Population biology of a long-lived rhodolith: the consequences of becoming old and large

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ABSTRACT: Life history characteristics of long-lived organisms make them particularly vulnerable to disturbances. Demographic studies of such populations are essential for evaluating susceptibility to disturbance and recovery potential, especially for ecosystem engineers supporting many dependent species. This type of demographic information, including population structure and mortality risk, is limited for long-lived rhodoliths (unattached non-geniculate coralline algae), which harbor a high biodiversity of cryptofaunal organisms. Population structure, *in situ* seasonal growth rates, age, and mortality estimates were determined in 2003–2004 for the subtidal rhodolith *Lithothamnion muelleri* in the Gulf of California, México. Individuals ranged in size from 0.5 to 16 cm diameter and the population was dominated by those <4 cm. Average annual growth (mean ± SE) was slow (0.71 ± 0.04 mm yr^{-1}), but faster in summer (March–October). Age projections suggest that large individuals could live for 100–300 yr. In 2003, numerous rhodoliths ≥8 cm diameter died after being cast on shore by Hurricane Marty. Slow growth and increased mortality of larger individuals suggests that recovery from disturbances is slow and that smaller (younger) individuals are more resilient. Larger, older rhodoliths support a more diverse cryptofauna and thus not only are they more vulnerable to disturbances, but their mortality contributes disproportionately to the loss of community structure.

KEY WORDS: *Lithothamnion muelleri* · Hurricane disturbance · Population persistence · Age and growth · Mortality · Gulf of California

INTRODUCTION

Life history characteristics of organisms, along with disturbance type, size, severity, and frequency, all influence population recovery following a disturbance (Connell & Slatyer 1977, Sousa 1979, 1984). Long-lived hard and soft corals (Hughes & Tanner 2000, Andrews et al. 2002), fish (Stevens et al. 2000, Reynolds et al. 2005), coralline algae (Foster 2001, Wilson et al. 2004, Nelson 2009), and seagrasses (Arnaud-Haond et al. 2012) may be particularly slow to recover from, and are vulnerable to, population declines or extinction following disturbances due to slow growth rates, delayed age of first reproduction, low adult survival and/or recruitment impacts. In terrestrial environments, long-lived organisms may be biologically slow to respond to environmental degradation, and even small amounts of habitat loss can lead to rapid population declines (Doak 1995). Reduction of larger and often older individuals within a population represents a significant ecological loss, as they are often more fecund (Birkeland & Dayton 2005) or support a greater number of associated species (Buhl-Mortensen & Mortensen 2005). Demographic studies of long-lived

organisms that include estimates of growth, age, population structure, and mortality are therefore essential to understanding population persistence. Such studies are of particular importance when these long-lived individuals serve as ecosystem engineers (Jones et al. 1994) which produce habitat that support many other species such as corals (Enochs 2012) and rhodoliths (Foster et al. 2007).

Coral reef population declines due to anthropogenic and natural disturbances are well documented (Hughes 1994, Pandolfi et al. 2003, De'ath et al. 2012) and predicted to continue in the absence of management efforts (Kennedy et al. 2013). The slow growth rates and longevity of corals make them vulnerable to disturbance, and these life history characteristics are shared by rhodoliths (unattached non-geniculate coralline algae). Like corals, rhodoliths form a biologically diverse and ecologically important marine habitat. These long-lived individuals form high-density beds, or aggregations, throughout the world's oceans (Foster 2001). They produce carbonate (Martin et al. 2006, Amado-Filho et al. 2012, Halfar et al. 2012), and provide habitat for many marine plants and animals (Bosence 1979, Grall & Glémarec 1997, James 2000, Steller et al. 2003, Hinojosa-Arango & Riosmena-Rodríguez 2004, Foster et al. 2007, Riera et al. 2012). They are economically valuable (and vulnerable to destruction) when harvested (Blunden et al. 1975) or when beds are fished for associated vertebrates and invertebrates (Hall-Spencer & Moore 2000, Kamenos et al. 2004, Steller & Cáceres-Martínez 2009).

A number of studies have determined rhodolith growth rates, but few have examined how growth rates combined with other population parameters affect rhodolith population dynamics. Growth rates range from <1.0 mm yr^{-1} (reviewed in Foster 2001) to >5.0 mm yr^{-1} (Steller et al. 2007) depending on species and estimation technique. Direct field measurements (Adey & McKibbin 1970), changes in calcium carbonate weight (Potin et al. 1990), ^{14}C dating (Littler et al. 1991, Frantz et al. 2000, Goldberg 2006), Mg:Ca ratios (Halfar et al. 2000, Kamenos et al. 2008), Alizarin Red staining (Blake & Maggs 2003, Rivera et al. 2004, Steller et al. 2007, Amado-Filho et al. 2012), or a combination of these techniques (Darrenougue et al. 2013) have all been used to determine growth rates and/or age. Growth is typically more rapid in summer than in winter (Adey & McKibbin 1970, Potin et al. 1990, Steller et al. 2007), with one report of faster growth in winter (Rivera et al. 2004). Although growth estimates are variable, all have concluded that rhodoliths are slow-growing and some may live for

>100 yr (Frantz et al. 2000, Rivera et al. 2004). Growth rates, therefore, indicate that the recovery of populations after disturbance will be slow, but do not show how this might affect size distributions and associated species, except in the case of massive disturbances.

Our objective was to combine growth rate, size frequency, and mortality data for the rhodolith *Lithothamnion muelleri* at a site in the Gulf of California, México, to better understand bed persistence and vulnerability to a disturbance. We determined growth rates (seasonal, annual, and size-based) and estimated rhodolith age during 2003 and 2004 to test if there was a relationship between growth rate and rhodolith size, and if growth rates varied seasonally. Size distributions were determined before and after a disturbance from a hurricane, and used to assess size-dependent mortality risk. We hypothesized that mortality would not be size-dependent and that all sizes would be equally affected by the storm.

MATERIALS AND METHODS

Study site

The study site was accessed using a small inflatable boat, and subtidal fieldwork was conducted with the aid of SCUBA during March and October 2003 and 2004 in Baja California Sur, México. The study site, Cabo Los Machos (near the mouth of Bahía Concepción; 26.84° N, 111.89° W), is a mixed rocky and sandy bottom at a depth of 2–8 m, dominated by a perennial bed of the rhodolith *Lithothamnion muelleri* in sandy areas, with abundant growth of the fucoid *Sargassum horridum* on rocks in winter and spring. The study site is described in detail in Foster et al. (2007) along with a quantitative assessment of the site's diversity and community composition. We initiated a growth experiment at 2 sites in the middle of the rhodolith bed (~5 m depth) in 2003. Temperature loggers placed at each site from March 2003 to May 2004 indicate temperature ranges from ~16 to 32°C, with these extremes occurring in January and August, respectively. These site-specific temperature data also show that tidal flushing at the mouth of Bahía Concepción reduces water temperature by 5–6°C during May–July 2003 (Fig. 1).

Growth

In October 2003, ~72 rhodoliths were collected, representing 3 size classes (small: 4–6 cm, medium:
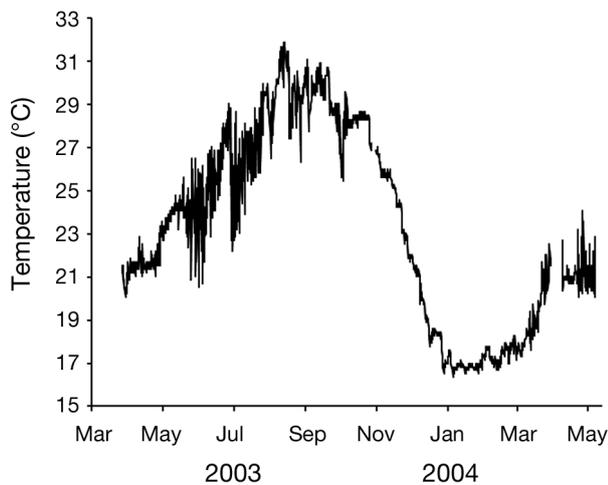
Fig. 1. Bottom temperature (~5 m) at Cabo Los Machos, March 2003 to May 2004. Data gaps during October 2003 and March 2004 occurred when logger was temporarily removed to download data

6–8 cm, and large: >8 cm) from ~5 m depth. Each was tagged with thin stainless steel wire and a small piece of plastic surveyor's tape. All were soaked for 24 h in an aerated container of seawater and the calcium carbonate-binding vital stain Alizarin Red (0.25 g l^{-1} seawater). Alizarin Red binds to the outer medullary and epithelial cells of the rhodoliths, producing a band that serves as a marker to track further growth *in situ* (see Steller et al. 2007 for method). We marked the 2 sites with metal stakes and returned 36 rhodoliths (12 from each size class: small, medium, large) to each area.

The first set of rhodoliths (n = 31) was recovered (approximately half from each site) during March 2004, representing 5 mo of winter growth. The second set (n = 33) was recovered from the sites after 12 mo in October 2004 and represents annual growth. Recovered samples were air-dried, and 10 branch tips were haphazardly removed from each rhodolith and attached to a glass slide using Cytoseal 60 mounting medium. Branch tips were ground down using a grinding wheel and wet/dry sandpaper to expose the Alizarin Red band. The distance from the red band to the apical tip of each branch, indicating radial growth of an individual tip, was measured using a compound microscope. Not all branches absorbed Alizarin stain. The average growth rate per rhodolith (mm yr^{-1}) was calculated from a minimum of 4 and a maximum of 10 branch tips per individual, depending on how many branches revealed stain.

Differences in seasonal growth were assessed by converting average radial growth rates for winter

(October 2003 to March 2004; n = 31 recovered) and the entire year (October 2003 to October 2004; n = 33 recovered) to millimeters of growth per month. Given rhodolith staining and collection times (none were left in the field for the period March–October only), it was not possible to directly determine summer growth rates; therefore, they were approximated using annual and winter growth rate data. Because of similarities among rhodoliths of the same size within and between sites, we treated each rhodolith as an independent replicate and calculated average annual growth rates based on radial extension of branch tips for rhodoliths in the field for the entire year. Since rhodoliths are free-living and growth occurs in all directions, these average radial growth estimates were doubled to give the average diametric growth of the entire rhodolith. Significant differences in monthly growth rates between winter and the entire year were assessed with a *t*-test. Regression analysis of annual diametric growth rate versus size (average diameter based on *x*, *y*, *z* measurements) for each rhodolith stained and left in the field for an entire year was used to determine if growth varied with size. In both cases, data met the assumptions of normality and homogeneity of variances.

Age estimates

Annual diametric growth rate estimates were used to determine age for each of the 33 rhodoliths grown in the field for one year. Rhodolith age was calculated by dividing rhodolith size by total diametric annual growth. Ages were not estimated for the 31 rhodoliths out-planted for 5 mo over winter because growth varied seasonally (see 'Results'). Age projections for all sizes (0.5–16 cm diameter [diam]) in the Cabo Los Machos population were calculated in 4 ways: by dividing rhodolith size (in 2 cm intervals) by average, minimum, maximum, and incremental (size-dependent) growth rates obtained from these 33 rhodoliths. For incremental growth rates, ages were determined by first calculating the average growth rates measured for individuals that were 4–6 cm, 6–8 cm, and >8 cm diam, and then dividing rhodolith size by its respective growth rate while in that size class. This calculation allowed for age projections that took into consideration the slight increase in growth rate with size. All age projections were calculated assuming growth rates for smallest (<4 cm) and largest (>11 cm) individuals in the unmeasured population would be equal to the smallest and largest rhodoliths measured in our study.

Population size structure

Rhodolith population size structure was previously determined *in situ* (using SCUBA) at 8 sites within Cabo Los Machos in March 2003 (data reported in Foster et al. 2007). These data were obtained by counting and measuring the greatest diameter (most rhodoliths were nearly spherical) of all individuals >0.5 cm diam in eight 3.14 m^2 quadrats randomly placed within the bed between 2–8 m depth. Time constraints did not allow for adequate sampling of smaller size classes (<2.5 cm diam), which can be more easily overlooked in an underwater survey. To better determine the abundance of individuals in these smaller size classes, we analyzed additional samples from March 2003 obtained from cores. One core (12.7 cm diam, 8 cm height) was taken from inside of each of the eight 3.14 m^2 quadrats. Core samples were sieved (on shore) through a 0.5 cm mesh bag, the largest diameter of each pigmented (live) rhodolith was measured, and abundance scaled up to the size of the 3.14 m^2 quadrat. Rhodoliths at the site are sorted such that individuals >2.5 cm were typically found in surface sediment layers (top 8 cm) or at the sediment–water interface and are easily observed during *in situ* quadrat counts. Double counting of small or large individuals was unlikely given the sampling design. These additional core data were combined with quadrat data from Foster et al. (2007) to provide a more detailed assessment of the population structure and allow for a comparison of methodology.

Mortality

Mortality from a major disturbance was assessed by sampling beach-cast rhodoliths in October 2003 that were deposited on shore following Hurricane Marty (18–24 September 2003; Franklin 2004). The hurricane generated a tropical storm that moved over the study site, and rhodoliths, which do not live intertidally at this site, were abundant in high intertidal and splash zones following this disturbance. Many were still pigmented, while others appeared stressed (began to turn green or had white patches) or were dead when sampled ~1 mo after the storm. In the high intertidal and splash zone, six 20 m long transects were placed parallel to shore and the diameter of each beach-cast rhodolith closest to the meter marks was measured (n = 20 per transect). Beached rhodoliths were less abundant in the mid to low intertidal zone. In this area, the diameter of each rhodolith found within a 100 × 2 m^2 diagonal swath was meas-

ured. Data from all zones were combined and used to analyze which size rhodoliths were most affected by the hurricane.

RESULTS

Growth

Average monthly radial growth rates over the winter (0.04 ± 0.003 mm mo^{-1}) were significantly lower than those calculated for the entire year (0.06 ± 0.003 mm mo^{-1}; *t*-test: t_{62} = 4.29, p < 0.0001). Monthly growth rates were greater over the entire year than during winter months (October–March), thus it can be inferred that *Lithothamnion muelleri* grew almost twice as fast (~0.07 mm mo^{-1}) during summer months (March–October). Rhodoliths used for growth rate estimates ranged in size from ~4–10 cm and individual growth rates ranged from 0.27–1.13 mm yr^{-1}, with an average annual growth rate (based on radial extension) of 0.71 ± 0.04 mm yr^{-1}. Regression analysis based on diametric extension suggests that smaller individuals may grow slower than larger ones, but this was largely driven by 3 slow-growing individuals (Fig. 2a), and differences were not statistically significant (linear regression: r^2 = 0.11, $F_{1,31}$ = 3.83, p = 0.06).

Age estimates

Rhodolith ages based on measured growth rates for the 33 rhodoliths in the field for 1 yr were estimated to range from ~29–119 yr old, with the majority between 40–80 yr old (Fig. 2b). Age projections incorporating variation in growth rates according to size (incremental growth rates) gave age estimates for individuals 4–14 cm slightly greater than those calculated using average growth rates. Despite this slight curvilinear relationship between size and age, the maximum predicted ages for the largest rhodoliths seen at Cabo Los Machos were similar for the 2 sets of age projections (113 vs. 117 yr old using average and incremental growth rates, respectively). Age projections using minimum and maximum growth rates put the largest individuals at ~300 and 70 yr old, respectively (Fig. 3).

Population size structure

Combining the data from Foster et al. (2007) with our core data allowed size-frequency determination
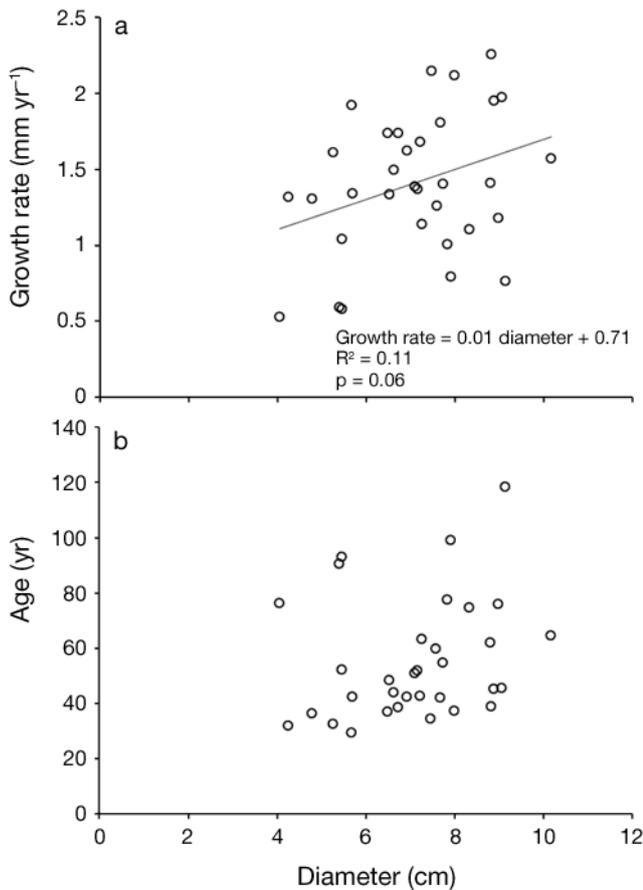
Fig. 2. *Lithothamnion muelleri* diameter vs. (a) annual growth rates (based on diametric extension); (b) age for stained rhodoliths growing in the field between October 2003 and October 2004 (n = 33 for both)

In panel (a):

Growth rate = 0.01 diameter + 0.71
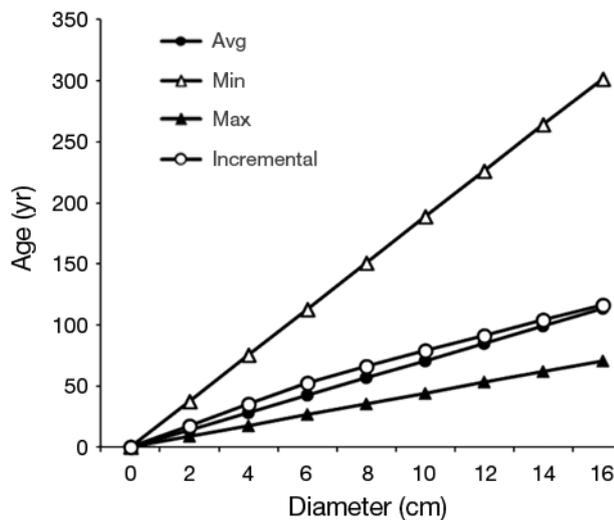$R^2 = 0.11$
$p = 0.06$

Fig. 3. Age projections for *Lithothamnion muelleri* 0–16 cm in diameter based on average (Avg), minimum (Min), maximum (Max), and incremental growth rates

from a total of 14 489 individuals. Small rhodoliths (<2 cm diam) represented ~80% of the entire population, while the largest (>8 cm diam) represented <1% of the sampled population (Fig. 4).

Mortality

Rhodoliths from 1.2–13.7 cm diam were transported on shore as a result of Hurricane Marty (Fig. 5a). Larger rhodoliths were disproportionately affected by the storm. Of the 149 individuals measured 1 mo after the hurricane, 62% were >8 cm diam, while medium (6–8 cm diam) and small (<6 cm diam) rhodoliths accounted for 10% and 28%, respectively (Fig. 5b).

DISCUSSION

Our data show that *Lithothamnion muelleri* is slow-growing, and that large (older) individuals are rare and particularly vulnerable to large disturbances. Average annual growth rates of 0.71 ± 0.04 mm yr^{-1} fall within the low end of the range reported by others studying growth in rhodoliths (Foster 2001, Blake & Maggs 2003, Steller et al. 2007). The slow growth rate may be related to the heavily calcified thalli of *L. muelleri*. Estimates in our study, and likely others, are underestimates of growth due to abrasion of surface layers. Three other studies of *L. muelleri* populations in the southern Gulf of California all indicated similar growth rates: 0.60 mm yr^{-1} (Frantz et al. 2000, Rivera et al. 2004) and 0.25–0.45 mm yr^{-1} (Halfar et
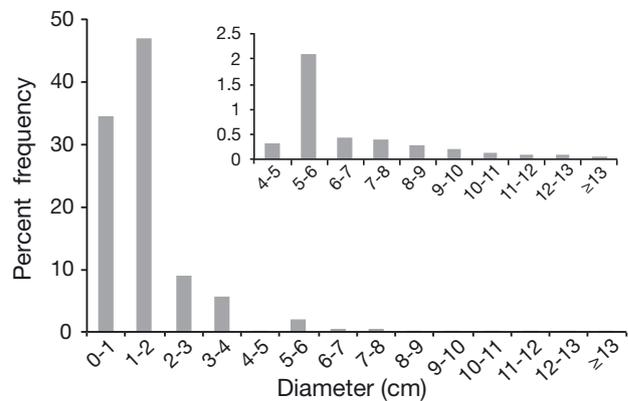

Fig. 4. Percent frequency of *Lithothamnion muelleri* (in cores and 3.14 m^2 quadrats) in March 2003 (n = 14 489 rhodoliths). Inset graph shows percent frequency of rhodoliths between 4–13 cm diameter re-plotted on a more appropriate scale
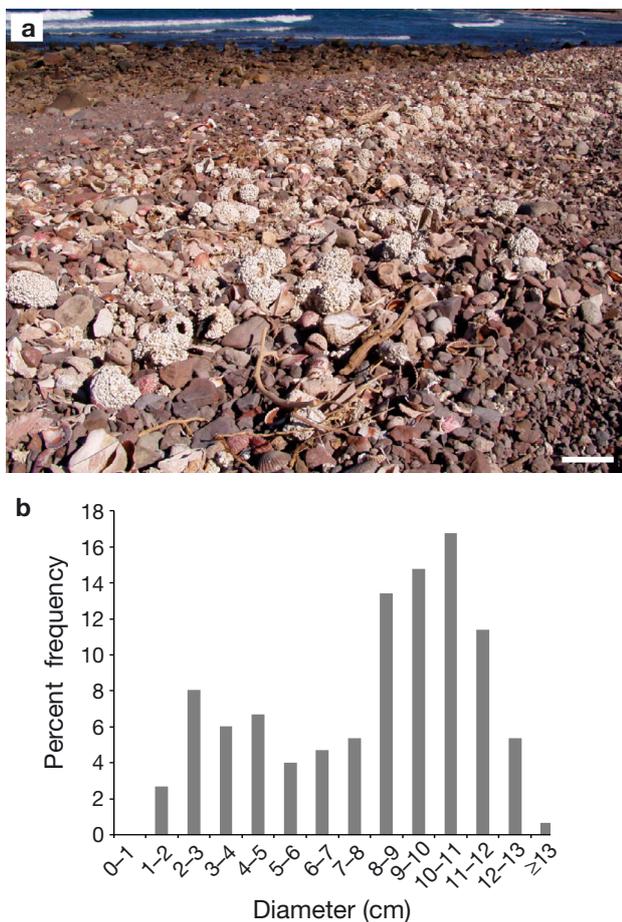
Fig. 5. *Lithothamnion muelleri*. (a) Dead, shore-cast rhodoliths (white bumpy spheres) in October 2003 after a tropical storm produced by Hurricane Marty (September 2003) passed over the study site (scale bar = ~10 cm); (b) size-frequency distribution of shore-cast rhodoliths encountered along transects (n = 149)

al. 2000). These independent assessments of growth for the same species were obtained using ^{14}C dating, Alizarin Red, and Mg:Ca ratios correlated to growth bands, respectively. Together, all 4 studies of *L. muelleri* from the Gulf of California provide some of the most detailed growth rate data for any rhodolith species studied to date.

Differences in rhodolith monthly growth rates calculated over the winter and the entire year suggest that growth is affected by seasonal environmental variables, with the greatest growth occurring over summer months. Rhodoliths in the field for the entire year (October 2003 to October 2004) grew nearly twice as fast over summer compared to those in the field between October and March. The difference may be due to increased light in summer, including increases related to the annual nature of the *Sargas-*

sum horridum canopy at the site that develops in winter–spring and degenerates in early summer (Foster et al. 2007). Summer growth may also be stimulated by tidal flow that brings cold (and likely higher-nutrient) water to the site, as temperature data (Fig. 1) showed a strong tidal signature at the mouth of Bahía Concepción. Cryptofauna living inside rhodoliths also produce an additional, localized nutrient supply which may aid in growth (L. A. McConnico unpubl. data). Interestingly, Rivera et al. (2004) found *L. muelleri* growth rates at a site near La Paz, México were greater in winter than summer. They attributed the difference to higher than average water temperatures during their study, which took place during an El Niño year. Elevated summer growth rates were, however, reported for the rhodoliths *Lithothamnion corallioides* (Adey & McKibbin 1970, Potin et al. 1990), *Lithophyllum margaritae* (Steller et al. 2007), *Lithothamnion glaciale* (Kamenos & Law 2010, Burdett et al. 2011), and *Sporolithon durum* (Darrenougue et al. 2013), and were attributed to nutrient availability, increased light, water temperature, reduced wind and sedimentation, and/or reduced abrasion which enhanced growth relative to winter months. Although they did not measure growth rates, Martin et al. (2006) also found calcification rates and primary production were greater for *L. corallioides* during summer when irradiance was higher.

The slight but statistically insignificant variation in growth rate versus size that suggests growth rate may increase with size has not been previously reported for this species. Rivera et al. (2004) determined that growth rates for *L. muelleri* were not size-dependent and suggested this was because only the outer edge of the rhodolith is alive and growing regardless of diameter. Steller (2003) did find growth rate increased with size in *L. margaritae*. It is possible that smaller rhodoliths are more readily or completely buried so their growth is reduced. Most studies on rhodolith growth have not considered the relationship between size and growth rates, and more studies are required to better understand this aspect of rhodolith demography.

Age estimates based on field measurements and all age projections, combined with size-frequency data, indicate the Cabo Los Machos *L. muelleri* population is dominated by smaller rhodoliths that are <40 yr old. While larger, older individuals can range from 70 to 100+ yr old (and may be as old as 300 yr using minimum growth rates), they represent a small portion of the entire population. This 200+ yr difference in maximum age estimates is a reflection of the large

variation in an individual rhodolith's growth. Repeated site visits during 2001–2014 indicate that rhodoliths are frequently buried and exhumed seasonally as a result of strong winter winds out of the north (Merrifield et al. 1987) and less frequent summer tropical storms from the south (NOAA 2013). The exact duration (likely weeks to months) of complete or partial burial is unknown; however, growth rates would no doubt be affected by the extent to which an individual is covered or for how long burial persists. Burial would affect not only light availability, but also scour growing edges and potentially limit access to nutrients. Additionally, although Alizarin Red staining was an effective tool for measuring growth, not all branches within an individual absorbed or retained the stain. This has been reported or suggested by others using the stain (Blake & Maggs 2003, Rivera et al. 2004, Kamenos & Law 2010). Thus, growth rates reported in the present study include variation within individual rhodoliths (4–10 branch tips), but may do so inconsistently. This is an inherent limitation of the staining technique and may account for some of the observed variability in reported ages. Variation may also be partially driven by size-dependent growth rates, but since average and incremental growth rates were similar and variation in growth based on size was not statistically significant, it suggests those differences do not largely influence age projections. All of these possibilities warrant further exploration and consideration in future rhodolith age and growth studies.

In general, our age ranges are similar to those proposed by others working on *L. muelleri* in the Gulf of California, but lower than those reported for other species worldwide. Frantz et al. (2000) and Rivera et al. (2004) determined that growth in *L. muelleri* is continuous and the largest individuals in their studies were 100+ yr old. Like Rivera et al. (2004), we also found that maximum rhodolith size was 15–16 cm diam, suggesting that there may be a finite maximum size (and thus measurable age) for this species. It is possible that rhodoliths could grow larger, but size-related mortality suggests that survivorship beyond 15–16 cm is low. Age estimates based on radiocarbon dating of other rhodolith species have ranged from hundreds to several thousand years (Littler et al. 1991, Goldberg 2006, Amado-Filho et al. 2012), with authors suggesting very old rhodoliths likely represent fossil rhodoliths that have been recolonized, creating age discontinuities within a single individual. In some cases, carbon dating techniques used in previous studies likely overestimated rhodolith age (Foster 2001). More field-based growth studies of

rhodolith species outside of the Gulf of California would enhance current understanding of rhodolith age and growth, but our data further show that rhodoliths are long-lived.

While relatively rare, large individuals may be important demographically and are important ecologically. We did not investigate sexual reproduction, but given the reproductive phenology of *L. muelleri*, it is probable that as surface area increases in larger organisms, so does their reproductive potential, as active conceptacles are in surface cell layers (R. Riosmena-Rodríguez pers. obs.). However, demographic models (Foster 2001) suggest that most reproduction in rhodoliths is likely due to fragmentation, and the abundance of small rhodoliths without a core or nucleus at our study site suggests that fragmentation may be the most common source of new individuals in this population. Any small fragments that do not continue to grow, and dead rhodoliths which break down into small pieces, form carbonate sand that can provide habitat for other organisms (Steller et al. 2003). Studies that have examined diversity of crypto-faunal communities living inside or on top of rhodoliths also indicate that larger and more structurally complex rhodoliths harbor more species and more individuals (Steller et al. 2003, Foster et al. 2007). Similar patterns are also reported for benthic invertebrates that function as habitat builders (Buhl-Mortensen et al. 2010).

Aside from our study and a few exceptions (Steller 2003, Rivera et al. 2004, Goldberg 2006), the majority of rhodolith age and/or growth studies do not include assessment of population structure and are often based on small sample sizes (Adey & McKibbin 1970, Potin et al. 1990, Littler et al. 1991, Frantz et al. 2000, Halfar et al. 2000, Blake & Maggs 2003, Kamenos et al. 2008, Amado-Filho et al. 2012, Darrenougue et al. 2013). Rivera et al. (2004) did measure 117 individuals in a 1 h survey of their site, and resulting size-frequency data was also indicative of a population dominated by smaller (<5 cm diam) individuals. The relative abundance of various ages/sizes of rhodoliths is particularly important when trying to assess potential impacts and recovery from disturbances. Moreover, size-frequency data from the present study and Foster et al. (2007) show that surveys that do not include live rhodoliths from sediment cores can severely underestimate the abundance of small (<2.5 cm diam) individuals in a population.

Size-frequency data from ~6 mo prior to Hurricane Marty, coupled with growth rate data and the size-frequency distribution of rhodoliths deposited on shore following the storm, provided a unique oppor-

tunity to assess mortality and resilience of rhodoliths following a large-scale disturbance. The largest and oldest rhodoliths appear to be most susceptible to this type of wave-driven storm damage. This was also observed after the same storm, for the same species, at a nearby site (Johnson et al. 2012). Percent cover data in Foster et al. (2007) suggest there was little change in the abundance of rhodoliths before and after the storm. This could be due to the effects of burial and emergence of rhodoliths during storm events. Regardless, changes in cover are not indicative of changes in size-frequency because of the effects of fragmentation. Given the thousands of rhodoliths deposited on shore (many more than the 149 sampled) and their dominance by larger individuals, there was no doubt an impact to the surviving subtidal population structure. Slow growth rates and ease of fragmentation suggest the storm caused an increase in small individuals and a significant loss of larger, older, more ecologically important rhodoliths. Similar loses in rhodolith (maerl) habitat due to fragmentation or burial, and slow recovery potential, have also been reported following trawling disturbance (Hall-Spencer & Moore 2000).

The observed shoreward transport of rhodoliths during storm events has also been reported for other macroalgae. Black & Peterson (1987) found that the brown alga *Hormosira banksii* could be dislodged during storms and cast on shore to die. Those authors hypothesized that *H. banksii* grew more frequently on larger bivalve species at their study site because bigger molluscs provided a more secure anchor and were less likely to be dislodged by wave forces. Given this logic, it may seem counter-intuitive that the largest rhodoliths would be the most likely to be transported toward shore, but previous surveys of Cabo Los Machos (Fig. 4 in Foster et al. 2007) showed rhodolith size increased closer to shore in shallower water. The shoreward transport of these larger rhodoliths may be enhanced because they are filled with cryptofauna and partially excavated by stomatopods, which may in turn reduce rhodolith density and increase the likelihood they would be moved by storm surge. Larger rhodoliths may also be more prone to shoreward transport because they project higher in the water column. Lastly, it is possible that all size classes were cast on shore during the initial storm event, but that smaller (lighter) rhodoliths were more easily carried back down the beach slope into the subtidal zone and thus less represented in the beach-stranded population. If the latter is true, then smaller, younger rhodoliths are perhaps most resilient.

The population structure of *L. muelleri* at Cabo Los Machos, and likely other sites in the Gulf of California, is driven by fragmentation, slow growth, and episodic large disturbances such as hurricanes and tropical storms. During the past 64 yr, 5 hurricane-related disturbances (tropical depression up to a Category 3 hurricane) have crossed over the study site and at least 9 others were near enough to potentially affect the area (NOAA 2013). Therefore, while episodic, these disturbances are frequent relative to the ~100 yr lifespan of the rhodoliths. Observations by others (e.g. Schlanger & Johnson 1969, Johnson et al. 2012) have suggested the importance of hurricane disturbance to rhodolith distribution and carbonate deposition in the Gulf. The frequency of such disturbances and consequent death by fragmentation and stranding of large, old individuals documented here indicate that such disturbance may be the most important phenomena affecting rhodolith population structure in the region. Because large individuals harbor a more diverse and abundant fauna, their loss has community effects disproportionate to their abundance. Changes in hurricane frequency and intensity due to global climate change are uncertain (IPCC 2012), but any increase in storm events would accelerate the elimination of large individuals from the population. This degradation could add to that which may occur from ocean acidification (Jokiel et al. 2008, McCoy 2013, Ragazzola et al. 2013, McCoy & Pfister 2014).

LITERATURE CITED

Adey WH, McKibbin DL (1970) Studies on the maerl species *Phymatolithon calcareum* (Pallas) nov. comb. and *Lithothamnium coralloides* Crouan in the Ria de Vigo. Bot Mar 13:100–106

Amado-Filho GM, Moura RL, Bastos AC, Salgado LT and others (2012) Rhodolith beds are major CaCO$_3$ bio-factories in the tropical South West Atlantic. PLoS ONE 7:e35171

Andrews AH, Cordes EE, Mahoney MM, Munk K, Coale KH, Cailliet GM, Heifetz J (2002) Age, growth and radiometric age validation of a deep-sea, habitat-forming gorgonian (*Primnoa resedaeformis*) from the Gulf of Alaska. Hydrobiologia 471:101–110

Arnaud-Haond S, Duarte CM, Diaz-Almela E, Marbà N, Sintes T, Serrão EA (2012) Implications of extreme life span in clonal organisms: millenary clones in meadows of the threatened seagrass *Posidonia oceanica.* PLoS ONE 7:e30454

Birkeland C, Dayton PK (2005) The importance in fishery management of leaving the big ones. Trends Ecol Evol 20:356–358

Black R, Peterson CH (1987) Biological vs. physical explanations for the non-random pattern of host occupation by a macroalga attaching to infaunal bivalve molluscs. Oecologia 73:213–221

Blake C, Maggs CA (2003) Comparative growth rates and internal banding periodicity of maerl species (Corallinales, Rhodophyta) from northern Europe. Phycologia 42:606–612

Blunden G, Binns WW, Perks F (1975) Commercial collection and utilisation of maërl. Econ Bot 29:141–145

Bosence DWJ (1979) Live and dead faunas from coralline algal gravels, Co. Galway. Palaeontology 22:449–478

Buhl-Mortensen L, Mortensen PB (2005) Distribution and diversity of species associated with deep-sea gorgonian corals off Atlantic Canada. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer-Verlag, Berlin, p 849–879

Buhl-Mortensen L, Vanreusel A, Gooday AJ, Levin LA and others (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Mar Ecol 31:21–50

Burdett H, Kamenos NA, Law A (2011) Using coralline algae to understand historic marine cloud cover. Palaeogeogr Palaeoclimatol Palaeoecol 302:65–70

Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. Am Nat 111:1119–1144

Darrenougue N, De Deckker P, Payri C, Eggins S, Fallon S (2013) Growth and chronology of the rhodolith-forming, coralline red alga *Sporolithon durum*. Mar Ecol Prog Ser 474:105–119

De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proc Natl Acad Sci USA 109: 17995–17999

Doak D (1995) Source sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. Conserv Biol 9:1370–1379

Enochs IC (2012) Motile cryptofauna associated with live and dead coral substrates: implications for coral mortality and framework erosion. Mar Biol 159:709–722

Foster M (2001) Rhodoliths: between rocks and soft places. J Phycol 37:659–667

Foster MS, McConnico LM, Lundsten L, Wadsworth T and others (2007) The diversity and natural history of a *Lithothamnion muelleri-Sarassum horridum* community in the Gulf of California. Cienc Mar 33:367–384

Franklin JL (2004) Tropical cyclone report. Hurricane Marty 18-24 September 2003. National Hurricane Center, National Centers for Environmental Prediction, National Weather Service, NOAA, Miami, FL. www.nhc.noaa.gov/ 2003marty.shtml (accessed on 20 Oct 2013)

Frantz BR, Kashgarian M, Coale K, Foster MS (2000) Growth rate and potential climate record from a rhodolith using ^{14}C accelerator mass spectrometry. Limnol Oceanogr 45: 1773–1777

Goldberg N (2006) Age estimates and description of rhodoliths from Esperance Bay, Western Australia. J Mar Biol Assoc UK 86:1291–1296

Grall J, Glémarec M (1997) Biodiversité des fonds de maerl en Bretagne: approche fonctionnelle et impacts anthropogeniques. Vie Milieu 47:339–349

Halfar J, Zack T, Kronz A, Zachos JC (2000) Growth and high-resolution paleoenvironmental signals of rhodoliths (coralline red algae): a new biogenic archive. J Geophys Res 105(C9):22107–22116

Halfar J, Eisele M, Riegl B, Hetzinger S, Godinez-Orta L (2012) Modern rhodolith-dominated carbonates at Punta Chivato, México. Geodiversitas 34:99–113

Hall-Spencer JM, Moore PG (2000) Scallop dredging has profound, long-term impacts on maerl habitats. ICES J Mar Sci 57:1407–1415

Hinojosa-Arango G, Riosmena-Rodríguez R (2004) Influence of rhodolith-forming species and growth-form on associated fauna of rhodolith beds in the central-west Gulf of California, Mexico. Mar Ecol 25:109–127

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265: 1547–1551

Hughes TP, Tanner JE (2000) Recruitment failure, life histories, and long-term decline of Caribbean corals. Ecology 81:2250–2263

IPCC (2012) Field CB, Barros V, Stocker TF, Qin D and others (eds) Managing the risks of extreme events and disasters to advance climate change adaptation. A special report of Working Groups I and II of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

James DW (2000) Diet, movement, and covering behavior of the sea urchin *Toxopneustes roseus* in rhodolith beds in the Gulf of California, México. Mar Biol 137:913–923

Johnson ME, Perez DM, Baarli BG (2012) Rhodolith stranding event on a Pliocene rocky shore from Isla Cerralvo in the lower Gulf of California (Mexico). J Coast Res 28: 225–233

Jokiel PL, Rodgers KS, Kuffner IB, Andersson AJ, Cox EF, Mackenzie FT (2008) Ocean acidification and calcifying reef organisms: a mesocosm investigation. Coral Reefs 27:473–483

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Kamenos NA, Law A (2010) Temperature controls on coralline algal skeletal growth. J Phycol 46:331–335

Kamenos NA, Moore PG, Hall-Spencer JM (2004) Attachment of the juvenile queen scallop (*Aequipecten opercularis* (L.)) to maerl in mesocosm conditions; juvenile habitat selection. J Exp Mar Biol Ecol 306:139–155

Kamenos NA, Cusack M, Moore PG (2008) Coralline algae are global palaeothermometers with bi-weekly resolution. Geochim Cosmochim Acta 72:771–779

Kennedy EV, Perry CT, Halloran PR, Iglesias-Prieto R and others (2013) Avoiding coral reef functional collapse requires local and global action. Curr Biol 23:912–918

Littler M, Littler DS, Hanisak MD (1991) Deep-water rhodolith distribution, productivity, and growth history at sites of formation and subsequent degradation. J Exp Mar Biol Ecol 150:163–182

Martin S, Castets MD, Clavier J (2006) Primary production, respiration and calcification of the temperate free-living coralline alga *Lithothamnion corallioides*. Aquat Bot 85: 121–128

McCoy SJ (2013) Morphology of the crustose coralline alga *Pseudolithophyllum muricatum* (Corallinales, Rhodophyta) responds to 30 years of ocean acidification in the Northeast Pacific. J Phycol 49:830–837

McCoy SJ, Pfister CA (2014) Historical comparisons reveal altered competitive interactions in a guild of crustose coralline algae. Ecol Lett 17:475–483

Merrifield MA, Badan-Dangon A, Winant CD (1987) Temporal behavior of lower atmospheric variables over the Gulf of California, 1983–1985: a data report. Reference Series 87-6. Scripps Institution of Oceanography, La Jolla, CA

Nelson WA (2009) Calcified macroalgae — critical to coastal ecosystems and vulnerable to change: a review. Mar Freshw Res 60:787–801

NOAA (2013) Archive data. Past track seasonal maps for the East Pacific Basin since 1949. National Hurricane Center, National Weather Service, Miami, FL. www.nhc.noaa.gov/data/ (accessed on 24 Oct 2013)

Pandolfi JM, Bradbury RH, Sala E, Hughes TP and others (2003) Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955–958

Potin P, Floc'h JY, Augris C, Cabioch J (1990) Annual growth rate of the calcareous red algae *Lithothamnion corallioides* (Corallinales, Rhodophyta) in the Bay of Brest, France. Hydrobiologia 204–205:263–267

Ragazzola F, Foster LC, Form AU, Büscher J, Hansteen TH, Fietzke J (2013) Phenotypic plasticity of coralline algae in a high CO_2 world. Ecol Evol 3:3436–3446

Reynolds JD, Dulvy NK, Goodwin NB, Hutchings JA (2005) Biology of extinction risk in marine fishes. Proc R Soc Lond B Biol Sci 272:2337–2344

Riera R, Delgado JD, Rodríguez M, Monterroso O, Ramos E (2012) Macrofaunal communities of threatened subtidal maërl seabeds on Tenerife (Canary Islands, north-east Atlantic Ocean) in summer. Acta Oceanol Sin 31:98–105

Rivera MG, Riosmena-Rodríguez R, Foster MS (2004) Age and growth of *Lithothamnion muelleri* (Corallinales, Rhodophyta) in the southwestern Gulf of California, Mexico. Cienc Mar 30:235–249

Schlanger SO, Johnson CJ (1969) Algal banks near La Paz, Baja California — modern analogues of source areas of transported shallow-water fossils in pre-alpine flysch deposits. Palaeogeogr Palaeoclimatol Palaeoecol 6:141–157

Sousa WP (1979) Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60:1225–1239

Sousa WP (1984) The role of disturbance in natural communities. Annu Rev Ecol Syst 15:353–391

Steller DL (2003) Rhodoliths in the Gulf of California: growth, demography, disturbance and effects on population dynamics of catarina scallops. PhD dissertation, University of California, Santa Cruz, CA

Steller DL, Cáceres-Martínez C (2009) Coralline algal rhodoliths enhance larval settlement and early growth of the Pacific calico scallop *Argopecten ventricosus*. Mar Ecol Prog Ser 396:49–60

Steller DL, Riosmena-Rodríguez R, Foster MS, Roberts CA (2003) Rhodolith bed diversity in the Gulf of California: the importance of rhodolith structure and consequences of disturbance. Aquat Conserv Mar Freshw Ecosyst 13: S5–S20

Steller DL, Hernández-Ayón JM, Riosmena-Rodríguez R, Cabello-Pasini A (2007) Effect of temperature on photosynthesis, growth, and calcification rates of the free-living coralline alga *Lithophyllum margaritae*. Cienc Mar 33:441–456

Stevens JD, Bonfil R, Dulvy NK, Walker PA (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES J Mar Sci 57:476–494

Wilson S, Blake C, Berges JA, Maggs CA (2004) Environmental tolerances of free-living coralline algae (maerl): implications for European marine conservation. Biol Conserv 120:279–289