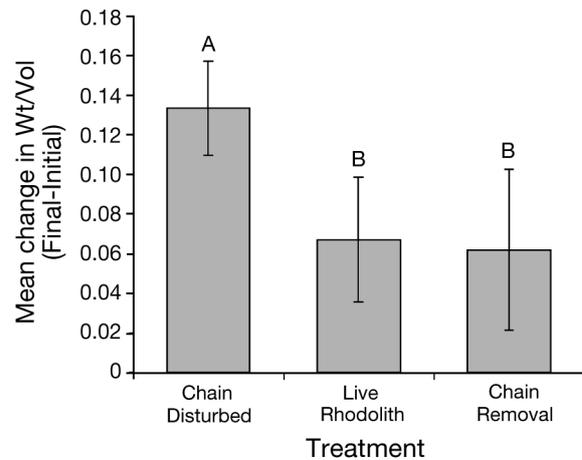


Fig. 3. Experimental results of mooring chain disturbance on rhodolith structural complexity (change in mean \pm SD weight vol^{-1} , $n = 5$ replicates per treatment) in the Cherry Cove rhodolith bed, Santa Catalina Island. Letters represent significant post hoc differences using a Tukey's test ($\alpha = 0.05$)

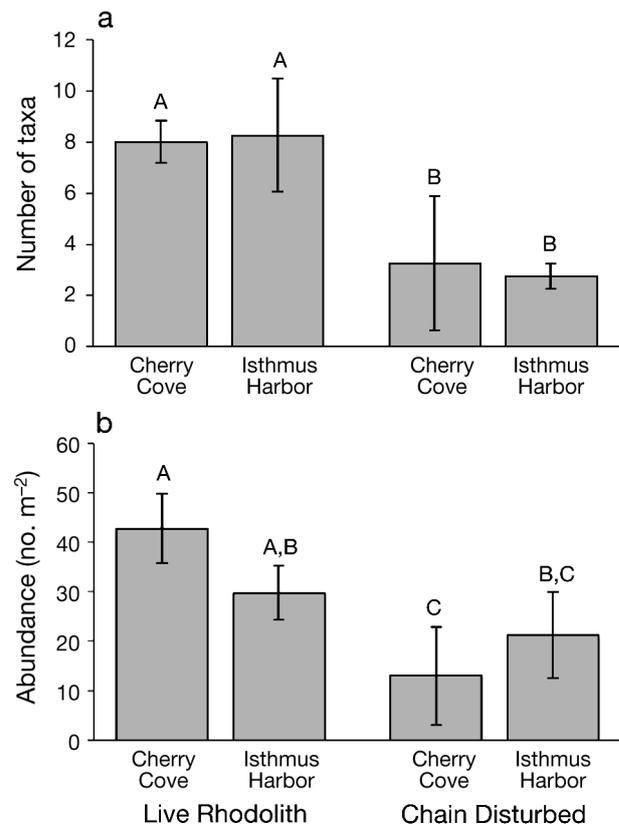


Fig. 4. Mean (a) number of taxa and (b) abundance of macroinvertebrates (no. m^{-2}) relative to disturbance level in live rhodolith and mooring chain disturbed habitats within Cherry Cove and Isthmus Harbor, Santa Catalina Island, rhodolith beds (mean \pm SD, $n = 4$). Letters represent significant post hoc differences using a Tukey's test ($\alpha = 0.05$)

Rhodolith growth

The Alizarin Red staining rate of rhodoliths in this study was very low. Of roughly 1000 total branch tips examined and potentially stained (approximately 10 branch tips ind.⁻¹, 100 total individuals, 50 per season) only 68 total branches from 11 rhodoliths showed reliably measurable stains (6.8% return, ranging from 1 to 13 branches per rhodolith). Growth rates were generated for individual rhodoliths by averaging across all stained branches within an individual. An annual growth rate of 1.25 ± 0.62 mm yr⁻¹ was then estimated by averaging across those 11 individual rhodolith means. Several rhodoliths only produced 1 or 2 stained branches. Due to between-branch growth variability within any individual thallus, seasonal growth rates were generated using the 4 rhodoliths per season that revealed stain on 3 or more branches. Seasonal growth rates (mm yr⁻¹) varied significantly ($t_{1,3} = 3.98$, $p = 0.007$); the average rate in Fall 2008 (1.56 ± 0.42 ; $n = 4$) was almost double that of Spring 2010 (0.89 ± 0.21 ; $n = 4$).

DISCUSSION

Carbonate-based biogenic habitats are susceptible to increasing human disturbance (Hoegh-Guldberg & Bruno 2010), with slow predicted recovery. This study provides the first quantitative characterization of rhodolith bed ecosystems in coastal California, USA. While Parnell et al. (2006) provided a description of Catalina rhodoliths, our study is the first comprehensive investigation of the topic, describing location and disturbance details for Catalina rhodolith beds to provide an inventory of these habitats for conservation purposes and as an aid for future research. The discovery of carbonate rhodolith habitat along the populated California coast suggests that rhodolith beds worldwide are possibly more abundant than previously thought.

Catalina rhodolith beds are found in similar bathymetric settings to those described globally: shallow, gently sloping, protected embayments (Bosence 1980, Scoffin et al. 1985, Peña & Bárbara 2009, Rosas-Alquicira et al. 2009, Gagnon et al. 2012). The 7 Catalina beds are small in areal extent (collectively 0.66 km²) relative to the many beds reported to extend from 10s to 1000s km² (Bosence 1983, Littler et al. 1991, Foster 2001, Rosas-Alquicira et al. 2009, Amado-Filho et al. 2012). The small areal extent and low live cover at Catalina may result from numerous

factors including the restricted extent of embayments in conjunction with high anchoring and mooring disturbance.

The size range of the *L. australe* rhodoliths from Catalina (3–25 mm) was much smaller than those reported for other eastern Pacific rhodoliths. This may be a result of species differences between locations: Bahia Concepcion, Mexico, 5–130 mm (McConnico et al. 2014, *L. muelleri*), and 5–100 mm (Steller & Foster 1995, *Lithophyllum margaritae*); Herring Bay, Alaska, 20–70 mm (Konar et al. 2006, *Phymatolithon calcareum*). In addition, the proportion of dead material measured in Catalina rhodolith beds was highly variable and relatively large (up to 70% of total area) compared to other beds worldwide (e.g. Galician beds, only 1.4% dead material, Peña & Bárbara 2009; Gulf of California, commonly 100% live cover in undisturbed beds, Steller et al. 2003). Both the small mean thallus size (10.6 ± 0.8 mm) and low live rhodolith cover likely contributed to the failure of the multibeam survey effort to detect rhodoliths relative to background large-grain carbonate sand, although side-scan methods have proven effective on areas with larger size and higher cover of rhodoliths (e.g. Kendrick et al. 2005, Hetzinger et al. 2006).

The limited and variable extent of live cover and relatively small size of rhodoliths at Catalina may be influenced by the high frequency of anchoring and mooring disturbances. These activities can locally eliminate marine vegetation (Walker et al. 1989) and disturb invertebrate communities (Herbert et al. 2009). The manipulative mechanical disturbance experiment in Cherry Cove measured the reduction of rhodolith 3-dimensional structure due to mooring chains. While greater spatial replication would aid in separating the effects of mooring disturbance from natural patterns of variability known to exist in areas with rhodoliths (Bosence 1980), the physical deterioration of rhodoliths was rapid and dramatic. These findings support prior work measuring the long-term impact of scallop dredging on reducing habitat heterogeneity in maerl beds (i.e. rhodoliths, Hall-Spencer & Moore 2000, Kamenos et al. 2003). The extensive banks of dead rhodolith sediment at Catalina combined with the large size of a few dead rhodoliths found at the bed surface and exhumed from the sediments (~30–50 mm diameter, larger than any live material found; P. A. Tompkins pers. obs.) suggest that rhodoliths have long contributed to carbonate production around the island. We suggest that the historic high level of disturbance from mooring and anchoring activity in the sheltered bays of Catalina

has likely reduced both structural integrity and areal extent of these rhodolith beds.

Many marine communities are supported by biogenic reefs, and vegetated marine habitats are highly productive systems compared to less structurally complex, or non-vegetated counterparts (Edgar 1990, Ferrell & Bell 1991, Bustamante et al. 1995, Graham 2004, Hosack et al. 2006, Thrush et al. 2006). Biodiversity associated with rhodolith beds has been shown to be a function of their small-scale habitat complexity (Bosence 1979, Steller et al. 2003, Gagnon et al. 2012, Teichert 2014), with the matrix of interstitial spaces providing predation refuge for small invertebrates and important settlement and nursery substrates for epiphytes and epifauna (Bárbara et al. 2004, Kamenos et al. 2004b, Leliaert et al. 2009, Steller & Cáceres-Martínez 2009, Felder et al. 2014, Teichert 2014). Thus, similar to dredging, mooring-related destruction of rhodoliths likely has community-level consequences for benthic biodiversity (Kamenos et al. 2003). This is supported by our finding of reduced numbers of motile invertebrates in disturbed areas relative to live rhodoliths. In other marine benthic habitats, organic material and oxygen supply are positively influenced by invertebrate bioturbators (Rhoads 1974, Aller 1983, Hansen 1998), suggesting that these fluxes would also decline with live rhodolith loss. In addition, loss of rhodolith extent and integrity could have bottom-up implications for fish or other mobile marine species that capitalize on rhodolith secondary productivity, with potential implications across larger-scale food webs (Jackson et al. 2001, Dobson et al. 2006).

Crustose corallines are considered slow-growing compared to many other species of marine macroalgae (McCoy & Kamenos 2015). Most studies report rhodolith growth rates of $<1 \text{ mm yr}^{-1}$ (Bosence 1980, De Grave et al. 2000, Frantz et al. 2000, Rivera et al. 2004, Steller et al. 2007, Kamenos et al. 2008). Reported rates range from 0.11 to 2.56 mm yr^{-1} for *L. corallioides* (Adey & McKibbin 1970) and *Lithophyllum margaritae* (Steller et al. 2007), respectively. The average growth rate of 1.25 mm yr^{-1} measured for *L. australe* in this study fell within the range of previously reported values. The seasonally higher growth rates in fall relative to spring measured in this study are consistent with other rhodolith-forming species from the eastern Pacific (Frantz et al. 2000, Steller et al. 2007). Collectively, the slow annual growth rates suggest that disturbed rhodolith beds would take decades to recover from major disturbance, underlining the need for further study and long-term protection.

While this study focused on mooring-related disturbance, we predict that the cumulative impacts of multiple stressors may have detrimental effects on rhodolith beds, as demonstrated in other marine habitats (Crain et al. 2008). The direct destruction of rhodolith habitat observed during this study could be compounded with long-term environmental changes, such as increases in ocean acidification (Kuffner et al. 2008, McCoy & Kamenos 2015), El Niño/Southern Oscillation (ENSO) intensity, and coastal development. A reduction in structural integrity due to decalcification would make rhodoliths more susceptible to breakdown from physical disturbance, and more sensitive to locally intensifying levels of wave energy associated with ENSO events (Barnard et al. 2015). Sediments can smother and quickly kill rhodoliths (Wilson et al. 2004), and strong ENSO events result in increased local sedimentation from rainfall runoff (Barnard et al. 2015, Hendy et al. 2015), a process exacerbated by coastal development. Thus further studies of rhodolith disturbance should ideally use multi-factor approaches and consider examining the combined effects of changing pH, wave energy, sedimentation, nutrients, and temperature.

Destruction and limited recovery of marine biogenic reefs are an ongoing process and a major threat to marine biodiversity (Beatley 1991, Gray 1997, Roberts & Hirshfield 2004, Airolidi et al. 2008). The degradation or loss of autogenic ecosystem engineers like rhodoliths (Barbera et al. 2003) can lead to local-scale trophic simplification, a process similar to the conversion of hard and soft coral reefs to rubble (Koslow et al. 2001, Fox et al. 2003) or kelp forests to urchin barrens (Graham 2004). However, unlike the problems faced by other biogenic ecosystem engineers, reducing disturbance and enhancing restoration of rhodolith habitats at Catalina may simply require re-engineering of the mooring system to minimize benthic impacts. Without such action, the degradation of these unique and novel habitats is likely to continue. We propose a standardized monitoring scheme based on the mapping and characterization methods in this paper to quantify future changes. Although globally important for primary and secondary marine productivity (Martin et al. 2007), rhodolith beds have not been recognized as a priority habitat in local or national-level marine conservation planning. Given their ecological sensitivity, currently degraded state, and current limited recovery potential, these unique carbonate habitats should be considered a conservation priority.

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