UNIVERSIDAD AUTÓNOMA DE BAJA CALIFORNIA SUR

ÁREA DE CONOCIMIENTO DE CIENCIAS DEL MAR Y DE LA TIERRA
DEPARTAMENTO ACADÉMICO DE CIENCIAS MARINAS Y COSTERAS
POSGRADO EN CIENCIAS MARINAS Y COSTERAS

TESIS

EDAD, CRECIMIENTO, VARIACIÓN TEMPORAL Y DINÁMICA DE NUTRIENTES EN LOS MANTOS DE RODOLITOS EN BAJA CALIFORNIA SUR, MÉXICO

QUE COMO REQUISITO PARA OBTENER EL GRADO DE
DOCTOR EN CIENCIAS MARINAS Y COSTERAS
CON ORIENTACIÓN EN BIOLOGÍA MARINA

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LA PAZ, BAJA CALIFORNIA SUR, JUNIO DE 2016

UNIVERSIDAD AUTÓNOMA DE BAJA CALIFORNIA SUR
Área de Conocimiento de Ciencias del Mar y de la Tierra
Departamento Académico de Ciencias Marinas y Costeras
POSGRADO EN CIENCIAS MARINAS Y COSTERAS

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PRESENTE.**

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___EDAD, CRECIMIENTO, VARIACIÓN TEMPORAL Y DINÁMICA DE NUTRIENTES EN LOS MANTOS DE RODOLITOS EN BAJA CALIFORNIA SUR, MÉXICO._____

que presentó:

_____Laurie Anne McConnico_____

Otorgamos nuestro voto **aprobatorio** y consideramos que dicho trabajo está listo para su defensa, a fin de obtener el **Grado de Doctor** en Ciencias Marinas y Costeras, con Orientación en _____Biología Marina_____.

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A mi familia en Baja y Alta California

Y

A Rafael, quien se nos fue demasiado pronto

AGRADECIMIENTOS

Me gustaría expresar mi gratitud a los Drs. Rafael Riosmena Rodríguez[†] y Gustavo Hernández Carmona por darme la oportunidad de estudiar en México y brindarme su apoyo por completo durante todo el proceso. Agradezco al Dr. Carlos Armando Sánchez Ortíz por su servicio como co-director en las últimas etapas del doctorado y ayuda como un miembro del comité original. También agradezco a los demás miembros de mi comité: Drs. Diana Steller, Gustavo Hinojosa Arango, Juan Manuel López Vivas, Michael Foster y Jorge M. López Calderón por el tiempo, apoyo y asesoramiento necesario para completar mi tesis. A Mike, Diana, Gustavo y Rafael un gracias adicional por siempre cuidarme, motivarme, educarme y por su amistad. La ayuda prestada por todos ustedes ha servido para fomentar la colaboración entre investigadores de Estados Unidos y México.

Este trabajo fue verdaderamente logrado por el apoyo, amor y trabajo duro de Josué Sócrates Martínez Morales. Estoy en deuda con él por las muchas horas que invirtió en esta investigación. Su intelecto, creatividad y perspectiva positiva se encuentran entre algunas de sus mejores cualidades. Tengo la suerte de contar con él en mi vida y sigo impresionada por todo lo que logra.

El trabajo de ecología en el campo no sería posible sin la ayuda de un equipo, el cual se logró gracias a la ayuda de muchos asistentes de campo altamente capacitados y buzos de gran profesionalismo. En particular, Josué Sócrates Martínez Morales, Zvi Hoffman Ramírez, Yamaly Barragán Marín y Beatriz Torrano, que en mis horas de muestreo aportaron incontables horas de trabajo de campo. Son algunos de los más amables, trabajadoras y gente de buen espíritu que he conocido en mi vida. La asistencia de Juan Carlos González Boeta 'El Charly', Gustavo Ceballos, Zoideth Rocha, Kenia Castillo, Guadalupe Carolina Martínez Morales y Jason Felton que siempre fueron de gran ayuda.

Los capitanes de las embarcaciones, Julio 'El Iguano' Arce quien nos ayudó siempre en Bahía Concepción y Gilberto 'El Manotas' Ramírez en Bahía Magdalena son algunos de los hombres más amables, brillantes e interesantes en el agua. Sus conocimientos locales, corazones

Por último, tengo la suerte de tener el amor y el apoyo de mis padres John y Patti McConnico y mi familia en los Estados Unidos, no sólo durante este paso, sino por toda mi vida. Soy una chica con suerte. Mi segunda familia en México: Gustavo y Linda (todas sus hijas y nietos), Chuchis y el Chino (y sus hijos) y a Josué y su familia; gracias por hacerme aparte de sus familias, invitándome a sus vidas y hogares, así como el cuidado de esta gringa. Los amo a todos.

CAPÍTULO 1

BIOLOGÍA DE LA POBLACIÓN DE UN RODOLITO DE LARGA VIDA: LAS CONSECUENCIAS DE CONVERTIRSE EN VIEJO Y GRANDE

CAPÍTULO 2

VARIACIÓN TEMPORAL DENTRO DE LAS COMMUNIDADES ASOCIADAS A LOS MANTOS DE RODOLITOS EN BAJA CALIFORNIA SUR, MÉXICO

CAPÍTULO 3

REGENERACIÓN DE NUTRIENTES POR LOS CONJUNTOS DE CRIPTOFAUNA EN LOS MANTOS DE RODOLITOS DE BAJA CALIFORNIA SUR, MÉXICO

MATERIAL SUPLEMENTARIO

ÁREA DE ESTUDIO

CAPÍTULO 1

CAPÍTULO 2

CAPÍTULO 3

CAPÍTULO 2

CAPÍTULO 3

Los rodolitos son algas calcáreas rojas no geniculadas, que forman densos mantos en las zonas costeras de todo el mundo. Estas comunidades fotosintéticas crecen lentamente y forman el hábitat para cientos de especies crípticas y macroscópicas. Estos hábitats son particularmente vulnerables a las perturbaciones antropogénicas y naturales, pero existe poca información acerca la tasa de crecimiento de los mantos de rodolitos, la persistencia de especies asociadas con estos y los factores que afectan la persistencia y estabilidad de los rodolitos *e.g.* huracanes y la dinámica de nutrientes en los mantos. Considerando la gran diversidad y abundancia de criptofauna, es probable que éstos sean una fuente de nutrientes tanto a nivel individual como a nivel manto. Este trabajo abordó estos aspectos poco explorados, en ambos lados de la península Baja California. El primer objetivo del estudio fue a describir la estructura de una población de *Lithothamnion muelleri,* determinar los efectos de un huracán, determinar el crecimiento estacional y la edad de individuos en la población del manto en Bahía Concepción, usando muestreos de campo y técnicas de tinción rojo de alizarina. El segundo objetivo fue determinar la variación temporal de los componentes asociados en el manto de rodolitos en Bahía Magdalena y Bahía Concepción usando la técnica de RPQ (Random Point Quadrat) para estimar cambios en el porcentaje de macroalgas e invertebrados sésiles en los mantos y conteos de densidad para determinar la variación en invertebrados móviles. El último objetivo consistió en determinar la relación entre los rodolitos (*Lithothamnion muelleri* y *Lithophyllum margaritae*) y la producción de nutrientes por parte de la criptofauna. Se comparó la cantidad de nutrientes en muestras tomadas en la columna de agua, en los sedimentos y dentro de los rodolitos en Bahía Concepción y Bahía Magdalena, por último se relacionó esos datos con la cantidad de criptofauna en cada rodolito (2013-2014). Los resultados indicaron que la población de rodolitos en Bahía Concepción fue dominada por individuos pequeños (< 4 cm diámetro). Todos crecieron lentamente (~1.4 mm/ año), se estima que los más grandes tiene una edad de más de 100 años y estuvieron afectados negativamente por un huracán. Mientras las poblaciones de rodolitos estuvieron estables durante 2013-2015, la abundancia de las algas asociadas cambió estacionalmente, siendo más abundante en los primeros seis meses del año. No fue un efecto estacional distinto en la abundancia ni densidad de invertebrados sésiles o móviles asociados con los rodolitos *L. muelleri* o *L. margaritae*. Los análisis de nutrientes indicaron que hubo una alta concentración de nutrientes dentro de los rodolitos y los sedimentos en comparación a la concentración del agua en el ambiente. Los datos surgieren que la criptofauna pueda proveer una fuente de nutrientes adicional a los rodolitos de un manto. Los rodolitos son organismos de larga vida y lento crecimiento. En este estudio se demostró que contiene una criptofauna diversa que también puede fungir como una fuente abundante de nutrientes en un ambiente pobre en nutrientes. Se requieren más estudios para comprender mejor la dinámica de nutrientes en estos hábitats de gran valor ecológico y que son vulnerables a las perturbaciones.

Rhodoliths are red calcareous algae that form dense beds in coastal areas worldwide. These photosynthetic communities grow slowly and form a habitat for hundreds of cryptic and macroscopic species. These habitats are particularly vulnerable to anthropogenic and natural disturbances, but there is little information on the growth rate, persistence of species associated with beds and factors affecting the persistence of rhodoliths e.g. hurricanes and nutrient dynamics in the beds. Given the great diversity and abundance of cryptofauna, it is likely that they are a source of nutrients both for rhodoliths individually and at the bed level. This research addressed these relatively unexplored topics on both sides of Baja California peninsula. The first objective of the study was to describe the population structure of *Lithothamnion muelleri*, determine the effects of a hurricane and measure the seasonal growth and age of individuals in the population in Bahía Concepción, using field sampling techniques and alizarin red staining. The second objective was to determine temporal variation of organisms associated with rhodolith beds in Bahía Magdalena and Bahía Concepción using random point quadrats (RPQ) to estimate changes in the percent cover of macroalgae and sessile invertebrates and density counts to determine variation in mobile invertebrates. The last objective was to determine the relationship between rhodoliths (*Lithothamnion muelleri* and *Lithophyllum margaritae*) and the production of nutrients by cryptofauna. The amount of nutrients in samples taken from the water column, sediments and within rhodoliths in Bahía Concepción and Bahía Magdalena (2013-2014) and the data related to the amount of cryptofauna in each rhodolith was compared. The results indicated that the population of rhodoliths in Bahía Concepción was dominated by small individuals (< 4 cm diameter). All grew slowly (~ 1.4 mm/ year), with the largest living > 100 years, and they were negatively affected by a hurricane. While rhodolith populations were stable during 2013-2015, associated algae changed with seasons and were more abundant in the first six months of the year. No distinct seasonal effect of abundance or density of mobile or sessile invertebrates associated with *L. muelleri* or *L. margaritae* was detected. Analyses indicated there was a high concentration of nutrients within rhodoliths and sediment compared to ambient water column samples. Cryptofauna may provide an additional source of nutrients to rhodoliths and within beds. Long-lived and slow growing rhodoliths in this study support a diverse cryptofauna that may create an abundant source of nutrients in nutrient-poor environments. Further studies are needed to better understand the dynamics of nutrients in these habitats of great ecological importance, which are vulnerable to disturbances.

Los rodolitos y los mantos que estos forman son sin duda algunas de las comunidades marinas más importantes en aguas someras, cercanas a la costa (menos de 300 m Littler et al. 1991). Estas algas coralinas no geniculadas de vida libre están presentes en densidades altas y se pueden encontrarse en todos los océanos del mundo (Foster 2001). Tomando en cuenta su distribución y abundancia global, estas comunidades de algas calcificadas son tanto económica como ecológicamente importantes. El valor ecológico de estas especies radica en las muchas funciones ecosistémicas que se realizan a partir de la generación de carbonato (Martin et al. 2006, Amado-Filho et al. 2012, Halfar et al. 2012), al hábitat que proporcionan para muchas plantas marinas y animales asociados (Bosence 1979, Grall & Glémarec 1997, Steller et al. 2003, Hinojosa-Arango & Riosmena-Rodríguez 2004, Foster et al. 2007, Riera et al. 2012). El valor económico de los mantos de rodolitos se relaciona a menudo con la pesca comercial y artesanal en estos (Hall-Spencer & Moore 2000, Kamenos et al. 2004, Steller & Cáceres-Martínez 2009) o la extracción directa para fines agrícolas (Blunden et al. 1975). La importancia global de estas comunidades con mayor biodiversidad ha llevado a impulsar la continua investigación de su función ecológica/ biológica en todo el mundo, así como los estudios de impedimentos a su persistencia.

Las descripciones detalladas de rodolitos se remontan a la década de 1800 (Foslie 1894) y se reportó por primera vez en el Golfo de California, México por Hariot (1895) y también se documentó en encuestas realizadas por Dawson (1960). Bosence (1983) propuso algunos de los esquemas de clasificación inicial y Riosmena-Rodríguez et al. (1999) y Riosmena-Rodríguez (2002) han desempeñado un papel clave en la clasificación e identificación de los principales taxones de rodolitos en el Golfo de California, donde cuatro especies principales son reconocidos actualmente (*Lithothamnion muelleri*, *Lithophyllum margaritae*, *Neogoniolithon trichotomum* y *Mesophyllum engelhartii*; Riosmena-Rodríguez et al. 2010). En general, la taxonomía de rodolitos es difícil de resolver y complicada por la naturaleza altamente variable de la morfología de rodolitos dentro de una misma especie (Riosmena-Rodríguez et al. 2010).

Los rodolitos se han reportado en todo el mundo y son especialmente abundantes en el Mar Mediterráneo, Brasil, Australia, el Reino Unido y en Baja California, México (Foster 2001). Las

regiones de Baja California han sido particularmente estudiadas a fondo por Steller & Foster (1995) Foster et al. (2007), Ávila & Riosmena-Rodríguez (2011) y Riosmena-Rodríguez et al. (2012). Estos autores reporta altas densidades de rodolitos en mantos intermareal y/o submareal superficiales. Los estudios de la plataforma de Abrolhos en Brasil, confirmaron la presencia generalizada de los mantos a lo largo de su costa oriental (Amado-Filho et al. 2012), como se informó anteriormente por Kempf (1970). Se estima que estos mantos fueron tan grande como la Gran Barrera de Coral y se continuarán desarrollando estudios ecológicos y demográficos en la región (Amado-Filho et al. 2012). En general, muchos estudios iniciales se centran en la descripción de lugares de los mantos, las distribuciones locales, las poblaciones de rodolitos y especies asociadas.

A nivel de población, los estudios de las tasas de crecimiento de rodolitos han sido importantes en la comprensión de la longevidad y la vulnerabilidad a eventos estocásticos y amenazas antropogénicas. Las tasas de crecimiento varían desde menos de 1.0 mm año^{-1} (Foster 2001) a más de 5.0 mm año^{-1} (Steller et al. 2007), dependiendo de la especie y de la técnica de estimación. Mediciones directas de campo (Adey & McKibbin 1970), cambios en el peso de carbonato de calcio (Potin et al. 1990), el Carbono 14 (Littler et al. 1991, Frantz et al. 2000, Goldberg 2006), relaciones Mg/Ca (Halfar et al. 2000, Kamenos et al. 2008), tinción de rojo de alizarina (Blake & Maggs 2003, Rivera et al. 2004, Steller et al. 2007, Amado-Filho et al. 2012) o una combinación de estas técnicas (Darrenougue et al. 2013), se han utilizado para determinar las tasas de crecimiento y/o la edad. Algunos autores mencionan que el crecimiento es generalmente más rápido en verano que en invierno (Adey & McKibbin 1970, Potin et al. 1990, Steller et al. 2007), sin embargo un reporte de crecimiento menciona que es más rápido en invierno (Rivera et al. 2004). Aunque las estimaciones de crecimiento son variables, todos han llegado a la conclusión de que los rodolitos son de lento crecimiento y algunos pueden vivir más de 100 años (Frantz et al. 2000, Rivera et al. 2004). Por lo tanto, las tasas de crecimiento indican que la recuperación de las poblaciones después de la perturbación será lenta, pero no muestran cómo esto podría afectar la distribución de tamaño y las especies asociadas, excepto en el caso de alteraciones masivas.

4

A nivel comunitario, la variabilidad temporal en los mantos de rodolitos es común. La estacionalidad de las macroalgas asociadas se documentó ampliamente en los lechos de Europa (Maggs 1983, Hily et al. 1992, Piazzi et al. 2004, Bárbara et al. 2004, Grall et al. 2006, Peña & Bárbara 2008, 2010), México (Steller et al. 2003, Foster et al. 2007), Estados Unidos (Gabara 2014), Brasil (Amado-Filho et al. 2007, 2010, Pascelli et al. 2013) y Nueva Zelanda (Nelson et al. 2014). Pocos estudios se han centrado en los cambios temporales de las comunidades de invertebrados asociados con los mantos de rodolitos (Steller et al. 2003, Foster et al. 2007, Riosmena-Rodríguez & Medina-López 2011, Gabara 2014). En general, la diversidad y/o abundancia de especies tienden a ser afectados por la temperatura o las condiciones oceanográficas estacionales, perturbaciones, así como reclutamiento episódico y las características del ciclo vital. Muchos estudios florísticos existentes son en gran parte descriptiva y todos los estudios anteriores, excepto Maggs (1983) y Peña & Bárbara (2008), se basan en la comparación de dos extremos temporales o carecen de la replicación de temporadas. Se requieren estudios cuantitativos multianuales que nos permitan comprender mejor el papel de la estacionalidad vs otros factores que influyen en la estructura de los mantos de rodolitos.

La comunidad de rodolitos también se compone de organismos asociados que viven en y entre las ramas de los rodolitos (criptofauna). Los rodolitos actúan como especies fundamentales (Weber Van Bosse & Foslie 1904, Foster 2001), que pueden albergar cientos de organismos, incluyendo equinodermos, moluscos, crustáceos y anélidos (Steller et al. 2003, Hinojosa-Arango & Riosmena-Rodríguez 2004, Foster et al. 2007, Riosmena-Rodríguez & Medina-López 2011, Riera et al. 2012). La criptofauna que habita entre las ramas de los rodolitos está compuesta tanto de adultos como de organismos juveniles, aunque los rodolitos parecen ser más un sitio de reclutamiento importante para juveniles (Riosmena-Rodríguez & Medina-López 2011).

Considerando la abundancia de invertebrados que viven en asociación con rodolitos, es probable que esta criptofauna pueda ser tan importante para el crecimiento y persistencia de rodolitos, como los rodolitos son para la supervivencia de sus habitantes invertebrados. El papel del aporte de nutrientes a los rodolitos suministrado por criptofauna no se ha determinado, sin embargo, el trabajo de Martin et al. (2007) indica los flujos de nutrientes en los mantos de rodolitos pueden

estimular la producción primaria. Los investigadores que han trabajado en otros sistemas marinos han indicado que los nutrientes excretados por invertebrados como los mejillones pueden ser una fuente importante de nutrientes y afectar las tasas de crecimiento del alga roja carnosa *Odonthalia* (Bracken 2004). El alga verde *Cladophora*, también es capaz de dominar pozas intermareales, en parte, debido al amonio liberado por la meiofauna que vive entre sus talos ramificados (Bracken et al. 2007). De la misma manera, la determinación de los beneficios existentes entre los invertebrados y los rodolitos, mejorará la comprensión de la disponibilidad de nutrientes existentes en los mantos de rodolitos y de fuentes de nutrientes potenciales.

Por último, la investigación actual indica que los rodolitos son muy susceptibles a los cambios en las condiciones ambientales y los impactos antropogénicos que pueden agravar estas condiciones. Los rodolitos son fácilmente fragmentados por actividades como la pesca de arrastre, el dragado y el uso de anclajes (Steller et al. 2003 y observación personal). Por lo tanto, los mantos de rodolitos son propensos a tener impactos largos y duraderos en estas frágiles comunidades, de crecimiento lento, relacionado con las actividades de extracción y fauna asociada. El dragado practicado en Escocia para la extracción de bivalvos ocasiona el entierro de los rodolitos (Hall-Spencer & Moore 2000) y reportaron que los tiempos de recuperación relacionados con la extracción comercial de bivalvos en Baja California pueden ser de décadas (Steller et al. 2003). Wilson et al. (2004) demostraron experimentalmente que los talos de rodolitos son físicamente intolerantes a la sedimentación y sugirió que los mantos afectados por la eutrofización y la pesca de arrastre están en mayor riesgo de mortalidad. Aunque existe un creciente interés en los impactos del cambio climático y la acidificación de los océanos en los rodolitos (Jokiel et al. 2008, McCoy 2013, Ragazzola et al. 2013, McCoy & Pfister 2014), mucha menos atención se ha dedicado a la comprensión de la vulnerabilidad a las grandes tormentas y los huracanes que también se pueden incrementar o fortalecer como resultado del cambio climático.

El objetivo de esta investigación fue estudiar las algas calcáreas conocidas como rodolitos, en cuanto a su crecimiento, mortalidad, cambios temporales de las comunidades y dinámica de nutrientes en mantos Baja California Sur, México. En conjunto, los trabajos presentados en esta tesis sirven para avanzar en el conocimiento general de las poblaciones y comunidades de

rodolitos. En el capítulo uno, datos de la tasa de crecimiento, la frecuencia del tamaño y de la mortalidad para el rodolito *Lithothamnion muelleri* en el Golfo de California fueron utilizados para comprender mejor la persistencia del manto y la vulnerabilidad ante una perturbación. Se determinó la tasa de crecimiento (estacional, anual y el tamaño del manto) basándonos en la edad de los rodolitos estimada durante 2003 y 2004. Esto permitió comprobar si existía una relación entre la tasa de crecimiento y el tamaño de rodolitos, y si las tasas de crecimiento varían estacionalmente. Se determinó la distribución de tallas antes y después de una perturbación (huracán) y se evaluó el riesgo de mortalidad dependiente del tamaño. A pesar de que la tasa de crecimiento de los rodolitos han sido previamente estudiada (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), con excepción de Steller (2003), Rivera et al. (2004) y Goldberg (2006), la mayoría de los estudios no incluyen la evaluación de la estructura de la población y se basan en tamaños de muestra pequeños. Los datos de esta investigación son los primeros en analizar la tasa de crecimiento de los rodolitos con datos de la frecuencia de talla de la población y la mortalidad después de un huracán.

En la segunda parte de este trabajo se describe el conjunto de rodolitos dominados por *Lithophyllum margaritae* y *Lithothamnion muelleri* en lagunas costeras de Baja California Sur, México. Los cambios temporales en la cobertura y talla promedio, así como los cambios en las macroalgas e invertebrados asociados a un manto de rodolitos en el Golfo de California (Bahía Concepción) y dos en la zona Pacífico de la península de Baja California (Bahía Magdalena) durante 2013-2015. Este trabajo es uno de los pocos, estudios cuantitativos multianuales necesarios para comprender mejor el papel de la estacionalidad en función de otros factores que influyen en la estructura de los mantos de rodolitos.

El tercer capítulo de esta investigación se centró en la cantidad y la variabilidad temporal de los nutrientes (NH_4^+, NO_3^- y PO_4^{-3}) asociados con mantos de rodolitos en el Golfo de California y del Océano Pacífico en Baja California Sur, México. Se comparó la disponibilidad de nutrientes en la columna de agua, los sedimentos y entre las ramas de rodolitos, para evaluar la contribución de los nutrientes regenerados a partir de la criptofauna dentro de los rodolitos. Se estudió la relación entre la disponibilidad de nutrientes, el tamaño de los rodolitos y la biomasa

de la criptofauna para determinar si los rodolitos más grandes, albergan más criptofauna y así tener acceso a un reservorio de nutriente más abundante. Se analizaron las puntas de las ramas de los rodolitos para determinar el contenido total de nitrógeno y poder inferir las necesidades de nutrientes. Se realizaron incubaciones de campo para determinar la absorción de nutrientes por los rodolitos. Este trabajo es el primero en medir la dinámica de nutrientes en mantos de rodolitos en Baja California y en evaluar las posibles contribuciones de criptofauna. Tales nutrientes regenerados pueden ser de particular importancia en las zonas tropicales y subtropicales, donde los rodolitos son abundantes y potencialmente están limitados de nuevas fuentes de nutrientes. Esto puede ser importante para entender de manera más completa la variación estacional en las tasas de crecimiento, las cuales pueden ser más altas que las reportadas en el invierno. Se requieren más investigaciones en estas áreas poco estudiadas ya que se carece de datos completo que podrían ser una contribución significativa para entender cómo proteger estos hábitats, ecológica y económicamente importantes. Esto es especialmente cierta dada la propagación generalizada de mantos de rodolitos en gran parte de Baja California.

Objetivos Generales

1. Describir la demografía del rodolito *Lithothamnion muelleri* y los efectos de un huracán en Los Machos, Bahía Concepción, Baja California Sur, México.

2. Determinar la variación temporal de los conjuntos del manto de rodolitos en Bahía Magdalena y Bahía Concepción, Baja California Sur, México.

3. Determinar la relación entre los rodolitos y nutrientes producidos por criptofauna en Bahía Concepción y Bahía Magdalena, Baja California Sur, México.

Objetivos Específicos

1.1 Determinar las tasas de crecimiento en base estacional, anual y tamaño, así como las estimaciones de edad para *Lithothamnion muelleri*.

1.2 Determinar la estructura de la población de *Lithothamnion muelleri*.

1.3 Determinar los impactos en la población *Lithothamnion muelleri* después del huracán Marty de 2003.

2.1 Cuantificar la variación temporal del porcentaje de cobertura de algas e invertebrados sésiles y la densidad de macro-invertebrados asociados con los mantos de rodolitos.

3.1 Cuantificar la variación temporal de los nutrientes (amonio, nitrato y fosfatos) de las columnas de agua, sedimentos y rodolitos.

3.2 Cuantificar la biomasa de criptofauna asociado con rodolitos y endofauna asociado con los sedimentos, dentro y fuera de los mantos.

3.3 Relacionar la biomasa de criptofauna con el tamaño de rodolito y la cantidad de nutrientes de los rodolitos.

3.4. Medir el consumo de nutrientes por parte de los rodolitos utilizando incubaciones con luz y en la oscuridad.

Bahía Concepción

La investigación sobre la demografía de rodolitos, impactos de los huracanes, la variación temporal del conjunto de rodolitos y la dinámica de los nutrientes se realizó en Los Machos (Fig. 1), en la boca de Bahía Concepción en el Golfo de California, México (26°50' N, 111°53' W). El manto de rodolitos en Los Machos está ubicado entre 2-8 m de profundidad y está dominada por el rodolito *Lithothamnion muelleri*. Esta zona es una mezcla de arena, cantos rodados, rodolitos y la estacionalmente es abundante el fucoide *Sargassum horridum* (ver Foster et al. 2007, McConnico et al. 2014 para más detalles). El sitio de estudio se describe en detalle por Foster et al. (2007), junto con una evaluación cuantitativa de la composición de la diversidad y de la comunidad del sitio. La mayor parte de la investigación para el presente estudio se llevó a cabo a ~ 5 m de profundidad en el centro del manto usando buceo. En general, el centro del Golfo puede estar limitado de nutrientes, pero ocurren afloramientos estacionales en el golfo oriental en invierno/ primavera (impulsada por vientos del NW) y el afloramiento más débil que ocurre en verano, ya que los vientos vienen del sur, lo que resulta en una columna de agua estratificada la mayor parte del año (Álvarez-Borrego 1983). La temperatura del agua se monitoreó durante todo el estudio y varió de ~ 16-32°C, con las temperaturas extremas en enero y julio-septiembre agosto, respectivamente. Los datos de temperatura específicos del sitio también indican que la temperatura del agua puede disminuir 5-6°C durante finales de la primavera y el verano, tal vez debido al anegamiento.

Bahía Magdalena

La investigación acerca de la variación temporal de los conjuntos de rodolitos y dinámica de los nutrientes se llevó a cabo en dos sitios (Pedregoso y CFE; Fig. 1) dentro de Bahía Magdalena en la costa del Pacífico de Baja California Sur, México (entre 24°54' N y 24°48' N y 112°05' W y 112°06' W). Bahía Magdalena es una laguna poco profunda, compuesta por sedimentos de grano fino suave (< 500 μm) y fuertemente influenciados por las corrientes de marea, que puede exceder de 1 m s^{-1} en la boca (Zaytsev et al. 2003). Pedregoso se encuentra en un canal de

manglares sujetos a un mayor flujo de corriente y tiene un sustrato duro (roca carbonatada) en algunas regiones, mientras que la CFE está en una ensenada bordeada por manglares en su lado norte. Ambos sitios se encuentran en ~ 0.5-2.5 m de profundidad (dependiendo de la marea) y dominada por el rodolito *Lithophyllum margaritae* que alberga una comunidad de esponjas, tunicados y macroalgas en sus superficies. Los rodolitos en estos mantos se describieron originalmente y se identifican por Ávila & Riosmena-Rodríguez (2011). Este complejo lagunar representa un ecosistema de estuario anti-estuarino con nutrientes influenciados por la surgencia costera (Álvarez-Borrego et al. 1975, Cervantes et al. 2013). Los mantos de rodolitos se acceden utilizando pangas y una combinación de buceo o esnórquel, dependiendo de la altura de las mareas. La temperatura del agua varió de ~ 11-33°C con la temperatura más alta registrada durante julio- septiembre y la más fría en enero.
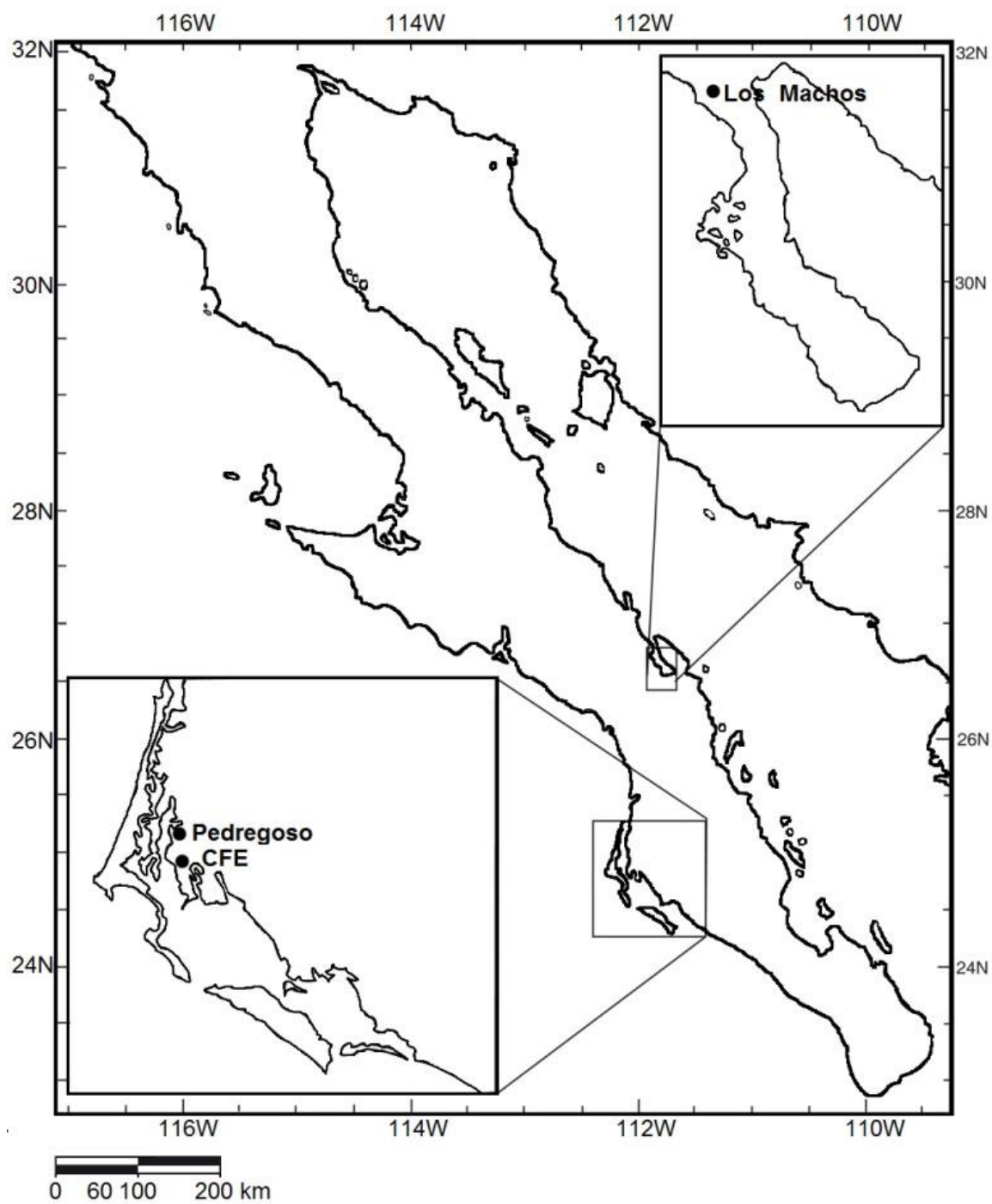
Fig. 1. Sitios de estudio en el Golfo de California (parte superior derecha: Bahía Concepción) y la Costa del Pacífico de (en el recuadro en la parte inferior izquierda: Bahía Magdalena) Baja California Sur, México. La escala corresponde con el mapa más grande, no las cajas pequeñas

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Biología de la población de un rodolito de larga vida: las consecuencias de convertirse en viejo y grande

Population biology of a long-lived rhodolith: the consequences of becoming old and large[1]

Resumen: Características del ciclo vital de los organismos de larga vida les hacen particularmente vulnerables a las perturbaciones. Los estudios demográficos de esas poblaciones son esenciales para evaluar la susceptibilidad a la perturbación y el potencial de recuperación, especialmente para los ingenieros ecosistémicos que apoyan a muchas especies dependientes. Este tipo de información demográfica, incluyendo la estructura de la población y el riesgo de mortalidad, es limitado para los rodolitos (algas coralinas no geniculados) de larga vida que albergan una gran biodiversidad de organismos criptofaunales. La estructura de la población, las tasas de crecimiento estaciónale, estimaciones de la edad y la mortalidad, se determinaron en el período 2003-2004 para los rodolitos de submareal llamados *Lithothamnion muelleri*, en el Golfo de California, México. Los rodolitos variaron en tamaño desde 0.5 hasta 16 cm de diámetro y la población estuvo dominada por los individuos < 4 cm de diámetro. El crecimiento promedio anual (media ± EE) fue lento (0.71 ± 0.04 mm año^{-1}), pero más rápido en verano (marzo-octubre). Las proyecciones de edad sugieren que los individuos grandes podrían vivir de 100 a 300 años. En 2003, numerosos rodolitos ≥ 8 cm de diámetro murieron después de ser arrastrados a la orilla por el huracán Marty. El crecimiento lento y aumento de la mortalidad de los individuos más grandes sugieren que la recuperación a las perturbaciones es lenta y que los individuos más pequeños son más resistentes. Los rodolitos más grandes y más viejos contienen criptofauna más diversa, y por lo tanto, no sólo son más vulnerables a las perturbaciones, pero su mortalidad contribuye de manera desproporcionada a la pérdida de la estructura de la comunidad.

Palabras Clave: *Lithothamnion muelleri* · Perturbación de Huracán · Persistencia Población· Edad y Crecimiento · Mortalidad · Golfo de California

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 (diam.) and the population was dominated by those < 4 cm diam. 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 from 100-300 years. In 2003, numerous rhodoliths ≥ 8 cm diam. died after being cast on shore by Hurricane Marty. Slow growth and increased mortality of larger individuals suggests recovery from disturbances is slow and that smaller (younger) individuals are more resilient. Larger, older, rhodoliths support a more diverse cryptofauna and are thus not only more vulnerable to disturbances, but their mortality contributes disproportionately to the loss of community structure.

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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 sea grasses (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 less than 1.0 mm yr^{-1} (reviewed in Foster 2001) to over 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, Franz 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 more than 100 yrs (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 all sizes would be equally affected by the storm.

Materials and Methods

Study site

The study site was accessed using a small inflatable boat (Zodiac) and subtidal fieldwork was conducted with the aid of SCUBA during March & 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 two sites in the middle of the rhodolith bed (~5 m depth) in 2003. Temperature loggers placed at each site from March 2003-May 2004 indicate temperature ranges from ~16-32°C with these extremes occurring in January and August, respectively. These site specific temperature data also show tidal flushing at the mouth of Bahía Concepción can reduce water temperature by 5-6°C during May-July 2003 (Fig. 1.1).
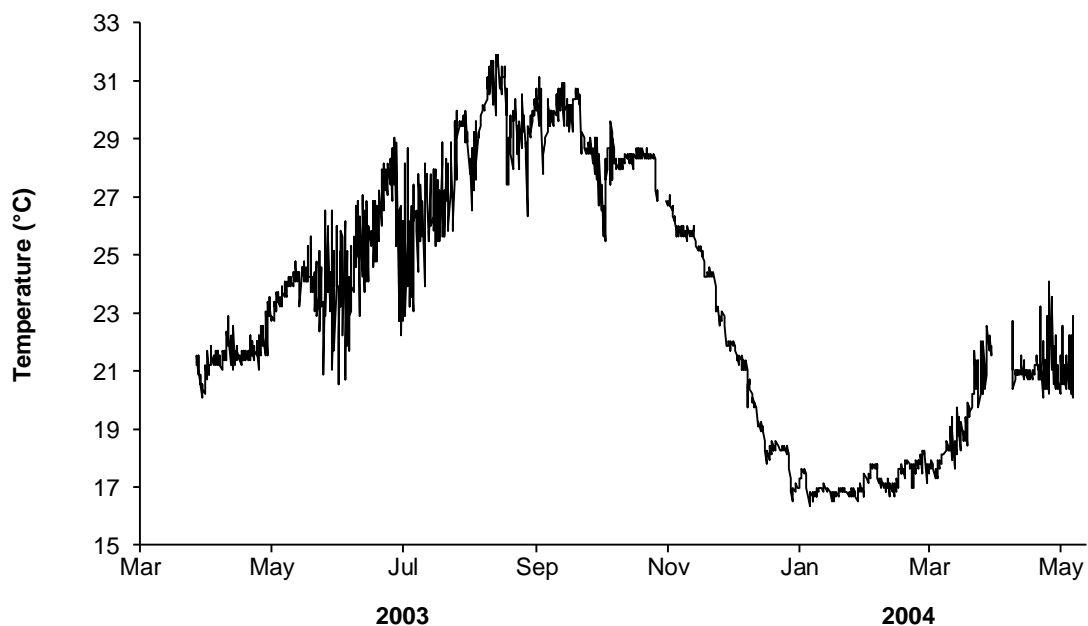
Fig. 1.1 Bottom temperature (5 m) at Cabo Los Machos, March 2003-May 2004. Data gaps during October 2003 and March 2004 occurred when logger was temporarily removed to download data

Rhodolith growth

In October 2003, ~72 rhodoliths were collected representing three size classes (small 4-6 cm, medium 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 surveyors tape. All were soaked for 24 h in an aerated container of seawater and the calcium carbonate binding vital stain Alizarin Red (0.3 g L^{-1} seawater; see Steller et al. 2007 for method). 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*. We marked the two 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) were recovered (~ half from each site) during March 2004, representing 5 months of winter growth. The second set (n = 33) was recovered from the sites after 12 months in October 2004 and represent 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-March 2004; n = 31 recovered) and the entire year (October 2003-October 2004; n = 33 recovered) to millimeters of growth month^{-1}. Given rhodolith staining and collection times (none were left in the field only March-October), it was not possible to explicitly 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.

Rhodolith 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 months 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 four ways: by dividing rhodolith size (in 2 cm intervals) by average, minimum, maximum, and incremental growth rates obtained from these 33 rhodoliths. For incremental growth rates, ages were determined by first calculating the average growth rates measured for individuals between 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. 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.

Rhodolith population size structure

Rhodolith population size structure was previously determined *in situ* (using SCUBA) at eight 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 over looked 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. 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. It should be noted that 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 therefore these individuals were easily spotted during the *in situ* quadrat counts and not double counted in core samples.

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 month 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 x 2 m^2 diagonal swath was measured. Data from all zones were combined and used to analyze which size rhodoliths were most affected by the hurricane.

Results

Rhodolith growth

Average monthly radial growth rates over the winter (0.04 ± 0.03 x 10^{-1} mm mo^{-1}) were significantly lower than those calculated for the entire year (0.06 ± 0.03 x 10^{-1} 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 *L. muelleri* grew almost twice as fast 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 three slow growing individuals (Fig. 1.2A) and differences were not statistically significant (Linear regression, $r^2 = 0.11$, $F_{1,31} = 3.83$, $p = 0.06$).

Rhodolith age estimates

Rhodolith ages (based on measured growth rates for the 33 rhodoliths in the field for one year) were estimated to range from ~29-119 yrs old, with the majority between 40-80 yrs old (Fig. 1.2B). Age projections which incorporated variation in growth rates according to size (incremental growth rates) showed that age estimates for individuals 4-14 cm were slightly greater than those calculated using average growth rates. However, the maximum predicted ages for the largest rhodoliths seen at Cabo Los Machos were similar for the two sets of age projections (113 vs 117 yrs old using average and incremental growth rates, respectively). Age projections using minimum and maximum growth rates put the largest individuals at ~300 and 70 yrs old, respectively (Fig. 1.3).

A

B
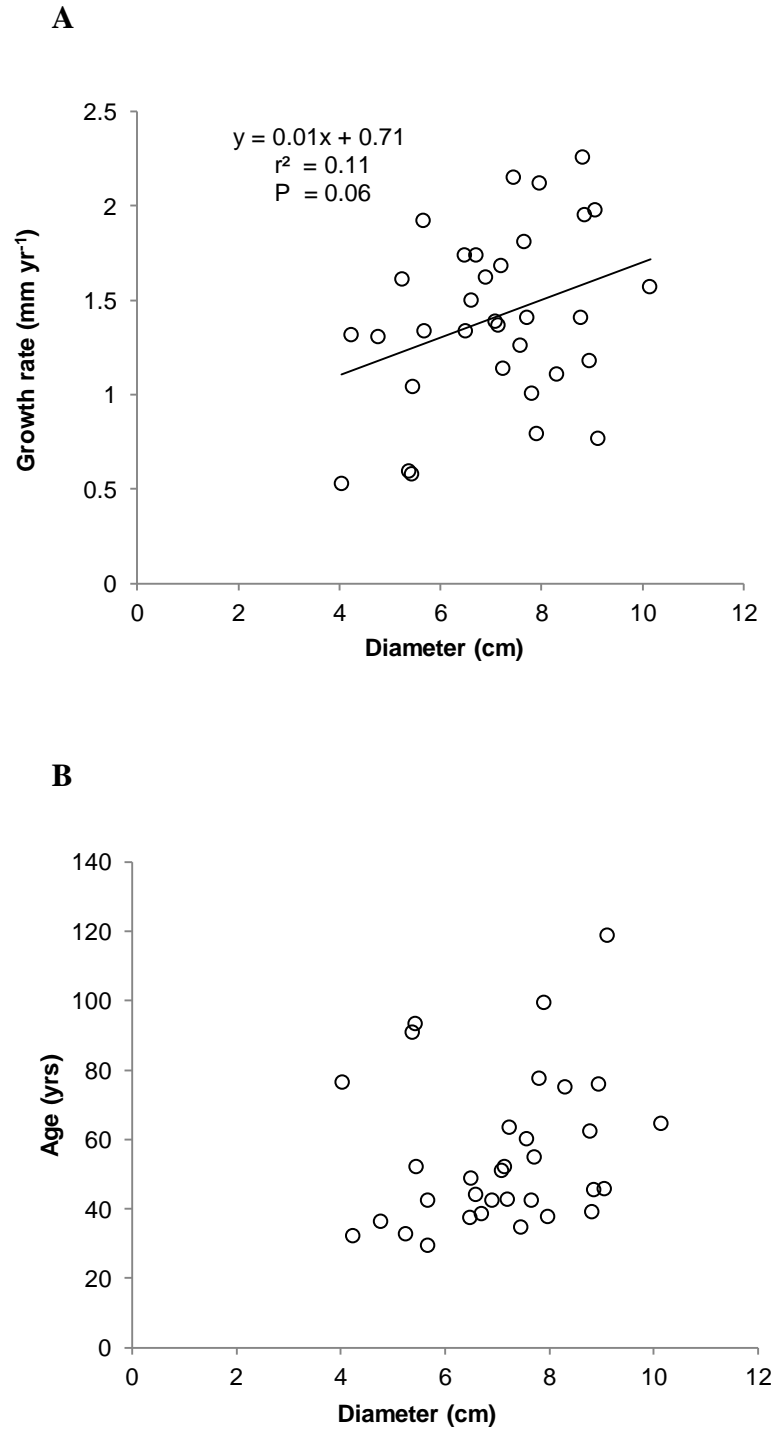
Fig. 1.2 *Lithothamnion muelleri* diameter vs. (A) annual growth rates (based on diametric extension); (B) age for stained rhodoliths growing in the field between October2003 and October 2004. (n = 33 for both)
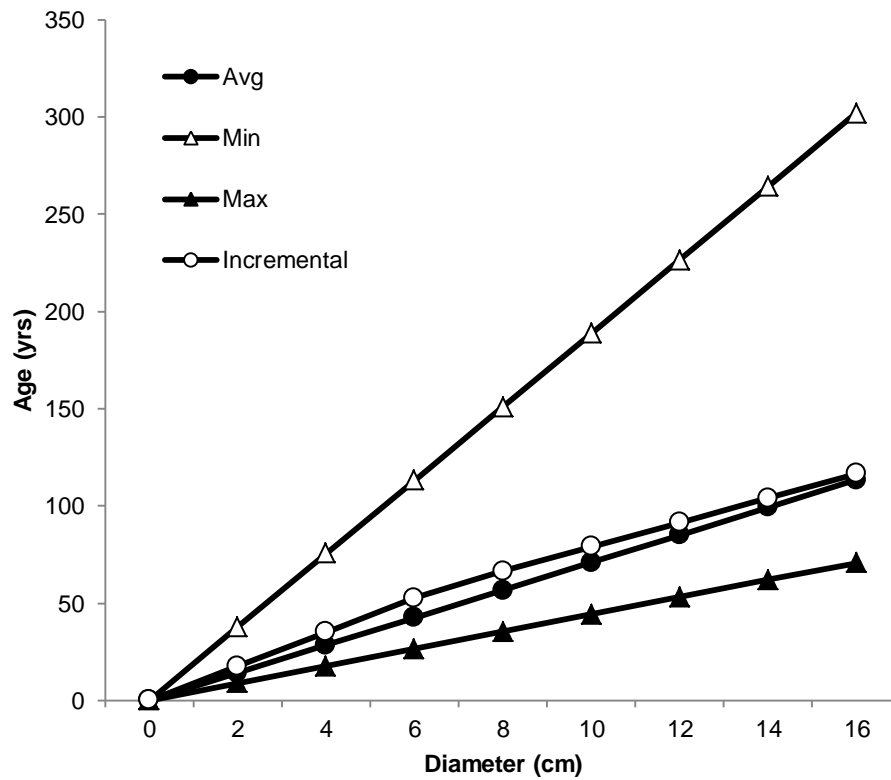
Fig. 1.3 Age projections for *Lithothamnion muelleri* 0−16 cm in diameter based on average (Avg), minimum (Min), máximum (Max), and incremental growth rates

Rhodolith population size structure

Combining the data from Foster et al. (2007) with our core data allowed size frequency determination 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 sampled population (Fig. 1.4).
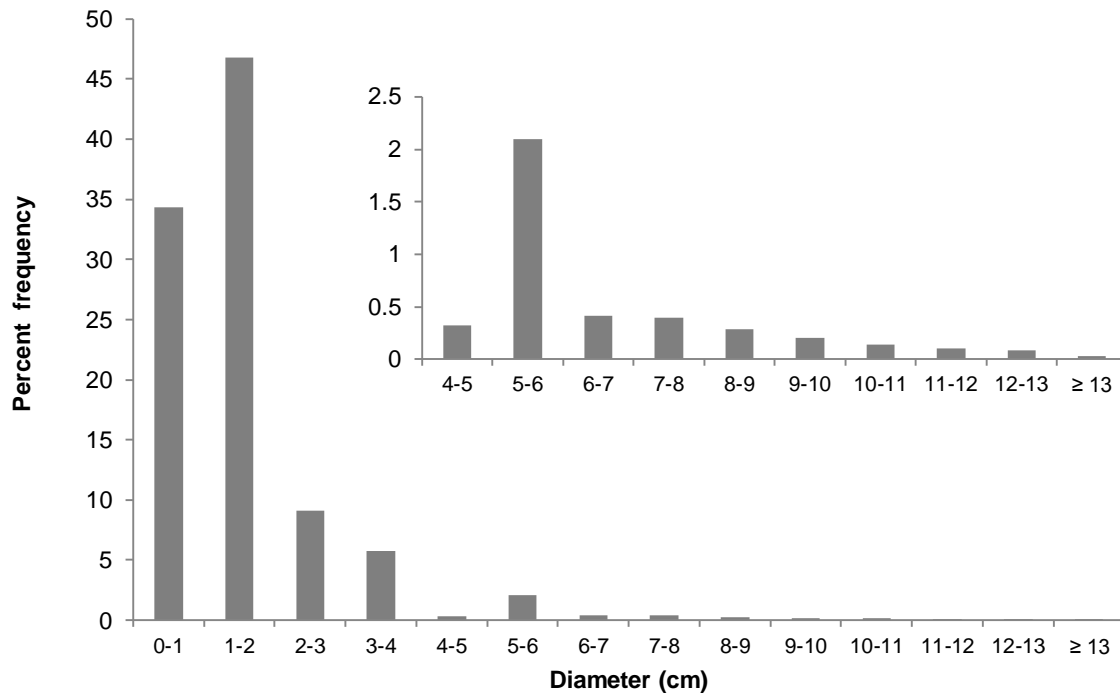
Fig. 1.4 Percent frequency of *Lithothamnion muelleri* (in cores and 3.14 m^2 quadrats) in March 2003 (n = 14, 489 rhodoliths). Inset graph shows percent frequency of rhodoliths between 4−13 cm diameter re-plotted on a more appropriate scale

Mortality

Rhodoliths from 1.2-13.7 cm diam. were transported on shore as a result of Hurricane Marty (Fig. 1.5A). Larger rhodoliths were disproportionately affected by the storm. Of the 149 individuals measured one month 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. 1.5B).
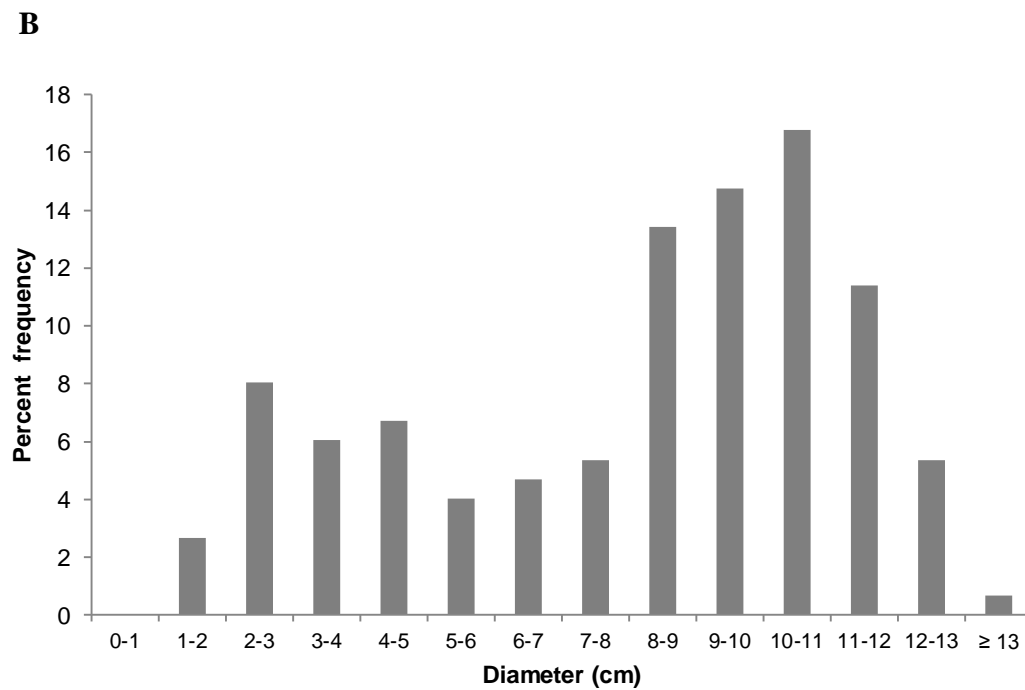
Fig. 1.5 *Lithothamnion muelleri*. (A) Dead, shore-cast rhodoliths (white bumpy spheres) in October 2003 after a tropical storm produced by Hurricane Marty (September 2003) passed over the study site (scale bar = ~10 cm); (B) size frequency distribution of shore-cast rhodoliths encountered along transects (n = 149)

Discussion

Our data show *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 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 four 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 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-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 S*argassum 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. 1.1) 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 (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 are, 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 are 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 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 less than 40 yrs old. While larger, older, individuals can range from 70-100+ yrs old (and may be as old as 300 yrs 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 this 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 growth in *L. muelleri* is continuous and that the largest individuals in their studies were 100+ yrs old. Like Rivera et al. (2004) we also found that maximum rhodolith size was 15-16 cm diameter 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 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 (Riosmena 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 suggest 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

breakdown into small pieces, form carbonate sand that can provide habitat for other organisms (Steller et al. 2003). Studies that have examined diversity of cryptofaunal 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 hour 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 this 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 months 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 opportunity to assess mortality and resilience of rhodoliths following a large scale disturbance. 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 and Peterson (1987) found that the brown alga *Hormosira banksii* could be dislodged during storms and cast on shore to die. The author's hypothesized *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 *Lithothamnion 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 years, five 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).

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Variación temporal dentro de las communidades asociadas a los mantos de rodolitos en Baja California Cur, méxico

Temporal variation within rhodolith assemblages of Baja California Sur, México[1]

Resumen: Las condiciones ambientales que cambian con la estacionaloda pueden causar variación temporal en las comunidades bentónicas marinas. Dicha variación temporal en los componentes asociados con los rodolitos (algas coralinas no geniculadas) no son bien conocidas, pero puede ser particularmente grandes, debido a la dependencia de rodolitos en las perturbaciones periódicas y en hábitats subtropicales, la gran variación estacional de la temperatura. Se evaluaron los cambios temporales (2013-2015) de tamaño de rodolitos y la cobertura, así como la variabilidad en las macroalgas e invertebrados asociados con un manto de rodolitos en el Golfo de California y dos en la Costa del Pacífico de Baja California Sur, México. Mientras el tamaño y la cobertura de los rodolitos estuvieron más constantes, los mantos en el Pacífico estuvieron más influenciados por las tormentas y las corrientes de marea, que cambiaron los mantos y redistribuyeron los sedimentos finos. Las macroalgas asociadas alcanzaron el pico de abundancia durante la primavera y el verano en la zona del Golfo, mientras que hubo una tendencia de mayor abundancia en invierno y primavera en el Pacífico, lo que sugiere que la temperatura puede influir en los componentes de todos los sitios. Los invertebrados no variaron estacionalmente, lo que sugiere el reclutamiento esporádico y cambios en la disponibilidad de alimento. El hábitat de los invertebrados puede influir más que los cambios de temperatura estacional. Se sugieren estudios del ciclo vital y datos ambientales detallados más completos para determinar detalladamente las relaciones entre los patrones biológicos observados en los mantos de rodolitos en todo el mundo con los factores ambientales asociados.

Palabras Clave: Variación Temporal · Comunidades de Rodolitos · Algas Marinas · Invertebrados Marinos · Bahías · Baja California Sur

Abstract: Seasonality in environmental conditions can cause temporal variation in marine benthic communities. Such temporal variation in assemblages of rhodolith (non-geniculate corallines) associates is not well understood, but may be particularly large given the dependence of rhodoliths on periodic disturbance and, in subtropical habitats, large seasonal temperature variation. We assessed temporal changes (2013-2015) in rhodolith size and cover, as well as variability in associated macroalgae and sessile and motile invertebrates in one rhodolith bed in the Gulf of California and two on the Pacific Coast of Baja California Sur, México. While rhodolith size/ cover were consistent, beds in the Pacific were more influenced by storms and tidal currents that shifted beds and redistributed fine sediments. Associated macroalgae reached peak abundance during spring and summer at the Gulf site, while there was a trend of greater abundance in winter and spring in the Pacific, suggesting temperature influences these assemblages at all sites. Invertebrate assemblages did not vary strictly seasonally suggesting episodic recruitment, and changes in food and habitat availability may influence invertebrates more than seasonal temperature changes. Detailed life history studies and more complete environmental data are needed to better connect relationships between biological patterns observed in rhodolith beds worldwide with associated environmental factors.

Key Words: Temporal Variation · Rhodolith Communities · Seaweeds · Marine Invertebrates · Bays · Baja California Sur

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Introduction

Temporal variation in marine benthic communities is often attributed to seasonal changes in environmental conditions. Marine plant-dominated communities, including seagrass meadows (Duarte 1989, Jankowska et al. 2014), kelp forests (Reed & Foster 1984) and those associated with rocky and sandy bottoms (Santelices 1977, McCourt 1984, Scrosati 2001) are no exception. Seasonal changes in temperature, light, nutrients, and/ or water motion can all contribute to periodic changes in abundance, biomass, growth or species richness. Declines or cyclic changes in primary producers can affect persistence and composition of associated algal and animal species (Klumpp et al. 1988, Kendrick & Burt 1997, Arkema et al. 2009). In addition to responding to seasonal changes in primary producers, macroinvertebrates themselves may be directly influenced by changes in temperature (Coma et al. 2000, Dijkstra et al. 2007, Ferretti et al. 2009), sediment deposition (Carballo 2006) and disturbances (Dayton 1971, Ebling et al. 1985).

Rhodoliths, free-living non-geniculate coralline algae, are considered foundation species supporting a wide range of associated organisms (Foster et al. 2001) which can respond to seasonal changes. Seasonality of associated macroalgae is widely reported in beds from Europe (Maggs 1983, Hily et al. 1992, Piazzi et al. 2004, Bárbara et al. 2004, Grall et al. 2006, Peña & Bárbara 2008, 2010), México (Steller et al. 2003, Foster et al. 2007), United States (Gabara 2014), Brazil (Amado-Filho et al. 2007, 2010, Pascelli et al. 2013) and New Zealand (Nelson et al. 2014). Fewer studies have focused on temporal changes in associated invertebrate communities (Steller et al. 2003, Foster et al. 2007, Riosmena-Rodríguez & Medina-Lopez 2011, Gabara 2014). In general, species diversity and/ or abundance are affected by temperature or seasonal oceanographic conditions, disturbances, as well as episodic recruitment and life history characteristics. Many existing floristic studies are largely descriptive and all of the above studies except Maggs (1983) and Peña & Bárbara (2008) are based on comparisons of two temporal extremes or lack seasonal replication. Quantitative, multi-year studies are required to better understand the role of seasonality vs. other factors influencing rhodolith bed structure.

This study describes rhodolith assemblages dominated by *Lithophyllum margaritae* and *Lithothamnion muelleri* in Baja California Sur, México. The temporal changes in rhodolith cover and average size were studied, as well as changes in associated macroalgae and invertebrates in one rhodolith bed in the Gulf of California and two on the Pacific Coast of the Baja peninsula from 2013-2015. Given the large seasonal variation in temperature on both sides of the peninsula, we hypothesized that all sites would exhibit strong seasonal changes in associated flora, while percent cover and average size of rhodoliths themselves would remain fairly constant given their slow growth rates and persistence at study sites. Additionally, we expected episodic increases and decreases of macrofaunal abundance and density, but that these fluctuations would not be strictly seasonal.

Materials and Methods

Study sites

Sampling was done ~ every 3 months Jan 2013-Apr 2015 at one site on the Gulf side of the Baja peninsula (Los Machos: not sampled Apr 2013) and two sites in Bahía Magdalena on the Pacific side of Baja California, México (Pedregoso and CFE: not sampled Apr 2014, Fig. 2.1). The Los Machos rhodolith bed is near the mouth of Bahía Concepción (~ 5 m depth) in the Gulf of California and is dominated by the rhodolith *Lithothamnion muelleri*. This area is a mixture of sand, boulders, rhodoliths, and the seasonally abundant fucoid *Sargassum horridum* (see Foster et al. 2007, McConnico et al. 2014 for details). Bahía Magdalena is a shallow lagoon composed of soft fine grain sediments (< 500 μm) and heavily influenced by tidal currents which can exceed 1 m s^{-1} at the mouth (Zaytsev et al. 2003). Pedregoso is in a mangrove lined channel subject to high current flow and has hard substratum (carbonate rock) in some regions, while CFE is in a scallop shaped embayment bordered by mangroves on its northern side and currents are reduced their relative to Pedregoso. Both sites are at ~ 0.5-2.5 m depth (depending on the tide) and dominated by *Lithophyllum margaritae* rhodoliths which host a community of sponges, tunicates and macroalgae on their surfaces. Rhodoliths in these beds were originally described and identified by Ávila & Riosmena-Rodríguez (2011). All sites were located using

GPS and/ or visual cues from land. Rhodolith beds were accessed by small boats and surveyed using SCUBA or snorkel depending on tidal height. Temperature was monitored hourly using Onset HOBO Pendant® data loggers (model UA-002-08; one per site) and monthly averages (+ SD) were determined for all sites.
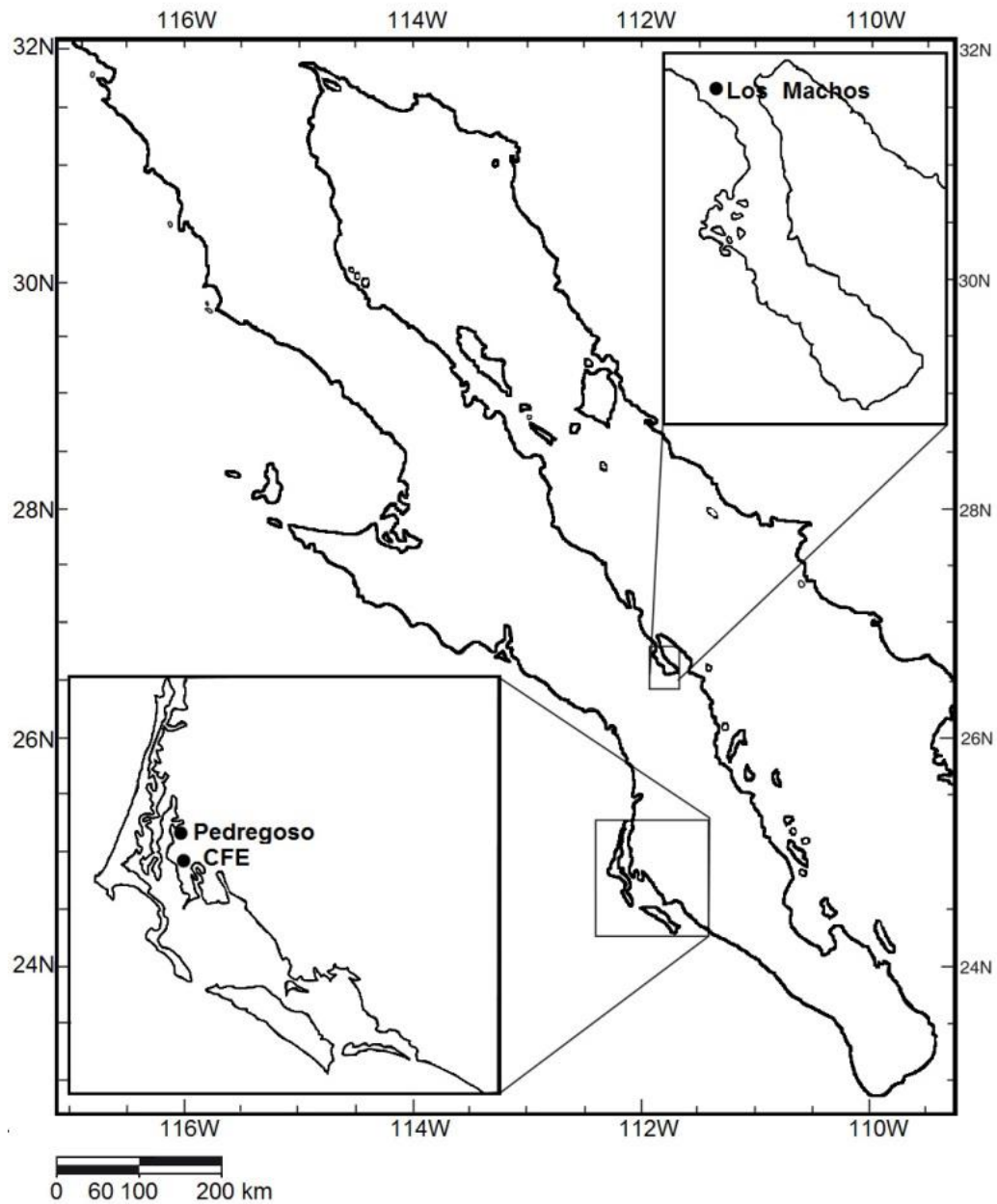
Fig. 2.1 Study sites in Gulf of California (inset at top right: Bahía Concepción) and on the Pacific Coast (inset at bottom left: Bahía Magdalena) of Baja California Sur, México. Scale at lower left corresponds to the larger map, not inset boxes

Rhodolith size

After surveying beds and locating the perimeter, one 30 m transect was placed in the middle of each bed. The longest diameter (diam.) of each rhodolith closest to the meter marks along the transect (n = 30 per site, per sampling time) was measured (to nearest mm) using calipers. Averages were calculated for each site as well as percent occurrence of small (< 4 or < 6 cm diam.), medium (4-8 or 6-8 cm diam.) and large (> 8 cm diam.) individuals. Ranges for the size categories were lower for the Pacific compared to the Gulf due to inherent differences in maximum size of the two species.

Percent cover

Percent cover of rhodoliths, other macroalgae, sessile/ colonial invertebrates and abiotic substrata was determined at all sites using the same 30 m transect described above. A random point quadrat (RPQ), consisting of a 1 m long bar with a loose string (1.20 m) attached to the ends like an archery bow, was placed at ten random locations along the transect. Five knots on the string were used to generate sampling points and the substratum or organism contacted below each knot was recorded for 10 random points per quadrat (5 points on each side of the bar; details in Foster 1975). Each point represented 10 % cover per quadrat and average cover for a site was based on 10 replicate quadrats. When layering occurred, all organisms or substrata beneath a point were recorded allowing for total cover to exceed 100 %. An exception to this occurred when rhodoliths were completely buried by a thick mat (>10 cm) of *Caulerpa sertularioides*. Under these circumstances, as when buried by sand, rhodolith cover could not be accurately determined.

Invertebrate density

Mobile/ solitary macroinvertebrate (molluscs, crustaceans, echinoderms, etc.) density was determined at the same time, at the same points, along transects used for percent cover estimates. Organisms typically occurred on sediments between adjacent rhodoliths or on top of rhodoliths. Cryptic organisms between rhodolith branches, under rhodoliths or hidden within a

quadrat were not quantified. All other obvious solitary macroinvertebrates (> 2 cm diam.) within ten 1 m^2 quadrats were identified and counted. Smaller (1-2 cm length), more numerous organisms (gastropods, hermit crabs, etc.) were sampled in a smaller quadrat (24 x 27 cm^2) and total counts scaled up to per 1 m^2. Site averages were calculated from the 10 replicate quadrats. When field identification of specimens was not possible, organisms were collected or photos were taken and used to identify organisms to the lowest possible taxon.

Data analysis

Data comparisons were made between sites within Bahía Magdalena, but given obvious differences in dominant species (*Sargassum horridum* only at Gulf site and distinct rhodolith species in the two regions), as well as variation in habitat and water motion between the Gulf and Pacific sites, the site in the Gulf was analyzed separately. With the exception of rhodoliths and the alga *S. horridum*, most organisms were lumped into broader categories (macroalgae, sessile invertebrates, crustaceans, molluscs, etc.) and their average percent cover or density plotted and examined for trends with time. Separate 1-way ANOVA's were used to evaluate significant differences in percent cover of rhodolith, sediment and bare rock at Los Machos. Separate 2-factor ANOVA's were used to evaluate differences in percent cover of rhodoliths and sediment between the sites Pedregoso and CFE. Data met assumptions of homogeneity of variances and were normally distributed.

Multivariate analyses were used to evaluate temporal and/ or spatial variation in rhodolith associated algal and invertebrate assemblages. For macroalgae, average cover of each taxon from each sampling month was square root transformed and used to create Bray-Curtis similarity matrices. The similarity matrix for Los Machos was used to assess variation among sampling seasons (replicate months), and the matrix for Bahía Magdalena was used to compare sampling seasons as well as sites (Pedregoso & CFE). Non-metric multidimensional scaling (nMDS) ordinations were used to illustrate temporal and/ or spatial variation and PERMANOVA analyses (999 permutations) were used to test the significance of the variation. If significant differences were present, SIMPER analyses were done to determine which taxa contributed to dissimilarity (Anderson et al. 2008). Bray-Curtis similarity matrices were also

generated based on mobile/ solitary invertebrate density (Gulf and Pacific sites analyzed separately). An additional Bray-Curtis matrix was created based on percent cover of sessile/ colonial invertebrates from Pacific sites. Due to the paucity of such data from Los Machos no formal analyses were done on these data. The same analytical procedure described for algal percent cover was applied to all other resemblance matrices. Multivariate data were analyzed using the software PRIMER-E (Clarke & Gorley 2006).

Results

Temperature

All sites experienced large seasonal and tidal driven temperature fluctuations during the year. Minimum average temperatures occurred in Jan and maximum in Aug. Average monthly water temperature Jan-Mar was cooler in the Gulf, but was ≥ 29 ℃ Jul–Sep 2014 at all three sites (Fig. 2.2). Tidal flushing at Pacific sites can produce temperature swings of 2-6 ℃ and may account for 3-5 ℃ temperature fluctuations at the mouth of the Gulf site May-Oct 2014.
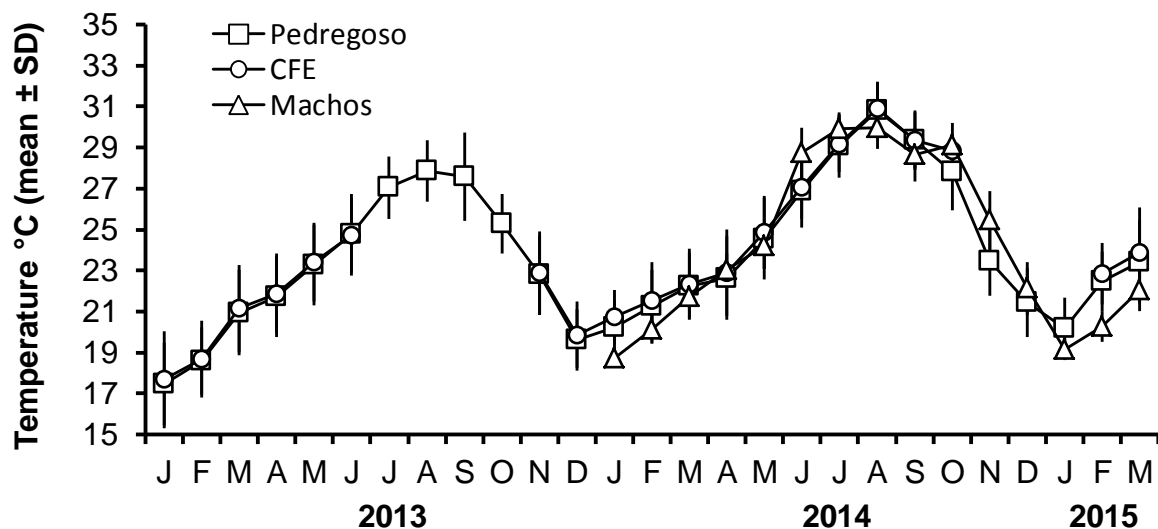
Fig. 2.2 Monthly average bottom temperature at Los Machos (~5 m depth) and Pedregoso & CFE (~0.5-2.5 m depth) during 2013-2015. No 2013 data for Los Machos and data gaps at CFE between Jul-Oct 2013 and Oct 2014-Jan 2015 were due to a logger malfunction

Rhodolith size

Gulf of California

Lithothamnion muelleri measured at Los Machos ranged in diam. between 3.5-15.5 cm. Average rhodolith diam. varied by < 2 cm during the study (Table 2.1). The majority of rhodoliths were medium to large; depending on sampling date 77-97 % of measured rhodoliths were > 6 cm diam. and remaining individuals < 6 cm diam.

Table 2.1 Minimum and maximum average rhodolith diameter (cm ± SE) at study sites 2013-2015. Sampling dates associated with measurements noted in parentheses

Diameter	Los Machos	Pedregoso	CFE
Minimum	7.66 ± 0.50 (Oct 2013)	4.78 ± 0.40 (Jan 2014)	5.01 ± 0.35 (Apr 2015)
Maximum	9.06 ± 0.43 (Jan 2013)	7.50 ± 0.25 (Jun 2013)	6.83 ± 0.27 (Jun 2013)

Pacific Coast of Baja California

Lithophyllum margaritae measured from Bahía Magdalena were between 2-14 cm diam. at Pedregoso and 2-12 cm diam. at CFE. Minimum and maximum average rhodolith diam. was similar for both sites (Table 2.1). Populations at both sites were dominated by individuals 4-8 cm diam.; accounting for 50-80 % of rhodoliths surveyed at Pedregoso and 63-93 % of rhodoliths at CFE depending on sampling date. Small individuals (< 4 cm diam.) accounted for 0-43 % of the population at Pedregoso and 0-30 % at CFE. Those > 8 cm diam. comprised 7-30 % of the sampled population at Pedregoso and 7-23 % at CFE.

Percent cover

Gulf of California

Cover of the rhodolith *Lithothamnion muelleri* at Los Machos ranged from 10-15 % and showed no significant intra- or inter-annual variation (Table 2.2, Fig. 2.3). Dead rhodoliths were seldom encountered (2 % cover in Jun 2014, 0 % in all other months). Bare rock varied significantly throughout the year with greatest cover seen in Oct and Jan sampling dates (Table 2.2, Fig. 2.3). Sediment cover also varied during the study (Table 2.2, Fig. 2.3) however, Tukey HSD Test showed that only cover in Oct 2013 was significantly greater than in Jun 2014 and Apr 2015.

Table 2.2 One-Way ANOVA (comparing sampling dates) for percent cover of substrata at Los Machos (Gulf of California)

Variable	Source	df	MS	F	*p* value
Rhodolith	Date	8	0.20	0.24	0.983
	Error	81	0.85		
Sediment	Date	8	11.99	2.94	0.006
	Error	81	4.08		
Bare Rock	Date	8	3.19	3.38	0.002
	Error	81	0.94		

Including *L. muelleri*, 30 algal taxa were observed at Los Machos (Table 2.3). While some encrusting algal species were found in all sampling seasons, *Sargassum horridum* was the only foliose alga present during all sampling periods. The highest percent cover of *S. horridum* was observed in Apr 2014 & 2015 and the lowest in Oct or Jan (Fig. 2.3). In 2013 *S. horridum* cover was greatest in June. Previous observations at this site suggest the true peak likely occurred in Apr 2013 when no data were taken. Percent cover of remaining macroalgal taxa increased during much of the year and declined between Jun/ Jul and Oct surveys (Fig. 2.3). Fewer algal taxa were recorded after summer in Oct 2013/ 2014 (6/8) compared to cooler months between Jan-Jun (12-15; Table 2.3).
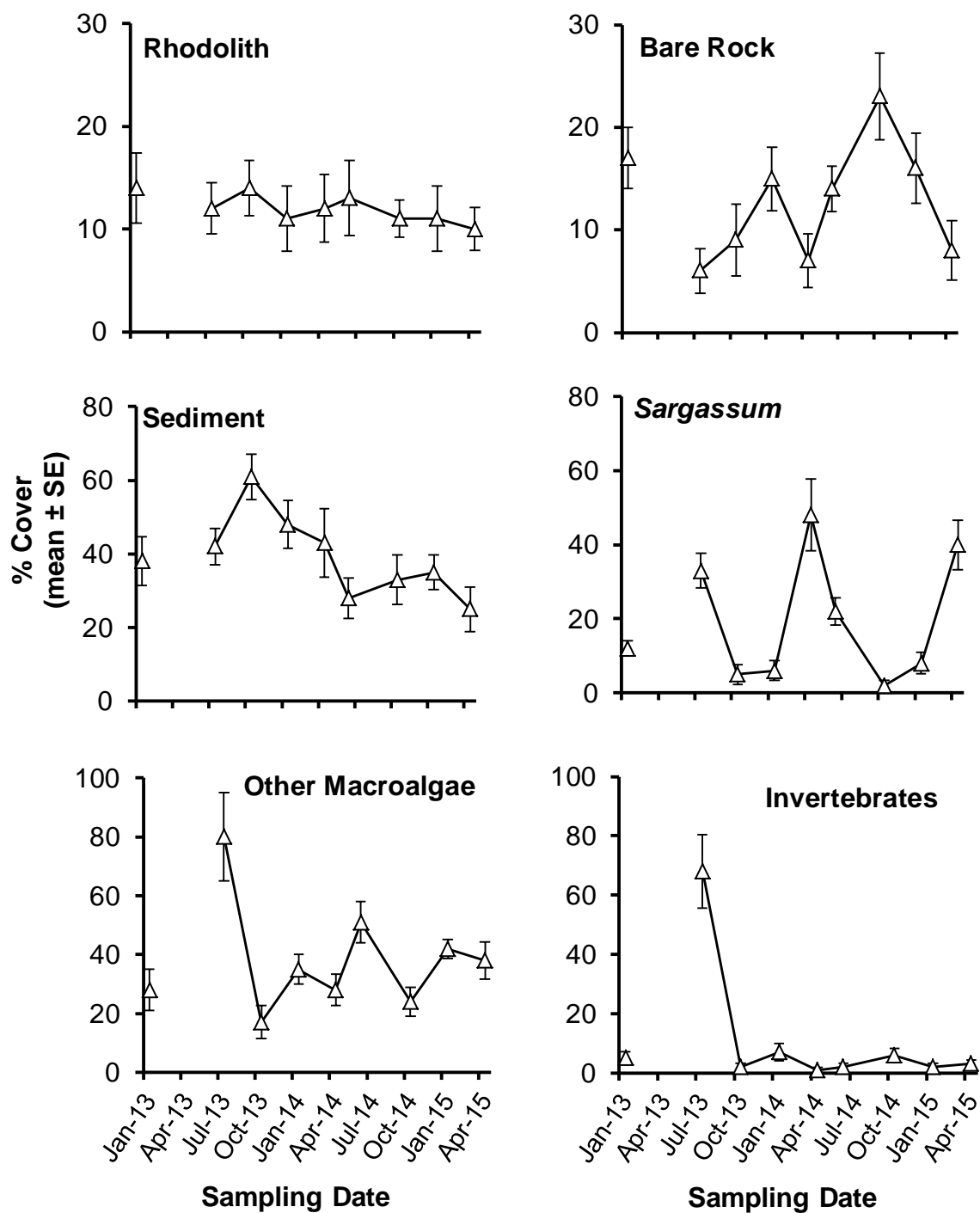
Fig. 2.3 Percent cover of dominant substrata at Los Machos (Gulf of California) 2013-2015. Invertebrates refers to sessile/ colonial taxa

Table 2.3 Algal and sessile/ colonial invertebrate taxa encountered ($\geq$ 10 % cover quadrat^{-1}) at Los Machos (Gulf of California) 2013-2015. No data (-) Apr 2013

TAXA	2013				2014				2015	
Rhodophyta	JAN	APR	JUN/JUL	OCT	JAN	APR	JUN/JUL	OCT	JAN	APR
Amphiroa valonioides	x	-	x	x	x	x	x		x	x
Antithamnion sp.		-							x	x
Callithamnion sp.		-	x							x
Ceramium sp.	x	-	x		x	x	x			
Champia parvula	x	-								
Dasya sinicola		-	x		x	x	x	x	x	
Halymenia sp.		-			x					
Helminthocladia australis		-				x				
Hypnea cervicornis		-								x
Jania sp.	x	-	x		x		x			x
Laurencia papillosa		-							x	
Lithothamnion muelleri	x	-	x	x	x	x	x	x	x	x
Myriogramme caespitosa	x	-							x	
Non-geniculate Coralline crust	x	-	x	x	x	x	x	x	x	x
Peyssonnelia sp.	x	-	x	x	x	x	x	x	x	x
Polysiphonia sp.		-	x		x	x	x		x	
Rhodymenia sp.		-							x	
Rosenvingea intricata		-				x				x
Scinaia latifrons		-			x					
Spyridia filamentosa		-					x			x
Heterokontophyta										
Dictyota crenulata		-	x				x	x	x	
Dictyota flabellata	x	-	x							
Dictyota vivesii	x	-								
Padina durvillei		-	x			x	x		x	x
Ralfsia sp.	x	-			x	x		x		
Sargassum horridum	x	-	x	x	x	x	x	x	x	x
Chlorophyta										
Caulerpa sertularioides	x	-	x	x	x		x			
Cladophora microcladioides		-	x				x		x	
Codium simulans		-			x					x
Ulva sp.		-			x			x		

Table 2.3 Continued Algal and sessile/ colonial invertebrate taxa encountered ($\geq$ 10 % cover quadrat^{-1}) at Los Machos (Gulf of California) 2013-2015. No data (-) Apr 2013

TAXA	2013				2014				2015	
Sessile/ Colonial Invertebrates	**JAN**	**APR**	**JUN/JUL**	**OCT**	**JAN**	**APR**	**JUN/JUL**	**OCT**	**JAN**	**APR**
Aglaophenia sp.	x	-			x					
Aplysina sp.		-						x		
Ascidiacea		-	x							
Eugorgia aurantiaca		-		x						
Phialoba steinbecki		-	x							
Plumularia sp.		-	x		x					
Porites panamensis	x	-	x	x	x	x	x	x	x	x

The nMDS ordination illustrated that algal assemblages associated with rhodolith beds varied seasonally (Fig. 2.4) and the PERMANOVA verified these differences were significant (Pseudo $f_{3,8}$ = 2.15, P = 0.004). SIMPER analysis revealed the average dissimilarity between Oct and Jun/ Jul sampling months was 57.3 %, with the taxa *S. horridum*, *Polysiphonia* sp., *Ceramium* sp. and *Dasya sinicola* (present in Jun/ Jul) accounting for more than half of this variation. Average dissimilarity between Oct and Apr was 55.2 %, with the taxa *S. horridum*, *Padina durvillei*, *Rosenvingea intricata*, *Dasya sinicola* and *Ralfsia* sp. (more abundant in Apr) accounting for more than half of this variation. Comparisons between Oct and Jan were only 46.3 % dissimilar and Jan and Jun/ Jul 45.7 % dissimilar, with several species present in low abundance contributing to this increased overlap between months (seasons).

Fig. 2.4 Non-metric multidimensional scaling ordinations (based on Bray-Curtis similarity matrix) of the macroalgal (all taxa except rhodoliths) and invertebrate assemblage associated with the Los Machos rhodolith bed (Gulf of California). Symbols represent site averages for replicate months (seasons) 2013-2015

Seven sessile/ colonial invertebrate taxa were identified (Table 2.3) and their cover was generally low (Fig. 2.3), except in Jul 2013 when the hydroid *Plumularia* sp. (an epiphyte on *S. horridum*) accounted for 63 % cover, only to fall to 0 % by Oct 2013. Of the remaining sessile invertebrates, the coral *Porites panamensis* was the only species present year round and accounted for 1-4 % cover. All other observed taxa (Table 2.3) accounted for 0-2 % cover depending on sampling date. Distinct seasonal patterns were not observed.

Pacific Coast of Baja California

In Bahía Magdalena *Lithophyllum margaritae* rhodolith cover ranged from ~ 40-64 % at CFE during 2013-2015 and was significantly greater than at Pedregoso (~ 41-57 %; Table 2.4, Fig. 2.5). Temporal variation in rhodolith cover was not significant (Table 2.4, Fig. 2.5). Dead rhodolith cover was generally ≤ 5 %, except in Oct 2014 and Apr 2015 at Pedregoso and in Jan and Apr 2015 at CFE (Fig. 2.5).

Table 2.4 Fixed Factor Two-Way ANOVA (comparing sites and sampling dates) for percent cover of substrata at CFE and Pedregoso (Pacific Coast of Baja) 2013-2015

Variable	Source	df	MS	F	*p* value
Rhodolith	Date	8	4.63	1.97	0.053
	Site	1	17.42	7.42	0.007
	Date x Site	8	3.51	1.49	0.163
	Error	162	2.35		
Sediment	Date	8	2.90	1.19	0.307
	Site	1	3.20	1.32	0.253
	Date x Site	8	3.23	1.33	0.234
	Error	162	2.43		
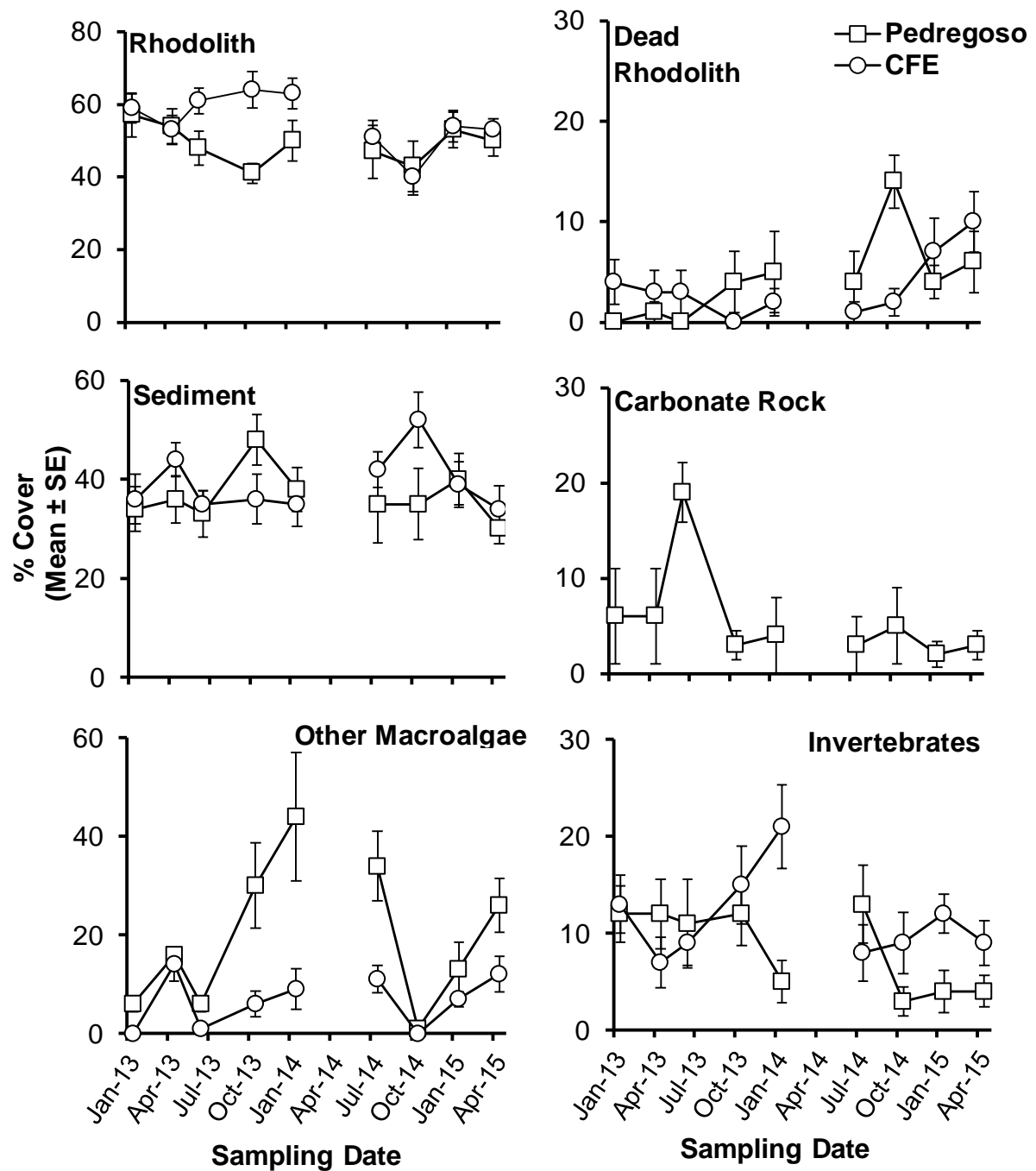
Fig. 2.5 Percent cover of dominant substrata at CFE and Pedregoso (Pacific Coast of Baja California) during 2013-2015. Invertebrates refers to sessile/ colonial taxa

Sediment cover ranged 30-48 % at Pedregoso and 34-52 % at CFE with no significant differences between sites or among sampling dates (Table 2.4, Fig. 2.5). Sediment cover did increase at Pedregoso in Oct 2013 and at CFE in Apr 2013 and Oct 2014. There was a significant inverse relationship between sediment and rhodolith cover at CFE (Regression: $R^2 =$ 0.74; ANOVA: $F_{1,8} = 19.93$, $P = 0.003$). The relationship was not significant at Pedregoso (Regression: $R^2 = 0.18$; ANOVA: $F_{1,8} = 1.55$, $P = 0.25$). Carbonate rock was present only at Pedregoso and varied little throughout the study, except in Jun 2013 (Fig. 2.5) when rhodoliths shifted and the bed center moved closer to this substratum.

Including *L. margaritae*, 14 macroalgal taxa were encountered at sites in Bahía Magdalena (Pedregoso: 12 taxa and CFE: 10 taxa; Table 2.5). Rhodolith associated macroalgae were generally more abundant in Jan and Apr and then declined in Jun/ Jul or Oct. All observed macroalgae typically recruited to rhodolith surfaces and were more abundant at Pedregoso than CFE (Fig. 2.5). Large changes in macroalgal cover between Jan and Apr 2013 were driven by a bloom of a brown filamentous alga (*Hincksia* cf. *mitchelliae*) and those between Oct 2013 and Jul 2014 by a bloom of *Caulerpa sertularioides* and *Callithamnion* cf. *acutum*. Together, remaining algal taxa (Table 2.5) accounted for 0-11 % cover depending on sampling date. *Amphiroa valonioides* was the only rhodolith associated alga consistently present throughout the study and others like *C. sertularioides*, *C.* cf *acutum*, *Cladophoropsis gracillima* and *Colpomenia* spp. were absent then appeared, and persisted for months. Increased algal diversity was not associated with a particular sampling month; the number of species found ranged from 2-7 in Jan, 3-9 in Apr, 3-7 in Jun/ Jul and in Oct 2-8 (Table 2.5). The nMDS ordination showed overlap between algal assemblages from Pedregoso and CFE and revealed no distinct seasonal patterns (Fig. 2.6). The PERMANOVA analysis for Site x Month further indicated no significant differences for either factor (Table 2.6).

Table 2.5 Algal and sessile/ colonial invertebrate taxa encountered ($\geq$ 10 % cover quadrat^{-1}) at CFE (c) and Pedregoso (p) on the Pacific Coast of Baja 2013-2015. No data (-) Apr 2014

TAXA	2013				2014				2015	
Rhodophyta	JAN	APR	JUN/JUL	OCT	JAN	APR	JUN/JUL	OCT	JAN	APR
Amphiroa valonioides	p	p	p, c	p, c	p, c	-	p, c		p	p, c
Callithamnion cf. *acutum*				p, c	p, c	-			p	
Gracilaria sp.				p		-				
Lithophyllum margaritae	p, c	p, c	p, c	p, c	p, c	-	p, c	p, c	p, c	p, c
Spyridia filamentosa						-				c
Heterokontophyta						-				
Colpomenia sinuosa						-			p, c	p
Colpomenia tuberculata						-			p, c	p
Dictyota flabellata				p		-		p		p
Hincksia cf. *mitchelliae*		p, c	p		p, c	-	c			c
Padina durvillei						-	p		p	p
Chlorophyta										
Bryopsis pennata				c		-				
Caulerpa sertularioides				p	p	-	p, c		p, c	p, c
Cladophora microcladioides						-	p, c			
Cladophoropsis gracillima				p		-	p			
						-				
Sessile/ Colonial Invertebrates										
Aptasia sp.	p, c	p	p		p, c	-	p, c			
Didemnum sp. 1			p			-				
Didemnum sp. 2				c		-				
Eudistoma sp.	p, c	p, c	p	p, c		-				
Halichondria cf. *semitubulosa*		p, c	c	p, c	p, c	-		p, c	c	c
Halichondria panicea					c	-			c	c
Mycale cecilia				p		-				
Porifera (unidentified sp.)						-	c	c	c	p, c
Scopalina sp.	p, c	p, c	p, c	p, c	p, c	-	p, c	p, c	p, c	p, c
Trididemnum sp.	p	p	c	p, c	c	-	c			

Macroalgae
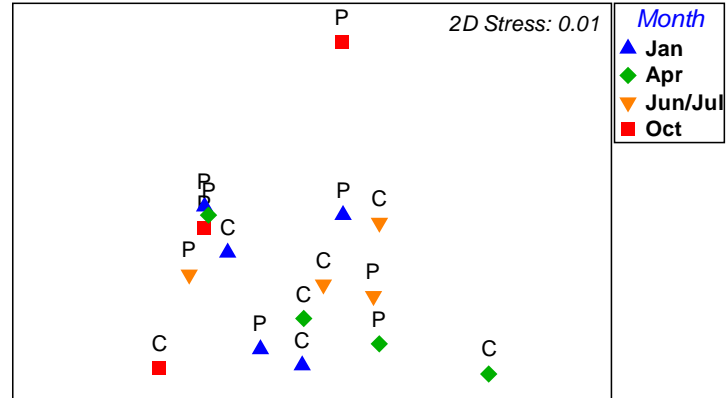
Sessile/ Colonial Invertebrates
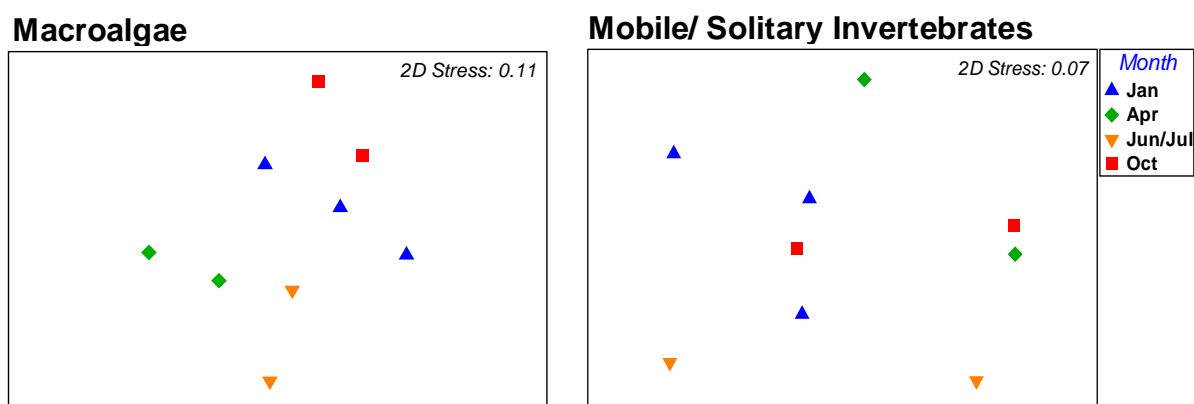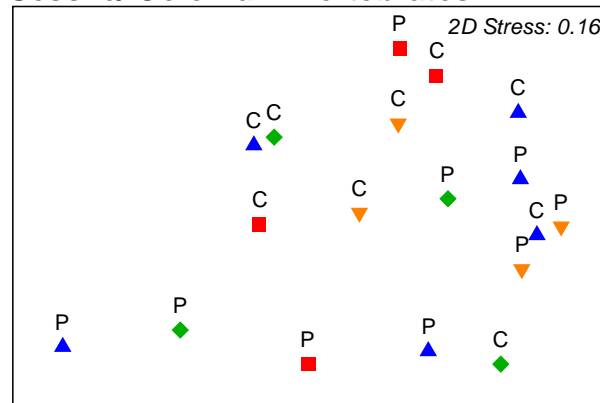

Mobile/ Solitary Invertebrates
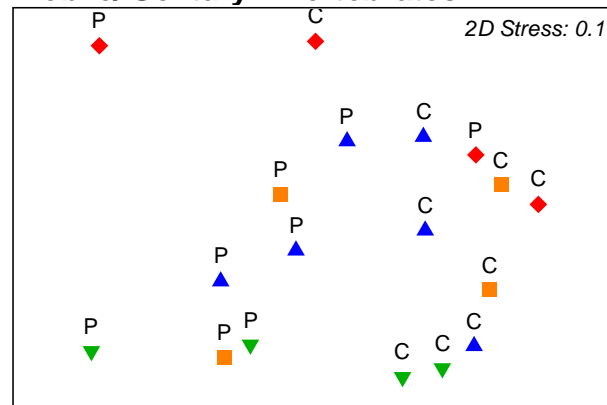
Fig. 2.6 Non-metric multidimensional scaling (nMDS) ordinations (based on Bray-Curtis similarity matrix) for macroalgal (all taxa except rhodoliths) and invertebrate assemblages associated with rhodolith beds at Bahía Magdalena (Pacific Coast of Baja). Symbols represent site averages for replicate months (seasons) 2013-2015; the letters C & P represent the sites CFE and Pedregoso, respectively. Note: in the sessile/ colonial invertebrate nMDS ordination two outlying months at CFE (Jan and Oct) are not shown in order to better visualize relationships among other sampling dates. These outliers were, however, included in the analysis

64

Table 2.6 PERMANOVA analyses between site (CFE and Pedregoso) and among months (sampling seasons) for algal and invertebrate assemblages at Bahía Magdalena 2013-2015

PERMANOVA				
Macroalgae	**df**	**MS**	**Pseudo-F**	**P (perm)**
Site	1	1	1.00	0.4
Month	3	3528.00	1.00	0.4
Site x Month	3	1437.80	0.40	1
Residual	10	3450.80		
Sessile/ Colonial Invertebrates	**df**	**MS**	**Pseudo-F**	**P (perm)**
Site	1	1049.30	0.80	0.5
Month	3	1043.30	0.80	0.7
Site x Month	3	707.70	0.50	0.9
Residual	10	1385.70		
Mobile/ Solitary Invertebrates	**df**	**MS**	**Pseudo-F**	**P (perm)**
Site	1	4048.70	5.05	0.005
Month	3	1273.30	1.59	0.113
Site x Month	3	465.66	0.58	0.894
Residual	10	801.37		

Ten sessile/ colonial invertebrate taxa (sponges, tunicates and one anemone) were found at sites in Bahía Magdalena, six of which occurred at both Pedregoso and CFE (Table 2.5). Of these taxa the sponges *Scopalina* sp. and *Halichondria* cf. *semitubulosa,* and tunicate *Trididemnum* sp. were the most common taxa (Table 2.5). Cover was variable between sites and showed no consistent seasonal trend. Invertebrate cover at CFE increased during much of 2013, peaked in Jan 2014 then declined and remained stable Jul 2014-Apr 2015, while cover at Pedregoso was consistent throughout 2013 and peaked in Jul 2014 and remained low thru Apr 2015. Invertebrate cover was often greater at CFE than Pedregoso Oct 2013-Apr 2015 (Fig. 2.5). Distinct seasonal variation of the entire invertebrate assemblages or differences between CFE and Pedregoso could not be identified in the nMDS ordination (Fig. 2.6) and the PERMANOVA showed no significant differences in either factor (Table 2.6).

Invertebrate abundance

Gulf of California

Nineteen mobile/ solitary invertebrate taxa were present in quadrats at Los Machos of which crustaceans, molluscs and echinoderms were the most common (Table 2.7). Crustaceans and molluscs exhibited intra- and/ or inter-annual variation in density, while echinoderms varied little over the study (Fig. 2.7). None of the observed variation appeared seasonal, although there was a trend of increasing arthropod density 2013-2015. The burrowing decapod *Neaxius vivesi* and bivalve *Chione californiensis* were the only two species consistently present and accounted for most of the variation in crustaceans and molluscs, respectively. Temporal variation in echinoderm density was driven by a variety of sea stars, urchins and brittle stars (Table 2.7). The average density of invertebrate taxa not reported graphically (e.g. Annelida, Platyhelminthes, Urochordata) ranged from 0-0.9 ind. m^{-2} during the study. The greatest number of taxa were present in Jan (5-9) compared to 4-6 in other sampling months. Of these species four could be found in both Oct and Jan (Table 2.7). The nMDS ordination showed overlap among sampling months for the mobile/solitary invertebrate assemblage (Fig. 2.4) and no significant differences were detected in the PERMANOVA analysis (Pseudo $f_{3,8} = 0.9$, P = 0.6), indicating no distinct seasonal variability in the invertebrate assemblage at this site.

Table 2.7 Mobile/ solitary invertebrate taxa encountered in 1m^2 quadrats at Los Machos (Gulf of California) 2013-2015. No data (-) Apr 2013

TAXA	2013				2014				2015	
Annelida	JAN	APR	JUN/JUL	OCT	JAN	APR	JUN/JUL	OCT	JAN	APR
Bispira rugosa monterea		-				x	x	x		
Arthropoda										
Anomura	x	-		x	x				x	x
Cancer setosus	x	-								
Decapoda		-					x			
Neaxius vivesi	x	-	x	x	x	x	x	x	x	x
Echinodermata										
Arbacia incisa		-								x
Echinaster tenuispina	x	-					x			
Eucidaris thouarsii		-				x				
Ophiactis sp.		-					x		x	
Phataria unifascialis	x	-	x	x					x	x
Mollusca										
Chione californiensis	x	-	x	x	x	x	x	x	x	
Gastropoda	x	-	x						x	
Megapitaria squalida		-			x					
Muricidae	x	-								
Pinctada mazatlantica		-						x		x
Pinna rugosa		-						x		
Tridachiella diomedea	x	-							x	
Platyhelminthes										
Pseudoceros bajae		-				x				
Urochordata										
Purple solitary tunicate		-	x		x					
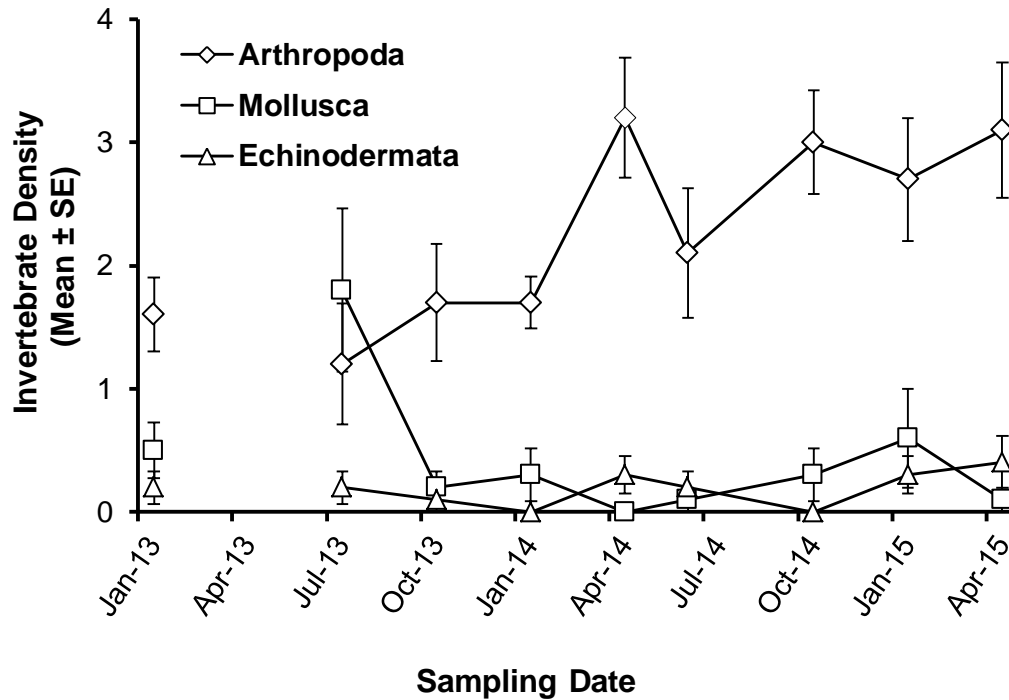
Fig. 2.7 Mobile/ solitary invertebrate density (individuals m^{-2}) at Los Machos (Gulf of California) 2013-2015

Pacific Coast of Baja California

Eighteen mobile/ solitary invertebrate taxa were observed in quadrats at Pedregoso and CFE, with many occurring at both sites (Table 2.8). Molluscs were the most common group (Table 2.8) and were generally more numerous at CFE than Pedregoso. Changes in their density were largely caused by two herbivorous gastropods (*Cerithium stercusmuscarum* and *Turbo funiculosus*). Maximum density occurred in Jun 2013 and Jul 2014 at CFE with declines by Oct 2013 and 2014. Density was less variable at Pedregoso except for a peak in Oct 2013 (Fig. 2.8). Crustaceans were the second most abundant invertebrate group (Fig. 2.8), of which only Anomura (hermit crabs) were consistently observed (Table 2.8). Their density peaked in Apr 2013 at CFE and in Jun 2013 at Pedregoso, with the lowest abundance at both sites occurring in Oct 2013. This increase in the first part of the year and decline by summers end was possibly repeated in 2014 and 2015, but data gaps are present (Fig. 2.8). Echinoderm density was greater and fluctuated more throughout the study at Pedregoso than at CFE (Fig. 2.8). Echinoderm temporal variability at Pedregoso was caused by increased abundance of *Ophiactis* spp. in Apr

68

2013, Jun 2013 and Jul 2014, which were less common or absent in Jan and Oct sampling dates. The seastar *Echinaster tenuispina* was present in low abundance at both sites and explains all of the variation in echinoderm density at CFE. The number of invertebrate taxa ranged from 4-8 in Jan, 6-8 in Apr, 5-9 in Jun/ Jul and 6-8 in Oct.

Table 2.8 Mobile/ solitary invertebrate taxa encountered in $1m^2$ quadrats at CFE (c) and Pedregoso (p) on the Pacific Coast of Baja 2013-2015. No data (-) Apr 2014

TAXA	2013				2014				2015	
Annelida	JAN	APR	JUN/JUL	OCT	JAN	APR	JUN/JUL	OCT	JAN	APR
Bispira rugosa monterea	p			p, c		-				p
Arthropoda										
Anomura	p, c	p, c	p, c	p, c	p, c	-	p, c	p, c	p, c	p, c
Iliacantha sp.	c		c			-				
Penaeidae						-		P		
Stomatopoda						-				p
Echinodermata										
Echinaster tenuispina	c	c		C	p	-			p	c
Ophiactis spp.	p	p	p		p	-	p			
Mollusca										
Aplysia californica					c	-				
Cerithium stercusmuscarum	p, c	p, c	p, c	p, c	p, c	-	p, c	p, c	p, c	p, c
Chione sp.		p, c		P		-				
Diodora inaequalis				P		-				
Megastraea sp.			c			-		C		
Octopus hubbsorum			c			-				
Oxynoe sp.			c		p	-		P		
Theodoxus sp.			c	c		-	c		c	p, c
Trivia sp.	c					-				
Turbo funiculosus	p, c	p, c	p, c	p		-	p, c	C	p, c	p, c
Turritella sp.						-				c

69
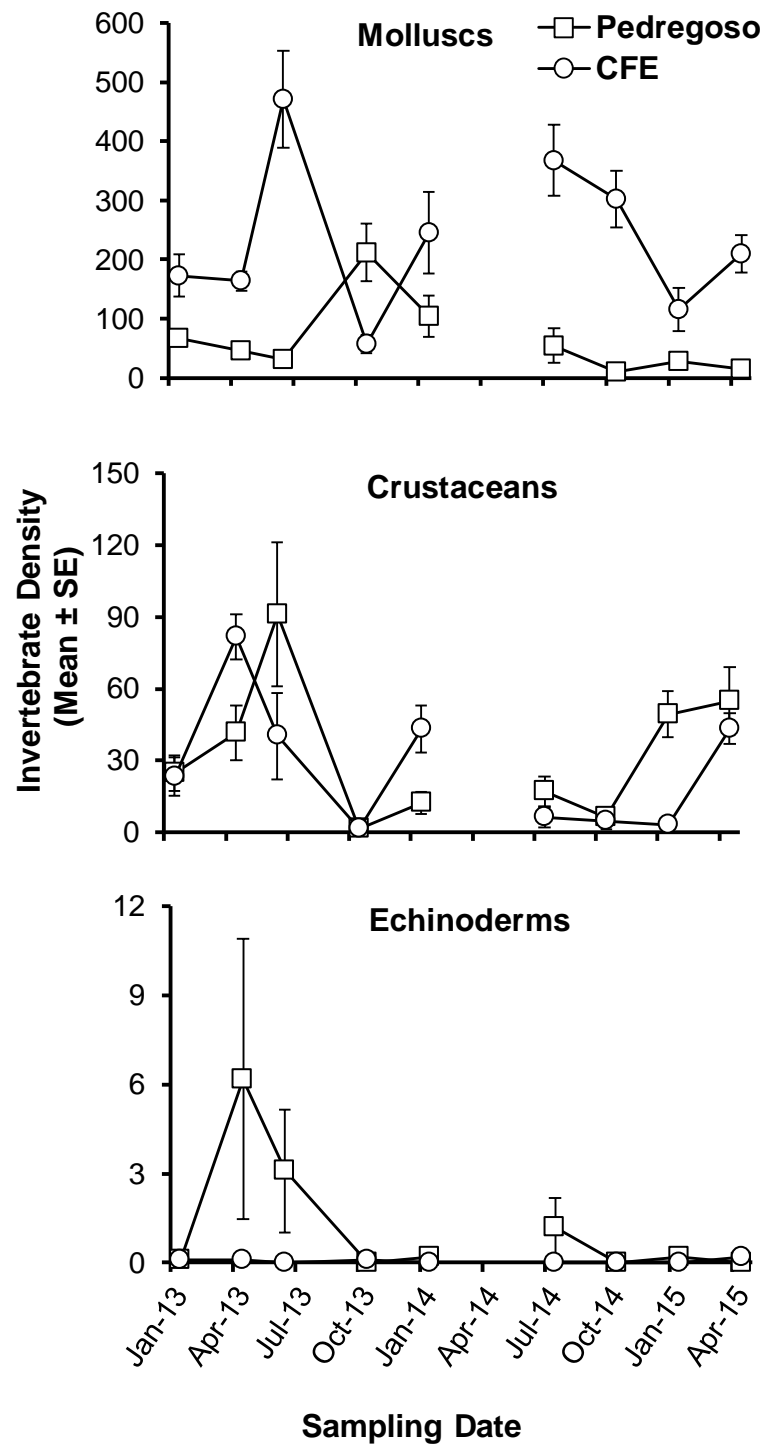
Fig. 2.8 Mobile/ solitary invertebrate density (individuals m^{-2}) at CFE and Pedregoso (Pacific Coast of Baja) over time (2013-2015)

The nMDS ordination showed overlap among sampling months for the mobile/ solitary invertebrate assemblages, however, assemblages at Pedregoso and CFE appeared distinct (Fig. 2.6). The PERMANOVA analysis indicated significant differences between sites, but not between seasons (Table 2.6). SIMPER analysis revealed an average dissimilarity of 43.55 % between Pedregoso and CFE, largely due to increased abundance of *C. stercusmuscarum* and *T. funiculosus* at CFE.

Discussion

This study is one of few quantitative accounts of temporal change and persistence in rhodolith assemblages over multiple sites and years. Two rhodolith beds formed by *Lithophyllum margaritae* on the Pacific Coast of Baja California and one dominated by *Lithothamnion muelleri* in the Gulf of California support a consistent and/ or high percent cover of rhodoliths, although more intra-annual variation was observed at sites in the Pacific. While rhodoliths persisted from year to year, the associated flora and fauna varied. Macroalgal abundance changed with seasonal changes in water temperature in the Gulf, and temperature may also influence macroalgae in Bahía Magdalena on the Pacific side of Baja. Invertebrate density and cover was variable at all sites throughout the 2+ yr study and did not respond predictably to seasonal temperature changes.

Gulf of California

The persistence and abundance of *L. muelleri* at Los Machos in the Gulf of California is consistent with reports by Foster et al. (2007) for the same site, where rhodolith cover ranged from ~ 10-15 % and formed a mixed bed with sediment and rock (Fig. 2.3). Larger rhodoliths (8-9 cm diam. on average) dominated the middle of the bed throughout the study. Smaller rhodoliths were seldom seen in the present study, but were reported by Foster et al. (2007) and McConnico et al. (2014). These differences are due to variation in sampling design, which in their studies included disturbing the sediment to look for buried rhodoliths, taking cores, and surveying many small sub sites within the bed instead of along one centrally placed transect.

While Foster et al. (2007) and McConnico et al. (2014) assessed rhodolith population structure more thoroughly, observations from our work further suggest that rhodoliths are a persistent feature at the site and do not vary seasonally, despite movement and variation in sediment cover (Fig. 2.3) which may bury or shift rhodoliths. Slow growth rates and longevity of *L. muelleri* (Frantz et al. 2000, Halfar et al. 2000, Rivera et al. 2004, McConnico et al. 2014) as well as a persistent, localized nutrient supply from cryptofauna (McConnico Thesis, Chapter 3) may contribute to rhodolith persistence in the absence of large disturbances. Although hurricanes have caused large episodic mortality events at this site (Foster et al. 2007; McConnico et al. 2014), no large storms passed sufficiently close to the area during 2013-2015 and did not impact rhodolith percent cover.

Macroalgal cover varied seasonally at Los Machos, with highest abundance in spring or summer suggesting temperature influenced algal populations. This was particularly evident in the annual growth and senescence cycle of the *Sargassum horridum* canopy which colonizes rocky substratum at this site, and occasionally on rhodoliths. As Foster et al. (2007) and others (McCourt 1984, Nuñez-López & Casas-Valdéz 1996) reported in the Gulf, *Sargassum* spp. begin to grow in the winter during cooler water temperatures, peak in the spring and degrade during summer as water temperature exceeds 30 ℃. Spring temperatures (21-23 ℃; Fig. 2.2) may be optimal for *S. horridum* growth as Rivera & Scrosati (2006) reported for *S. lapazeanum*. Nutrient availability can influence seasonality in kelp populations but has not been demonstrated for *Sargassum* (Rodríguez-Montesinos et al. 2008). Nitrate is seasonally more abundant in Jan than in Jun/ Jul at this site and may facilitate rapid spring growth, however, ammonium which is more easily assimilated by macroalgae (Lobban & Harrison 1994) is not always limited in Jun/ Jul (McConnico Thesis, Chapter 3). Thus, nutrient limitation is not likely the most important factor affecting temporal cycles of *S. horridum* at this site.

Remaining macroalgal cover also increased in winter and spring, but peaked in Jun/ Jul and declined by Oct after summer. This lag behind the *S. horridum* peak may be related to increases in light availability for understory algae once the *S. horridum* canopy degenerated. Much of the observed pattern was also related to increases in a mix of *Polysiphonia* sp., *Ceramium* sp. and

Dasya sinicola which epiphytized the remaining *S. horridum* canopy in Jul 2014, then declined after the summer temperature increase. These seasonal changes in algal abundance with spring boom and post summer collapse were also reported by Mateo-Cid et al. (1993) and Steller et al. (2003) in Bahía Concepción. Although the objective of our study was not a comprehensive investigation of species diversity, we (like Mateo-Cid et al. 1993 and Steller et al. 2003) found fewer species at this site in Oct (post summer) compared to other months, further suggesting that many species may not tolerate the warm conditions that develop in summer and last through Oct.

While we encountered ~26 different invertebrate taxa (mobile and sessile) at Los Machos, no group of organisms had strong seasonal cycles. Low sessile invertebrate cover, throughout much of the study, suggests macroalgae may out-compete them for space on rocky substratum or abrasion from sediments affects their abundance. Recruitment pulses, which are not strictly seasonal, may also influence abundance as was likely the case with the hydroid *Plumularia* sp. which peaked in Jul 2013, but was typically absent in other surveys. Among all mobile/ solitary macroinvertebrates, we found that only the bivalve *Chione californiensis* and burrowing decapod *Neaxius vivesi* were consistently present at the site throughout the study and neither species varied seasonally. Both species were reported as abundant during both Mar and Oct 2004, as well (Foster et al. 2007). Unlike previous reports for this site, we did not detect distinct changes in taxa from spring (Apr) to post summer (Oct), but did find more species in Jan (Table 2.7), when temperature was coolest. This could be related to differences in sampling protocols, as our methods focused on only abundant species. Some taxa (e.g. *Bispira* and *Phataria*) were present for 2-3 sampling periods (including spring and summer, or summer and winter), but then absent for months. These periodic gaps in species presence/ absence are consistent with other observations in the Gulf of California, but cannot be explained entirely by changes in water temperature alone and are likely related to episodic recruitment (Steller et al. 2003, Foster et al. 2007).Further investigation is required to better understand temporal variation in marine invertebrate communities in the Gulf of California, which are no doubt influenced by a range of biotic and abiotic factors.

Pacific Coast of Baja California

Both Pedregoso and CFE supported a high percent cover and dominance by the rhodolith *L. margaritae* (Fig. 2.5), with both populations comprised largely of individuals between 4-8 cm diam. This is similar to site descriptions and size frequency data previously reported by Ávila & Riosmena (2011) and Ávila et al. (2013) for these sites during 2008-2009, suggesting these beds may exhibit long-term stability. Such stability would continue to provide hard substratum for algal and invertebrate colonization not otherwise available at these sites and others where rhodoliths occur in Bahía Magdalena.

Despite the overall bed stability in Bahía Magdalena, tidal currents and storms appear to influence bed dynamics and could account for observed variation between sites and reduced rhodolith cover in Oct sampling months. Water motion allows for rhodolith persistence (Steller & Foster 1995) and strong tidal currents at our sites can cause them and fine sediments to shift periodically. The effects of which can be more pronounced at Pedregoso which occurs in a narrow channel. Such movements can disperse or clump rhodoliths resulting in changes in cover which would explain some of the between site variation, especially during months when wind or storm activity is reduced. As storm activity increases during the hurricane season, rhodolith beds in Bahía Magdalena can also be impacted. This was observed when tropical storm Juliette (August 29, 2013; NOAA 2015) passed directly over Bahía Magdalena (SW to NE) and likely caused burial and/ or movements of rhodoliths at Pedregoso. This is supported by increased sediment cover and dead rhodoliths at this site and a decrease in live rhodoliths (Oct 2013). Rhodolith and sediment cover at CFE during this time were similar to Jun 2013 (Fig. 2.5), suggesting that the storm trajectory could have varied enough to prevent similar effects at this site. Such *in situ* storm impacts including rhodolith burial and dispersal are also reported in Brazilian rhodolith beds (Pascelli et al. 2013).

Interestingly, although rhodolith cover did not vary significantly among sampling months (seasons), lowest cover occurred in Oct 2013 & 2014. As mentioned above the Oct 2013 data were taken after a large storm and the Oct 2014 data were taken after Hurricanes Norbert and Odile passed along the West and East sides (respectively) of Bahía Magdalena in Sep 2014

(NOAA 2015). That low rhodolith cover corresponded with a 10 % increase in dead rhodoliths at Pedregoso (the highest seen during the study) and 10 % increase in sediments at CFE further substantiates the impact large storms can have on rhodolith abundance *in situ*, in addition to the mass stranding and subsequent mortality on shore reported by others (Johnson et al. 2012; McConnico et al. 2014). The importance of storm disturbance to long-term persistence and temporal variability of rhodoliths requires increased exploration, especially in the tropics where such disturbances can be frequent (as is the case on the Pacific Coast of Baja California) to periodic (along the western Gulf of California; NOAA 2015).

Surprisingly, macroalgal assemblages did not vary significantly with season (sampling months), however percent cover peaked in months associated with cooler water temperature (Apr 2013 & Jan 2014) at both sites in Bahía Magdalena. This generally suggests that winter and spring months supported higher macroalgal abundance compared to summer or post summer months. This pattern of earlier growth/ peak abundance is in contrast to summer peaks observed by us in Los Machos and by others working in shallow lagoons (Nuñez-López et al. 1998, Ramírez et al. 2003) or rhodolith beds in Baja California (Steller et al. 2003, Foster et al. 2007). This may be because despite temperature similarities among sites, much of the observed increase and decrease in cover during 2013-2014 was produced by just 3 taxa: *Caulerpa sertularioides, Callithamnion* cf. *acutum* and *Amphiroa valonioides*, which can be found in Bahía Magdalena during cooler months (Sánchez-Rodríguez et al. 1989). Nutrient availability was probably not a factor influencing these algal blooms as seasonal upwelling is typically between Apr and May (Zaytsev et al. 2003) and does not correspond with the large increase in macroalgal cover seen at both sites in 2013-2014. Additionally, both sites are influenced by mangroves and may receive nutrients through leaf litter decay and from rhodolith cryptofauna throughout the year (McConnico Thesis, Chapter 3).

Caulerpa sertularioides blooms observed at our sites accounted for most of the total cover sampled at Pedregoso. Such blooms are common in the South Eastern Gulf of California during cool seasons (Piñon-Gimate et al. 2008) which may explain the peak abundance of macroalgae in cooler months like Dec-Apr. However, Sánchez Rodríguez et al. (1989) reported that *Caulerpa* was abundant in summer surveys of Bahía Magdalena and blooms in La Paz Bay have

been associated with warm temperatures (Scrosati 2001). Other *Caulerpa* blooms have been linked to high nitrogen, low phosphorus conditions (Fernández-García et al. 2012). At our sites blooms may not be entirely seasonally driven as they lasted for several months to a year. One bloom was first noted Oct 2013, peaked Jan 2014, and was still present by late Jun 2014 until it ended when a hurricane buried algal mats or tore them from the substratum. As we did not observe sites in late Jul or Aug 2014 we cannot rule out the role of increased temperature on bloom degradation. However, in Nov 2012 a similar hurricane induced collapse of a *C. sertularioides* bloom was noted and in this case blooms were present one week prior to the hurricane (McConnico & Martínez-Morales pers obs), suggesting that summer temperatures were not lethal to the alga. Regardless, large scale blooms can produce mats, some of which were measured at > 50 m long, which smother rhodoliths and other species. These blooms may also contribute to the measured decrease in rhodolith cover at Pedregoso during 2014 as well as changes in other algae, sponge and tunicate cover at Pedregoso, where blooms were more common. Changes in abundance of the Mediterranean invasive *C. racemosa* were shown to influence seasonal cycles of algae associated with rhodolith assemblages, but did not cause mortality of rhodoliths themselves (Klein & Verlaque 2009). The long-term impact of burial by such algal mats to rhodolith assemblages warrants further research.

Of the 14 algal taxa associated with rhodolith beds at Pedregoso and CFE, *A. valonioides* and *C. sertularioides* were the only two found in all seasons. Taxa which were present in 1-3 of the sampling months (seasons) may have responded to seasonal temperature changes (Table 2.5). However, others that were present in summer and winter tolerated a wide range of temperatures. The persistence and disappearance of these taxa requires further investigation to determine the source of such episodic recruitment within the bay. The extent to which algae recruit as spores, delivered during tidal movements, or recover from resting stages or fragments which may be present year round but only flourish in certain months, is unknown. In general, that we found few other algal species suggests diversity described by Sánchez Rodríguez et al. (1989) near the mouth of Bahía Magdalena and in other rocky areas (Hernández-Carmona et al. 2007) is greater than in these rhodolith beds, presumably due to increased tidal flushing, availability of stable hard substrata, and influence of the California Current at the mouth.

Variation in sessile/ colonial invertebrate cover between Pedregoso and CFE suggests that seasonality may be important, but is not the only factor influencing abundance. While cold water temperature associated with Jan sampling dates correspond to highest cover of sessile invertebrates at CFE, sessile invertebrates at Pedregoso were equally abundant throughout 2013 and in 2014 peak cover occurred in July. Fluctuations in abundance of the sponge *Scopalina* sp. accounted for much of the variation at both sites. Summer declines at CFE could be explained by a dormancy period or shrinkage in adverse conditions, as proposed by others (Coma et al. 2000; Blanquer et al. 2008). However, at Pedregoso the persistent *C. sertularioides* bloom which peaked in Jan 2014 could have outcompeted or smothered sponges (and tunicates) at this site, preventing a winter increase, while declines in Oct 2014 may be attributed to hurricane disturbance that occurred in Sep 2014. The same dominant species of sponges and tunicates are found at both sites, and these patterns of persistence and temporal change are likely influenced by a range of environmental conditions. In the absence of storm disturbance or over growth, it is possible that the sessile invertebrates cycle in response to cooler temperatures, which may be favorable for growth and/ or recruitment.

The dominant mobile/ solitary macroinvertebrates showed a range of temporal patterns which do not appear strictly seasonal and were variable between sites. As the two most abundant molluscs, *Cerithium stercusmuscarum* and *Turbo funiculosus* are herbivorous gastropods, it is possible that their populations were affected by changes in macro and microalgal abundance (and vice versa; Holguin-Quiñones & Michel-Morfín 2006). This may explain the higher abundance of gastropods at CFE in summer (Jun/ Jul) which would follow the winter and spring increased in macroalgae. Interestingly, adult *T. funiculosus* were commonly found attached to rhodoliths and *C. stercusmuscarum* were more common adjacent to rhodoliths, suggesting the two species have partitioned their niche and/ or consume different algal species. The lack of a cyclic pattern of abundance at Pedregoso suggests factors other than food availability influence gastropods at this site. Hermit crabs, the dominant crustacean at both sites, may have exhibited a trend of increased density in winter and spring then declines after summer (Fig. 2.5). This could be related to food availability, but also to disturbance impacts following storms and changes in shell availability. Since most of the hermit crabs in this study utilized shells from the most

abundant gastropod, *C. stercusmuscarum*, changes in the snail population could also account for increases/ decreases in hermit crab abundance in following months.

In general, mobile invertebrates were less diverse and/or less abundant at sites in Bahía Magdalena compared to other rhodolith beds in Baja California Sur (Steller et al. 2003, Foster et al. 2007). While gastropods and hermit crabs were abundant, few macroinvertebrates (e.g., seastars, urchins, bivalves and arthropods) were observed at Pedregoso and CFE. This could be related to high current velocities at these sites which may limit recruitment or reduced tolerance to temperature and salinity fluctuations within the bay. Fine sediments and sedimentation at both sites may also negatively impact species resulting in reduced invertebrates. While beds in Bahía Magdalena may support fewer macro invertebrates, inspection of rhodolith cryptofauna indicates they do harbor many small invertebrates (50-1700 individuals: McConnico Thesis, Chapter 3). Qualitative observations in adjacent muddy areas indicate that added heterogeneity provided by rhodoliths results in increased species abundance and diversity, as noted by others (Bosence 1979, Steller et al. 2003, Kamenos et al. 2004, Ávila et al. 2013).

Conclusion

In the absence of large episodic disturbances such as hurricanes or strong tidal movements, rhodolith populations remained stable throughout the study. Temporal declines in associated macroalgae corresponded with increasing temperature in the Gulf of California and possibly Bahía Magdalena in the Pacific. Marine invertebrates appeared to respond to a range of abiotic and biotic changes in the environment throughout the study, which did not always cause strong seasonal cycles in abundance. At present there are many reports of temporal variation in rhodolith assemblages (see introduction), however, detailed life history studies and more complete environmental data are needed to better connect relationships between biological patterns and environmental factors. These data along with field and lab experiments would allow for a more rigorous test of causes of observed temporal variation reported worldwide in rhodolith beds.

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Regeneración de nutrientes por los conjuntos de criptofauna en los mantos de rodolitos de

Baja California Sur, México

Nutrient regeneration by cryptofauna assemblages in rhodolith beds of

Baja California Sur, México[1]

Resumen: Las macroalgas son especies fundamentales que albergan fauna asociada a estas y ofrecen la oportunidad de explorar la aportación de los nutrientes de las excreciones de animales (nutrientes reciclados) en relación con la entrada de nuevas fuentes de nutrientes. Los rodolitos, son algas coralinas no geniculadas de vida libre, que albergan diversas agrupaciones de animales que podrían suministrar nutrientes regenerados para sus anfitriones. Sin embargo, los estudios sobre la dinámica de nutrientes de algas-criptofauna son limitados. Se evaluó la cantidad y variabilidad temporal de los nutrientes (amonio: NH_4^+, nitrato: NO_3^- y ortofosfato: PO_4^{3-}) asociados con los mantos de rodolitos en el Golfo de California y Pacífico de Baja California Sur, México y se consideraron las fuentes potenciales que contribuyen al suministro de nutrientes de la criptofauna. Los datos sugieren que los rodolitos y/o los sedimentos proporcionan NH_4^+, NO_3^- y PO_4^{3-} en exceso en comparación con la disponibilidad de la columna de agua, independientemente de la temporada o año. La biomasa de criptofauna se correlacionó positivamente con el diámetro de rodolitos en todos los sitios y en algunos casos también lo fue la concentración de nutrientes. El NH_4^+ y el enriquecimiento de PO_4^{3-} en los rodolitos sugieren que son suministrados por las excreciones o descomposición de criptofauna. Mientras que la entrega temporal de nuevos nutrientes (NO_3^-) proviene del movimiento del agua inducida por el viento que se produce en el Golfo de California, El NO_3^- en el Pacífico fue probablemente suministrado por agentes microbianos mediante el proceso de nitrificación. Las incubaciones de luz y oscuridad mostraron que el conjunto de rodolitos, pueden llevar a cabo inicialmente la absorción de NH_4^+, sobre NO_3^-, pero todos los nutrientes se consumen en presencia y ausencia de luz. Este estudio resalta la importancia de los rodolitos en ambientes

costeros y de estuario, no sólo como especies fundamentales, sino también por su papel en la regeneración de nutrientes (especialmente en áreas limitadas de nutrientes).

Abstract: Macroalgal foundation species harboring associated fauna provide an opportunity to explore nutrient contributions from animal excretions (recycled nutrients) relative to new inputs. Rhodoliths, free-living non-geniculate coralline algae, support diverse cryptofaunal assemblages which could supply regenerated nutrients to their host, but studies of the algal-cryptofauna nutrient dynamics are limited. We assessed the quantity and temporal variability of nutrients (ammonium: NH_4^+, nitrate: NO_3^-, and orthophosphate: PO_4^{3-}) associated with rhodolith beds on the Gulf and Pacific sides of Baja California Sur, México and considered potential nutrient contributions from cryptofauna and other sources. Data suggest rhodoliths and/or associated sediment communities provide NH_4^+, NO_3^- and PO_4^{3-} in excess of water column availability, regardless of season or year. Cryptofauna biomass was positively correlated with rhodolith size (diam.) at three sites, and in some cases nutrient concentration was also. Ammonium and PO_4^{3-} enrichment in rhodolith beds is likely supplied by cryptofaunal excretions or decomposition. While seasonal delivery of new nutrients (NO_3^-) via wind-induced water motion occurred in the Gulf, NO_3^- at Eastern Pacific sites was likely facilitated by microbial mediated nitrification. Light and Dark incubations showed rhodolith assemblages may initially uptake NH_4^+ over NO_3^-, but all nutrients were consumed in the presence and absence of light. This study highlights the role of rhodolith communities in nutrient regeneration especially in nutrient limited coastal and estuarine environments.

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[1]En Revisión como: McConnico LA, Hernández-Carmona G, Riosmena-Rodríguez R, (In Review) Nutrient regeneration by cryptofauna assemblages in rhodolith beds of Baja California Sur, México.

Introduction

Nutrient availability, namely nitrogen (N) or phosphorus (P), limits primary production (Lobban & Harrison 1994). Seaweeds may meet nutrient demands with N & P delivered via upwelling or from land (new nutrients), regenerated nutrients from excretion and decomposition of organisms, or mineralization within the euphotic zone. Nitrogen fixation in the euphotic zone can also be an important new nitrogen source (Dugdale & Goering 1967). The dependence on new or regenerated nutrients may be related to which form is most abundant in the environment or which is most easily assimilated. While seaweeds can uptake both nitrate (NO_3^-) and ammonium (NH_4^+), research suggests NH_4^+, the reduced form of N available in excretions (Wright 1995), may be more readily assimilated by some species (Hanisak 1983, Fujita 1985, Lobban & Harrison 1994, Bracken & Stachowicz 2006). Phosphorus is generally assimilated as orthophosphate (PO_4^{3-}; Lobban & Harrison 1994) and may come from new or regenerated sources (Paytan & McLaughlin 2007), but distinguishing between the two can be difficult (Eppley & Peterson 1979).

Investigations of nutrient availability or utilization focused on tightly coupled plant-animal associations provide a unique opportunity for evaluating the significance of regenerated nutrients in marine systems. Macroscopic primary producers which function as foundation species, harboring high densities of epifauna among their thalli, are particularly useful to address such questions. In these close associations, photosynthetic organisms can benefit from excretion and decomposition associated with the many animals they host. Foundation species including the macroalgae *Macrocystis* (Bray et al. 1986), *Carpophyllum* (Taylor & Rees 1998), *Cladophora* (Bracken et al. 2007) and *Sargassum* (Lapointe et al. 2014) can uptake NH_4^+ from animal associates and/ or experience increased growth (or abundance) in the presence of such invertebrate or vertebrate excretions. These studies and others (Williamson & Rees 1994, Bracken 2004, Pfister 2007, Aquilino et al. 2009) suggest that algal nutrient demands may be met by regenerated sources in both nutrient poor and upwelling regions.

Nutrient regeneration may occur within rhodolith ecosystems and current evidence comes from a sole detailed study (Martin et al. 2007). These non-geniculate coralline algae are foundation

species with a global distribution (Weber Van Bosse & Foslie 1904, Foster 2001). Aggregations, or beds, of the free-living algae provide habitat for numerous cryptofauna (macro and microscopic species hidden within and among their branches). Studies world-wide cite high biodiversity, unique species associations, and the importance of rhodolith beds to fisheries (Bosence 1979, Grall & Glemarec 1997, James 2000, Hall-Spencer & Moore 2000, Steller et al. 2003, Hinojosa-Arango & Riosmena-Rodríguez 2004, Kamenos et al. 2004, Foster et al. 2007, Riosmena-Rodríguez & Medina-López 2011, Bahia et al. 2010, Riera et al. 2012, Neill et al. 2015). Collectively these studies substantiate rhodoliths as foundation species, but none have considered how the myriad of associated species may benefit their algal host. As with other foundation species harboring animals (Myer et al. 1983, Taylor & Rees 1998, Bracken et al. 2007, Lapointe et al. 2014), it could be predicted that rhodolith associates, specifically cryptofauna, may provide additional N & P to their hosts. Such regenerated nutrients may be of particular importance in the tropics and subtropics where rhodoliths are abundant and potentially limited by new nutrient sources.

The goal of this study was to determine the quantity and temporal variability of nutrients (NH_4^+, NO_3^- and PO_4^{3-}) associated with rhodolith beds on the Gulf and Pacific sides of Baja California Sur, Mexico. We compared nutrient availability in the water column, sediments and from between rhodolith branches to assess if regenerated nutrients from rhodolith cryptofauna were greater than the available nutrient pool in surrounding environments. We investigated the relationship between nutrient availability, rhodolith size and cryptofaunal biomass to determine if larger rhodoliths harbor more cryptofauna and thus have access to more nutrients. Rhodolith branch tips were analyzed for total nitrogen content to infer nutrient requirements, and field incubations were done to determine nutrient uptake by rhodoliths.

Materials and Methods

Study sites

Research was done Jan 2013–Apr 2015 at two sites (Pedregoso and CFE) within Bahía Magdalena on the Pacific side of Baja California Sur, México (between 24°54´ N and 24°48´ N & 112°05´ W and 112°06´ W) and one site (Los Machos) at the mouth of Bahía Concepción on the Gulf of California side (26°50´ N, 111°53´ W). The shallow (0.5–2.5 m) rhodolith beds within Bahía Magdalena coastal lagoon are dominated by *Lithophyllum margaritae* and lined by mangroves on one or both sides. This lagoon complex represents a nutrient rich anti-estuarine ecosystem influenced by coastal upwelling (Alvarez-Borrego et al. 1975, Zaytsev et al. 2003, Cervantes-Duarte et al. 2013). Average surface water nutrients range from 1.4–3.7, 0.9–5.0 and 0.5–0.9 μM for NH_4^+, NO_3^- and PO_4^{3-}, respectively, with highest concentrations reported in the first half of the year and usually closer to the lagoon entrance. Bottom water nutrients (≤ 10 m) fall within these concentrations, except NH_4^+ and PO_4^{3-} can reach up to 12.2 and 2.08 μM, respectively, near the deeper (> 10 m) lagoon entrance (all data from Table 1 in Cervantes-Duarte et al. 2013). In the Gulf, the Los Machos bed ranges from 2–8 m depth and is a mixture of the rhodolith *Lithothamnion muelleri* and the brown alga *Sargassum horridum*. The central Gulf can be nutrient limited, but seasonal upwelling on the east coast occurs in winter (driven by NW winds) and weaker upwelling occurs during summer on the west coast as winds come from the south, resulting in a stratified water column for much of the year (Alvarez-Borrego 1983). Near the entrance to Bahía Concepción, water column nutrients are ~0.2–1.2, 1.0–6.4 and 0.8–2.4 μM for NH_4^+, NO_3^- and PO_4^{3-}, respectively, with highest concentrations reported during well mixed periods except for NH_4^+, where highest concentrations occurred during months when the water column was stratified (from Fig. 9 in Murillo Murillo 2005).

Detailed site descriptions, a map, temperature data, and temporal variation in rhodolith communities at all sites (during 2013–2015) are reported in McConnico et al. (in review; see McConnico Thesis, Chapter 2). Foster et al. (2007), Avila & Riosmena-Rodríguez (2011) and McConnico et al. (2014) also provide additional quantitative assessments of these same beds. Although sites on the two sides of the Baja peninsula are composed of different rhodolith

species, their morphology and size are similar and both species harbor a large number of cryptofauna. Rhodolith beds were accessed using small boats and a combination of SCUBA or snorkel depending on tidal height. Temperature was monitored during the study using HOBO Pendant® data loggers (model UA-002-08; one per site) and digital thermometers (from scuba consoles).

Temporal variation in NH_4^+, NO_3^- and PO_4^{3-}

Variation in nutrient production and availability was determined from water samples collected from inside and outside of rhodolith beds approximately seasonally, every 3–5 mo. Water samples varied relative to location. Within the bed, water was sampled from the water column, sediment and interstitial water from between rhodolith branches (n=10 taken at random locations along a 30 m transect placed at the middle of the bed). Outside the bed, only interstitial sediment water samples were collected (ten replicates taken 50-100 m from the bed edge; for logistical reasons these were obtained using random numbers of fin kicks). Water column samples were collected from 10 cm and 1 m above the rhodolith bed and sediment samples from the top 1-2 cm of sediments (inside and outside the bed), both were sampled with 50 ml sterile syringes. To obtain water samples from between rhodolith branches, a flexible plastic bag was gently wrapped over the surface of the alga and secured with a small piece of wire to retain interstitial water. Rhodoliths were brought to the surface, placed in a funnel, the plastic punctured and contents drained into a sterile container. Sample volume extracted varied from 10–100+ ml depending on rhodolith size. All samples were processed within ~ 30–60 min of collection. When < 30 ml of sample was available, nutrient analysis was prioritized as follows: NH_4^+, NO_3^- and then PO_4^{3-}. Thus, although water samples were always collected from 10 rhodoliths, the total replicates for each nutrient type varied from 7–10 depending on sample volume obtained. Foul weather prevented sample collection for sediments outside the bed at Los Machos Oct 2013.

All samples were field filtered using acid washed (10% HCL) Pall Gelman™ portable syringe filters outfitted with GF/F filters and immediately placed on ice in the dark. Ammonium concentrations were analyzed within 24–48 h and NO_3^- and PO_4^{3-} within ~one week of

collection. Samples not immediately analyzed remained frozen until the time of analysis. Samples were analyzed using standard analytical techniques for seawater (Strickland & Parsons 1972) at the accredited analytical facility El Centro de Investigaciones Biológicas del Noroeste, S.C. in La Paz, México. When nutrient concentrations were below detectable limits (0.5 μM for NH_4^+, and 0.1 μM for NO_3^- and PO_4^{3-}), minimum detection limits were used in the calculation of monthly averages. This estimation was used primarily for NH_4^+ in water column samples and occasionally in sediments outside of bed, which represent the lowest concentrations observed in the study. This approach was more conservative than using 0 μM and did not unfairly bias data interpretation.

The large variation in nutrient concentration associated with sediment and rhodolith samples relative to the homogeneous water column samples could not be corrected by data transformation. Data violated assumptions of homogeneity of variances and normality preventing parametric and non-parametric data analysis (Underwood 1997). Patterns in data, however, were clear and were compared as trends.

Temperature and nutrient concentration

Average NH_4^+, NO_3^- and PO_4^{3-} concentrations from water column samples (taken at 1 m) were plotted against average monthly temperatures to determine if the relationship was significant. As field temperature data were unavailable at Los Machos in 2013, average temperature for sites on the Pacific side were used in analyses and considered comparable (McConnico Thesis, Chapter 2). Analyses were done for all three sites and nutrient types, but only significant linear regressions are reported.

Fauna in rhodoliths and sediments

To determine the relationship between rhodolith size, cryptofaunal biomass and nutrient production, water samples were collected (using the technique described above) from 15 rhodoliths of varying sizes (~3–8 cm diam.) at the two sites in Bahía Magdalena and 20 rhodoliths (~3–13 cm diam.) at Los Machos in Bahía Concepción during Jan 2013. After

extracting interstitial water, rhodoliths were fixed in formalin (~10%) and 24 h later preserved in 70% EtOH until they could be measured, broken apart and sorted for fauna. Rhodolith diam. was determined based on average *x, y, z* axial measurements and all fauna retained on a 500 μm sieve were counted. Cryptofaunal biomass estimates were based on wet weights taken after blotting specimens dry on filter paper and then re-suspending them in DI water of a known mass. Regression analysis was used to determine if there was a relationship between rhodolith size (diam.) and cryptofauna biomass (g), and between rhodolith size (diam.) and nutrient (NH_4^+, NO_3^- and PO_4^{3-}) concentration of water collected from rhodolith between branches. The latter comparison was not made at CFE as nutrient data for rhodoliths were not available at this site in Jan 2013.

To determine if invertebrate biomass in sediments was similar to cryptofaunal biomass in rhodoliths, infaunal invertebrates were sampled at each of the three sites in Jun/ July 2014. Five 7 cm diam. cores (325 ml) were taken at random locations along a 30 m transect inside of beds and 5 were taken outside of beds using random numbers of fin kicks. Sediment cores were sieved and all invertebrates retained on a 500 μm mesh were preserved in 70% EtOH, subsequently counted and weighed as described above. All fauna from rhodoliths and sediments were sorted to phylum level using dissecting microscopes.

Light and Dark Incubations

To measure nutrient uptake by rhodoliths in the light and dark, field incubations of rhodoliths were done at Los Machos (Oct 2014) and Pedregoso (Apr 2015). Twelve rhodoliths (~ 6–8 cm diam., with < 5–10% epiphyte cover) were haphazardly collected from each bed. At the surface, each rhodolith was placed in a separate clear plastic container filled with 1500 ml of ambient filtered seawater (0.35 μm filter) collected from the study sites just prior to experimentation. All containers were covered with a clear lid and maintained at the sea surface in floating baskets for 2–3 h (~1100–1400 h). Six experimental units were exposed to ambient light [covered by a single layer of grey mesh screen (1 mm weave) to mimic subtidal light levels] and six were covered in black plastic to determine nutrient uptake without light. Forty ml of water were removed from experimental units prior to introducing rhodoliths and again at 30 min, 1 h and 2

h after rhodolith introduction. Samples were also collected after 3 h of incubation at Pedregoso. Temperature was monitored inside experimental units and was similar to subtidal temperatures. All water samples were GF/F filtered, kept on ice in the dark, and then frozen for 24–48 h before being analyzed for NH_4^+, NO_3^- and PO_4^{3-}. Data are reported as μmol rhodolith^{-1} except at time '0' prior to introducing rhodoliths, where nutrient concentrations are reported as μmol experimental container^{-1}.

Tissue nitrogen

To estimate nutrient requirements of rhodoliths, branch tips (10, ~ 2 mm pieces) were removed from 5 rhodoliths at each of the 3 sites during summer 2014. Samples were air dried and % N determined using an elemental analyzer at San Diego State University's analytical facility.

Results

Temporal variation in NH_4^+, NO_3^- and PO_4^{3-}

At the Los Machos site concentrations of all three nutrients were in general highest in the interstitial rhodolith water relative to the sediment or water column samples (Fig 3.1). Average NH_4^+ concentrations from all water samples at Los Machos (Gulf of California site) ranged seasonally from ~0.5–15 μM over 2013-2014 (Fig. 3.1A). Interstitial rhodolith water samples had the highest NH_4^+ content throughout much of the study relative to the water column and both sediment locations, except during summer 2013 when high NH_4^+ was also detected in sediments outside the bed. Intermediate concentrations were measured from sediment samples inside and outside the bed and lowest concentrations were observed in the water column (1 m and 10 cm above the bed). Interstitial rhodolith water showed seasonal nutrient cycles with highest levels in summer. NH_4^+ did not vary seasonally in the water column samples and data gaps prevented accurate assessment of seasonality in sediment samples (Fig. 3.1A)

Nitrate concentrations varied from ~0.1–8.0 µM at Los Machos during 2013-2014 (Fig. 3.1B). Concentrations were always highest in rhodoliths, followed by sediments inside the bed, while sediments outside the bed and water column samples were typically lowest throughout the study. Nitrate concentration was seasonally most abundant in Jan (2013 & 2014) for all sample types (Fig. 3.1B).

Phosphorus concentrations at Los Machos ranged from ~0.7–5.4 µM (Fig. 3.1C) with the highest concentrations typically observed in rhodoliths. An exception was during Jun/ Jul 2013 and 2014, when PO_4^{3-} peaked in sediments outside the bed. Similarly, sediments inside the bed typically had more PO_4^{3-} than sediments outside the bed, except during these summer peaks. In other months PO_4^{3-} concentration in sediments outside the bed was reduced (compared to rhodoliths) and/ or similar to water column samples (Fig. 3.1C).

A

B

C
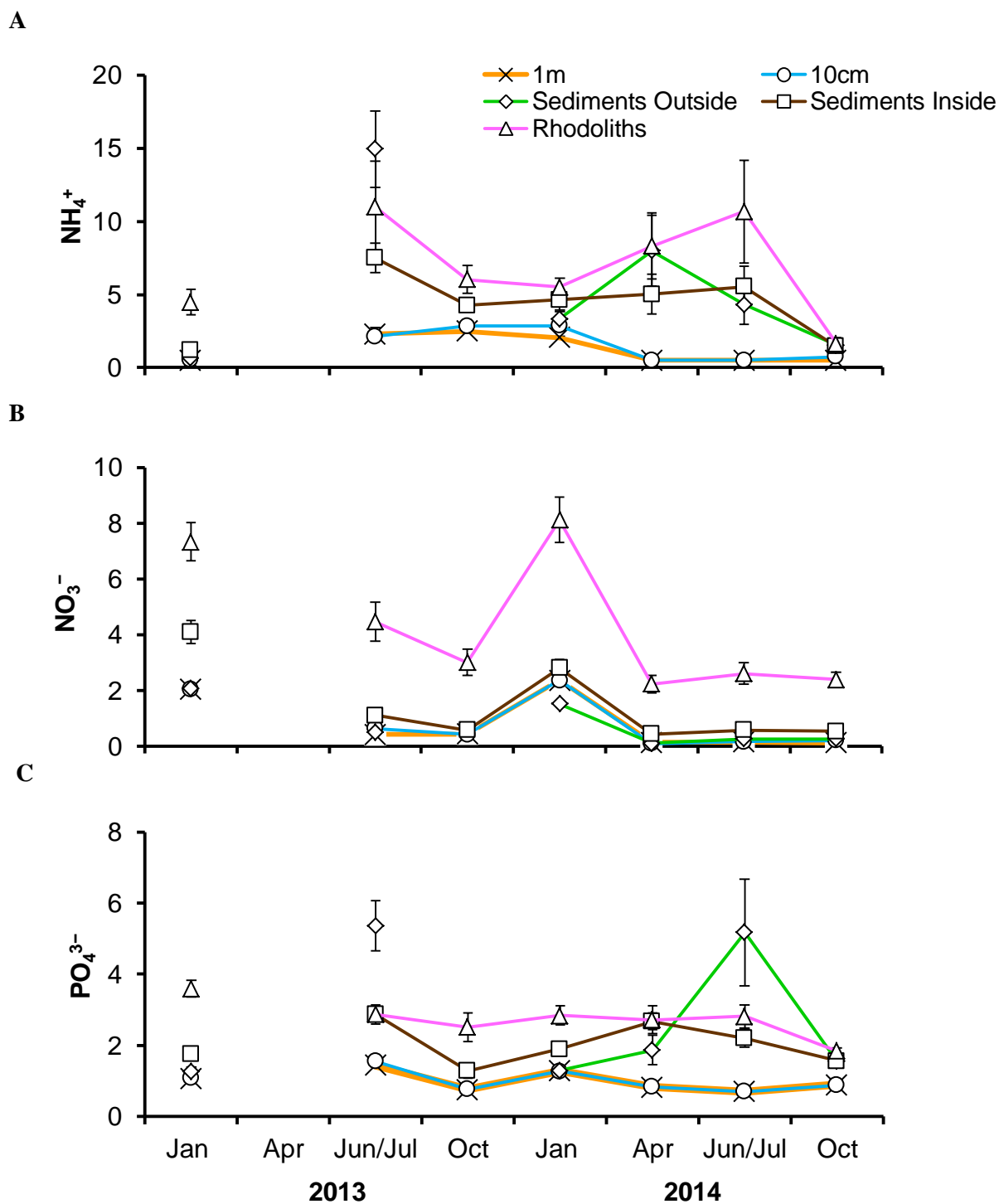
Fig. 3.1 Nutrient concentrations (Mean µM ± SE) at Los Machos (A) NH_4^+, (B) NO_3^- and (C) PO_4^{3-}. In the legend '1 m' and '10 cm' are distances above rhodolith in the water column, 'outside' and 'inside' sediments refer to samples taken from top layer of sediments outside and inside of rhodolith beds, respectively and 'rhodolith' refers to water samples collected from in between rhodolith branches. n=10 for all sample types except no samples taken for sediments outside of bed Oct 2013

Patterns of nutrient concentrations were more complex in the two Pacific sites at Bahía Magdalena. NH_4^+ ranged from 0.5–23.4 µM at Pedregoso and 0.5–16.4 µM at CFE (Figs. 3.2A & 3.3A). Sediments inside and outside the bed and rhodoliths often had the highest NH_4^+ content at both sites, with lowest NH_4^+ concentrations detected in water column samples. Ammonium concentration in sediments outside the bed was similar to low levels observed in the water column at Pedregoso in Jan and Jun/ Jul 2014 and Oct 2013 thru Jun/Jul 2014 at CFE (Figs. 3.2A & 3.3A).

Nitrate ranged from ~0.1–5.5 µM at Pedregoso and was usually higher than observed at CFE (~0.1– 3.0 µM; Figs. 3.2B & 3.3B). Nitrate concentrations were highest in rhodoliths relative to the other samples from both sites throughout study, except during Jun/ Jul 2013 when high levels were also detected in sediments inside the bed at CFE. Rhodolith samples at Pedregoso contained more NO_3^- than at CFE during all sampling dates. Sediments inside the bed were usually higher in NO_3^- than sediments outside of beds and the lowest concentrations were seen in water column samples at both sites. Nutrient concentration throughout the study was more variable from sampling date to sampling date at CFE compared to Pedregoso, especially for rhodolith samples (Figs. 3.2B & 3.3B)

Phosphorus concentrations at both sites were similar and ranged from 0.7–5.8 µM at Pedregoso and 0.6–6.1 µM at CFE (Figs. 3.2C & 3.3C). The highest concentrations were frequently associated with sediments inside the bed at both sites, except in Apr 2013 when PO_4^{3-} peaked in sediments outside of both beds and were high in rhodoliths at CFE during Jun/ Jul 2014. At Pedregoso, PO_4^{3-} in rhodoliths fell between values reported for sediments inside the bed and the water column. A similar pattern was observed at CFE, except rhodolith samples contained the greatest PO_4^{3-} concentration during Jun/ Jul 2014. Phosphorus concentrations were lowest in water column samples at both sites throughout the study (Figs. 3.2C & 3.3C).
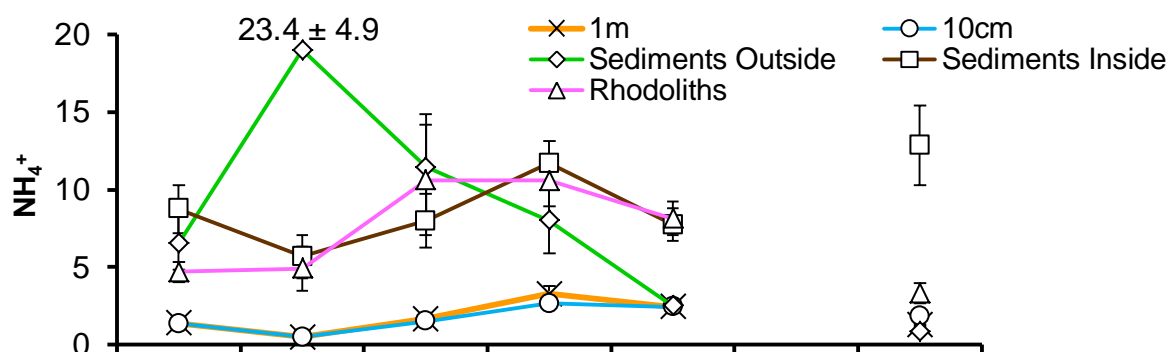
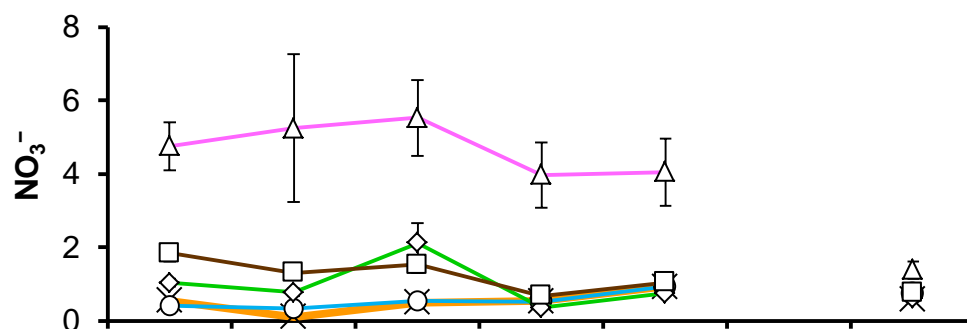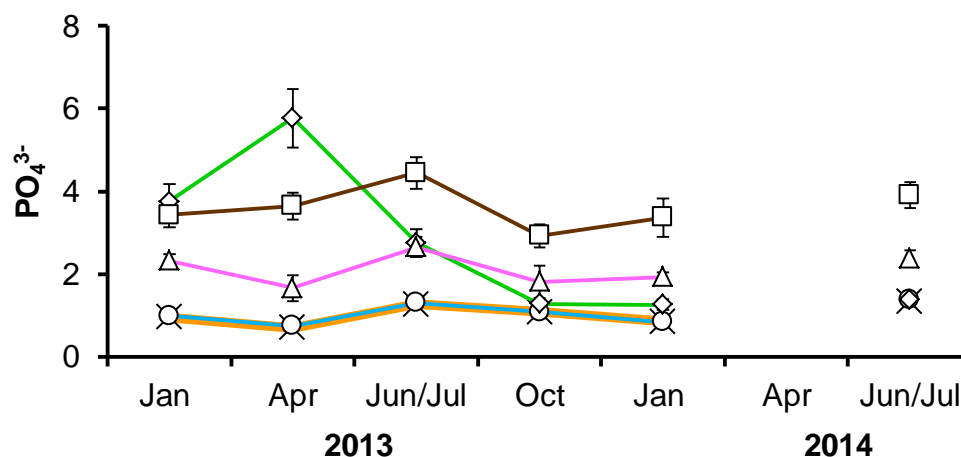**Fig. 3.2** Nutrient concentrations (Mean μM ± SE) at Pedregoso (A) NH_4^+, (B) NO_3^- and (C) PO_4^{3-}. In the legend '1m' and '10cm' are distances above rhodoliths in the water column, 'outside' and 'inside' sediments refer to samples taken from top layer of sediments outside and inside of rhodolith beds, respectively and 'rhodolith' refers to water samples collected from in between rhodolith branches. n=10 for all sample types except: n=9 for NO_3^- and n=7 for PO_4^{3-} in rhodoliths Apr 2013, and n=8 for NO_3^- in water samples from '10 cm' Jun/Jul 2014. In Fig. 3.2A '23.4 ± 4.9' is the mean for sediments outside the bed in Apr 2013
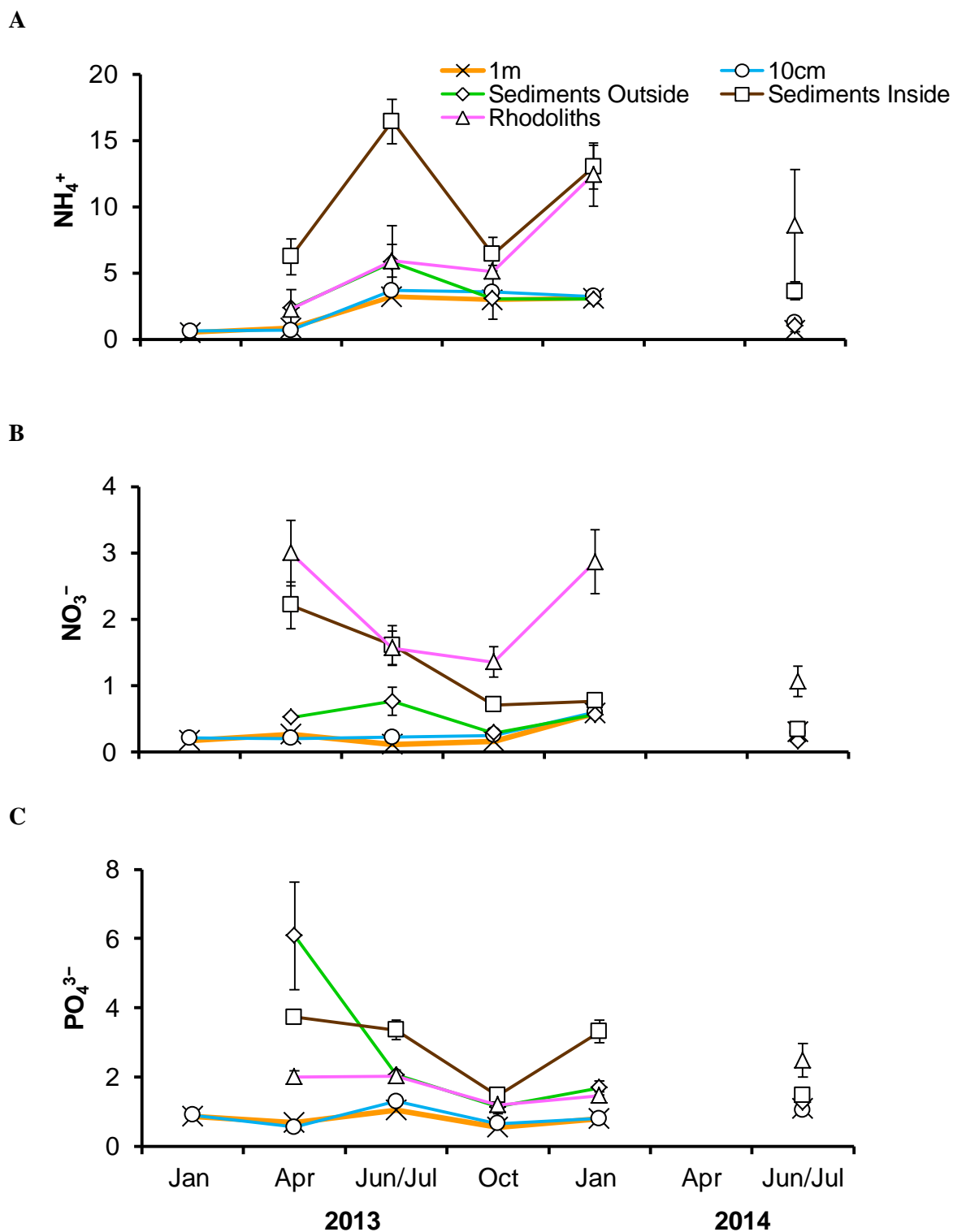
Fig. 3.3 Nutrient concentrations (Mean µM ± SE) at CFE (A) NH_4^+, (B) NO_3^- and (C) PO_4^{3-}. In the legend '1 m' and '10 cm' are distances above rhodolith in the water column, 'outside' and 'inside' sediments refer to samples taken from top layer of sediments outside and inside of rhodolith beds, respectively and 'rhodolith' refers to water samples collected from in between rhodolith branches. n=10 for all sample types except n=0 for sediments and rhodoliths Jan 2013, n=8 for PO_4^{3-} in rhodoliths Apr 2013

Temperature and nutrient concentration

Temperature was similar among all sites and varied seasonally. Average monthly temperatures ranged from ~17.5–20°C in Jan to 28–31°C during Aug/ Sept, with 2013 generally cooler than 2014/ 2015 (see Fig. 2.2 in McConnico Thesis, Chapter 2). Nitrate was negatively correlated to temperature at Los Machos ($R^2 = 0.77$, $F_{1,6} = 17.10$, $p = 0.01$). No other nutrient vs. temperature regressions were significant.

Fauna in rhodoliths and sediments

Cryptofaunal biomass ranged from 0.1–16.9 g per rhodolith at Los Machos, 0.3–12.1 g at Pedregoso and 0.4–14.0 g at CFE, with rhodoliths ~ 6–8 cm diam. averaging ~ 3–4 g biomass individual^{-1}. Cryptofauna biomass increased significantly with rhodolith diam. at all sites (Fig. 3.4). Cryptofauna were generally more numerous at Los Machos (11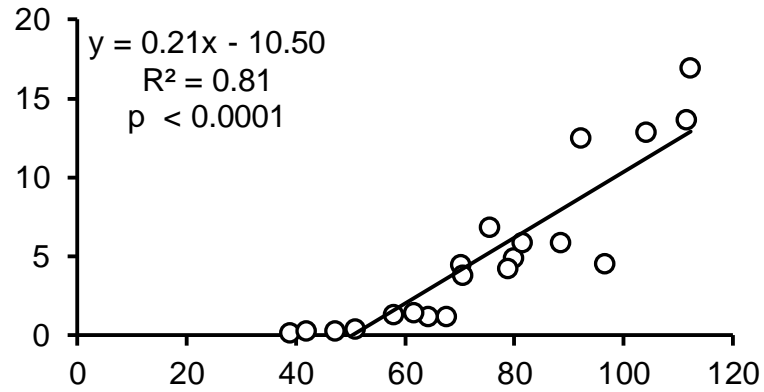8–3447 ind rhodolith^{-1}) than Pedregoso (57–1729 ind rhodolith^{-1}) and CFE (154–829 ind rhodolith^{-1}). Annelids, arthropods, molluscs and echinoderms accounted for much of the biomass (50-98 % of the total biomass for at least half of the samples) at all sites; however at Los Machos echinoderms and tunicates were particularly abundant, and at sites in Bahía Magdalena cnidarians and sponges were abundant. Interestingly, rhodoliths at CFE occasionally harbored solitary tunicates (~ 3 cm diam.) and fish (Labrisomidae and Tripterygiidae, 2-3 cm) inside thalli and larger gastropods (*Turbo funiculosus*, 2-3 cm) on top of thalli. This was not typical of other sites.

A

y = 0.21x - 10.50
R² = 0.81
p < 0.0001

B

y = 0.15x - 5.71
R² = 0.52
p = 0.002

Biomass Individual^{-1}
(g wet wt)

C

y = 0.21x - 9.13
R² = 0.68
p = 0.0002
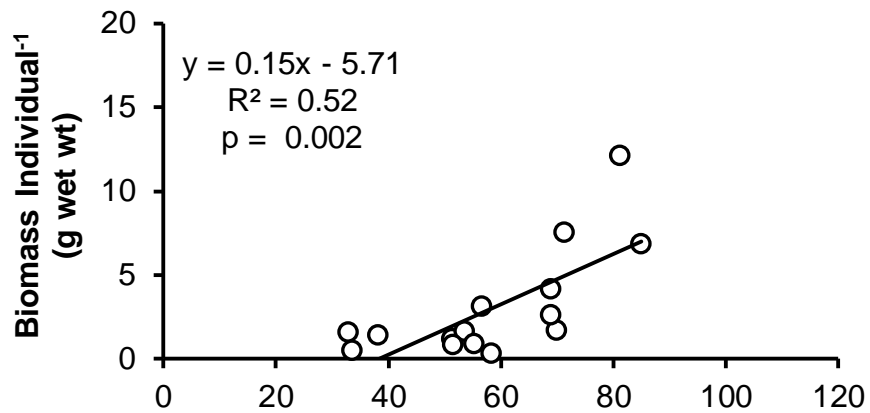
Diameter (mm)

Fig. 3.4 Cryptofauna biomass vs. rhodolith diameter (Jan 2013) at (A) Los Machos (n=20), (B) Pedregoso (n=15) and (C) CFE (n=15)

Infaunal biomass was low in sediment cores taken inside and outside of rhodolith beds (Table 3.1). Average biomass was < 0.2 g core^{-1} for all sites and sample types. At Los Machos and CFE there was a pattern of greater biomass from 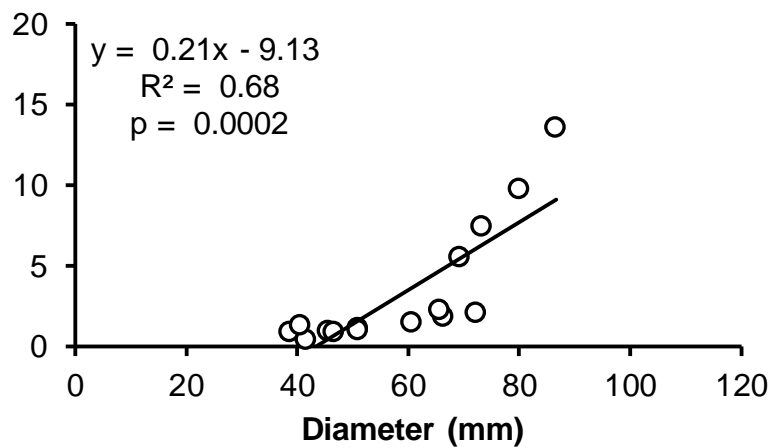cores inside the bed than outside, but at Pedregoso biomass was similar in and out of the bed. Cores from inside the Los Machos bed were dominated by annelids, tanaids and nematodes, while cores outside of the bed were dominated by an unidentified gastropod. On the Pacific Coast of Baja cores from inside the Pedregoso and CFE beds were dominated by annelids, nematodes and amphipods, while annelids and nematodes also dominated cores outside of both beds. Tanaids were also particularly abundant in cores outside of the bed at Pedregoso.

Table 3.1 Infaunal biomass (mean wet wt in g ± SE) from sediment cores (325 ml) inside and outside of rhodolith beds at Los Machos, Pedregoso and CFE during Jun/July 2014 (n = 5 for each site and core type)

Location of Core	Los Machos	Pedregoso	CFE
Inside Bed	0.13 ± 0.09	0.16 ± 0.15	0.04 ± 0.02
Outside Bed	0.03 ± 0.01	0.19 ± 0.03	0.01 ± 0.01

Nutrient concentrations relative to rhodolith size

Interstitial rhodolith water nutrient concentration was positively correlated with rhodolith diam. at Los Machos. This positive trend was similar but not significant at Pedregoso, due to data outliers (which could not be justifiably removed) (Table 3.2).

Table 3.2 R^2 and significance values for linear regression model (rhodolith diameter vs. nutrient concentration) based on samples collected from Los Machos and Pedregoso during Jan 2013

Site	NH_4^+	NO_3^-	PO_4^{3-}
Los Machos	$R^2 = 0.46$ p = 0.001	$R^2 = 0.58$ p = 0.0001	$R^2 = 0.39$ p = 0.01
Pedregoso	$R^2 = 0.001$ p = 0.90	$R^2 = 0.01$ p = 0.68	$R^2 = 0.04$ p = 0.54

Light and Dark incubations

Changes in nutrient concentrations during the 2 h incubation were similar in Light and Dark containers at Los Machos (Fig. 3.5). Ammonium concentrations declined by ~1–2 μmol rhodolith^{-1} over the 2 h experiment, while PO_4^{3-} was reduced only slightly. Nitrate increased during the first hour and then declined in the second hour.

Nutrient depletion was similar in Light and Dark containers at Pedregoso (Fig. 3.6). Ammonium and PO_4^{3-} declined steadily over the 3 h experiment (~3–5 and 0.1–0.2 μmol rhodolith^{-1}, respectively) while NO_3^- increased slightly or remained stable in the first 30 min, then declined by ~0.7 μmol rhodolith^{-1} and remained stable through the end of the experiment.

Tissue nitrogen

Tissue nitrogen estimates varied from rhodoliths in the Gulf of California and the Pacific Coast of Baja California. Average % N in rhodolith tissue from the Gulf was 0.14 ± 0.01, while in the Pacific % N was 0.26 ± 0.02 at Pedregoso and 0.21± 0.01 at CFE.

A

B

C
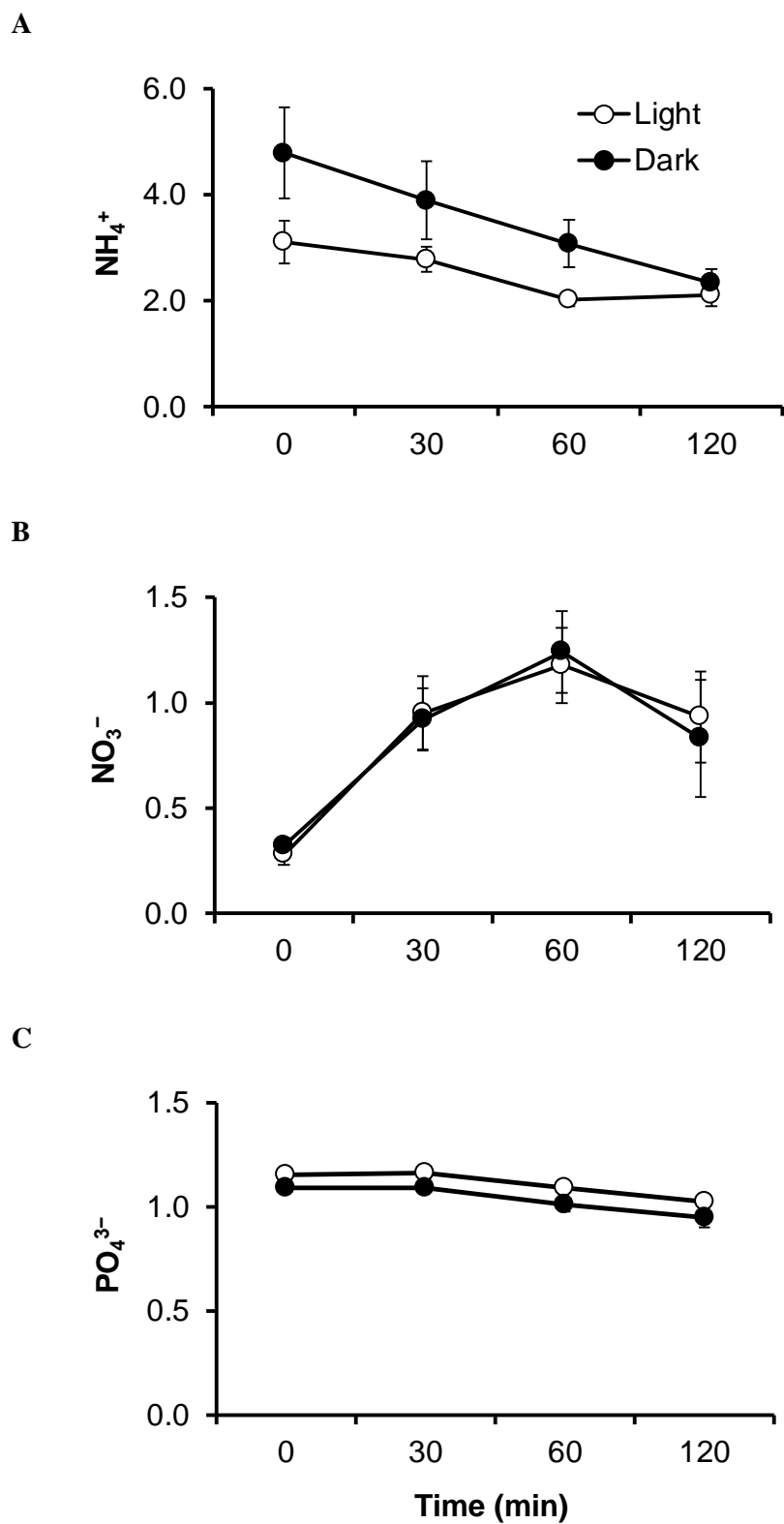
Fig. 3.5 Nutrient concentration (Mean µmol rhodolith^{-1} ± SE) for incubations under 'Light' and 'Dark' conditions at Los Machos in Oct 2014 (A) NH_4^+, (B) NO_3^- and (C) PO_4^{3-}; note n=6 per treatment and at time '0' nutrient concentrations are reported as µmol container^{-1}

A

B

C

Fig. 3.6 Nutrient concentration (Mean μmol rhodolith^{-1} ± SE) for incubations under 'Light' and 'Dark' conditions at Pedregoso in Apr 2015 (A) NH_4^+, (B) NO_3^- and (B) PO_4^{3-}; note n=6 per treatment and at time '0' nutrient concentrations are reported as μmol container^{-1}
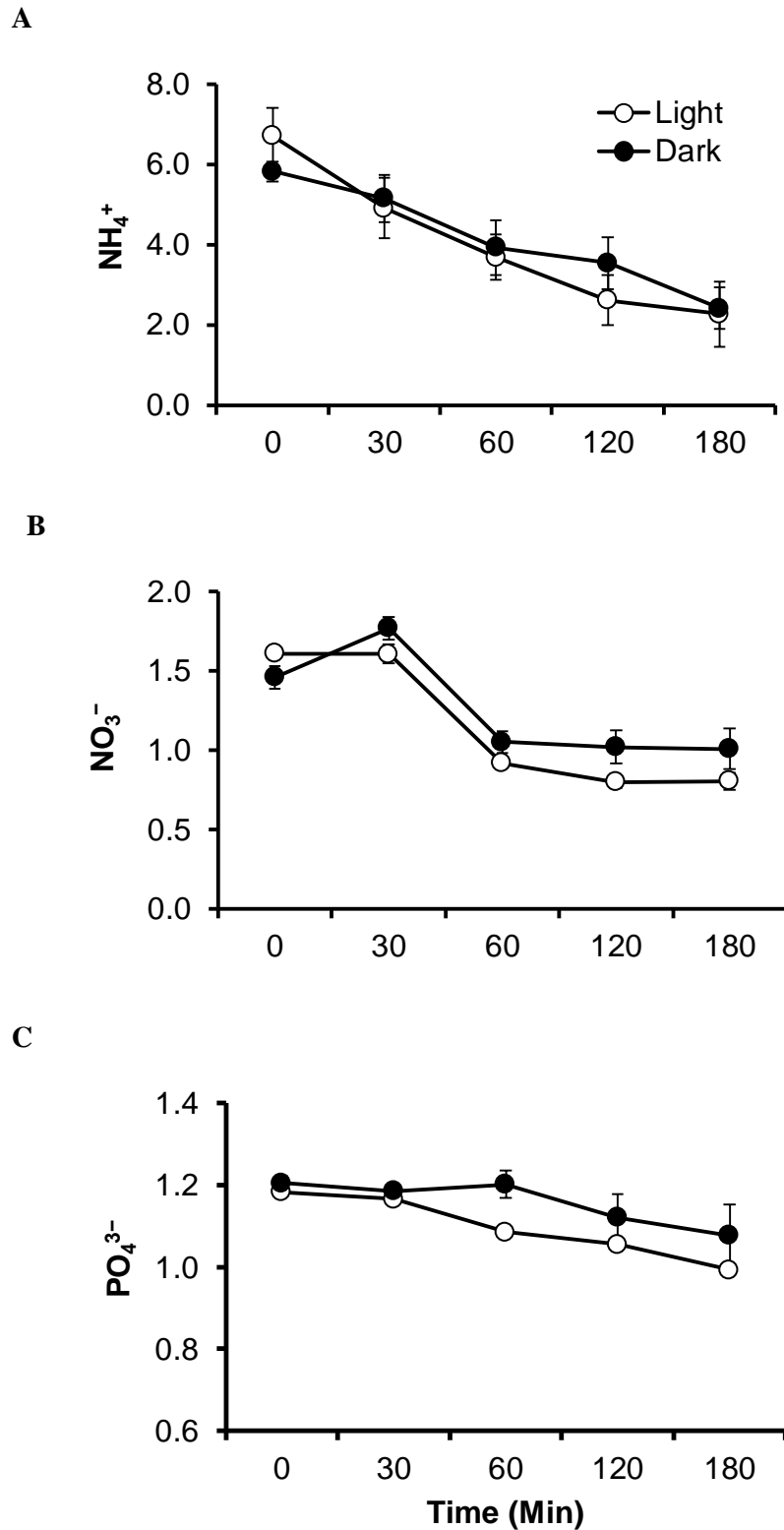
Discussion

Our data and field observations show rhodoliths on both the Gulf and Pacific sides of Baja California harbor numerous and diverse cryptofauna that may contribute substantially to the available nutrient pool within rhodolith beds. Elevated nutrient levels between rhodolith branches and sediments compared to water column samples were consistent at all three sites (Figs. 3.1–3.3) and in excess of surface water nutrient concentrations previously reported for Bahía Magdalena (Cervantes-Duarte et al. 2013) and near the entrance to Bahía Concepción (Murillo Murillo 2005). This supports the hypothesis that cryptofauna, along with microbial activity must account for much of these nutrient increases. Temporal trends in water column nutrient availability suggest new nutrients delivered via winds may influence rhodolith communities in the Gulf and that upwelling likely did not contribute new nutrients in the Pacific (discussed below).

Regenerated nutrients

Increases in NH_4^+ and PO_4^{3-} observed in rhodolith samples could be explained by organismal excretions and decomposition (i.e. recycled nutrients). This is supported by both the large number and high biomass of cryptofauna present in rhodoliths (Fig. 3.4A), but also in the positive correlation between increasing rhodolith size and nutrient concentration observed in the Gulf (Table 3.2). Interestingly, while cryptofaunal biomass was also high and positively correlated with rhodolith size in the Pacific (Fig. 3.4B), there was no significant relationship between rhodolith diam. and nutrient concentration (Table 3.2). This may be due to increased abundance of sponges present inside rhodoliths at the Pacific sites, which were generally absent in the Gulf. Sponges can harbor species specific microbes which influence nitrogen cycling (Fiore et al. 2010, Perea-Blázquez et al. 2012) and could account for some of the observed differences between sites. The extent to which filter feeders and their symbionts influence nutrient pools or nitrogen cycling within rhodoliths requires further study. Regardless of their specific impacts, the observed pattern of elevated nutrients in rhodoliths was consistent across sites, as was the high abundance of cryptofauna.

Comparative data on nutrient dynamics or sources in rhodolith beds are sparse. Ballesteros (1988) analyzed nutrients in water column samples from the surface and 40 m in a Mediterranean rhodolith bed, but did not measure NH_4^+. Nitrate (~0.0–1.6 μM) and PO_4^{3-} (~0.0–0.06 μM) concentrations reported in his study were within the range or lower than those we report for beds in Baja (Figs. 3.1–3.3). As a part of a larger study, Halfar et al. (2006) also examined water column nutrients (10 m depth) associated with two rhodolith dominated areas in the Gulf of California and found average annual NO_3^- and PO_4^{3-} concentrations of ~3–4 μM and ~0.6–1.0 μM, respectively. These PO_4^{3-} concentrations are similar to water column nutrients reported in the present study however their NO_3^- concentrations are higher (Fig. 3.1). They did not measure NH_4^+ and suggested the importance of upwelling to nutrient delivery in the Gulf. Martin et al. (2007) quantified nutrient fluxes (NH_4^+, NO_3^-, Nitrite, PO_4^{3-}, Silica) from sediments to the water column in a rhodolith bed from France. Net community increases in N & P were attributed to bacterial mineralization of organic matter and faunal excretions given the large number of organisms associated with rhodolith beds. This is consistent with our findings.

Marine invertebrates and fish, which are or can be common in rhodoliths at our sites, are also known to add regenerated nutrients (NH_4^+ and PO_4^{3-}) to both temperate and tropical systems which can help organisms meet nutrient demands. Coral growth, for example, can be enhanced by fish excretions (Myer et al. 1983, Shantz & Burkepile 2014), as can growth of the alga *Sargassum* (Lapointe et al. 2014). Similarly, mussels can cause sediment nutrient enrichment and when in their presence, seagrasses can exhibit increased production (Peterson & Heck 2001). Research from intertidal habitats in the North Eastern Pacific has consistently highlighted the role mussel excretions (NH_4^+) play in increasing growth or abundance of associated algal species, even in upwelling regions (Bracken 2004, Pfister 2007, Aquilino et al. 2009). *Cladophora*, a green turf forming alga, also harbors many cryptic species, whose excretions are sufficient to meet all of the alga's N requirements (Bracken et al. 2007). Data from our study add to these and along with Martin et al. (2007) provide the first detailed investigations of nutrient recycling in rhodolith assemblages.

Temporal variability in NO_3^- in the Gulf followed strong seasonal cycles compared to sites in the Pacific (Figs. 3.1B–3.3B) suggesting new nitrogen sources may be delivered to the Gulf site via allochthonous sources. Increased NO_3^- in Jan 2013 and 2014 coincided with strong northwest winter winds that are reported for the Gulf (Alvarez-Borrego 1983). During these well mixed periods winds may seasonally push water and nutrients from the Gulf of California into our study site at the mouth of Bahía Concepción and could account for new N sources within this rhodolith bed. The negative correlation between water temperature and NO_3^- concentration observed at this site also supports nutrient advection via winds. Additionally, the area just north of the Los Machos site (Bahía de Santa Inés) is rich in nutrients Jan–Apr (Murillo Murillo 2005) when winds are strong enough to homogenize the water column. This area and others in the northern Gulf could be a source of nutrients in Bahía Concepción as has been proposed by others when used to explain winter phytoplankton blooms within the bay (Martínez-López & Gárate-Lizárraga 1994, 1997, Lechuga-Devéze et al. 2000, Palomares-García et al. 2002). The main upwelling period along the west coast of the Gulf is reportedly spring to summer (Alvarez Borrego 1983, Badan-Dangon et al. 1985) and does not likely contribute much of the NO_3^- measured in our study (Fig. 3.1). Terrestrial inputs of N or P are also unlikely new nutrient sources as there is very little freshwater input (except for late summer and fall tropical storms, which does not correspond to winter NO_3^- nor early summer PO_4^{3-} peaks) and anthropogenic influences are limited in this remote area of Baja (Mendoza-Salgado et al. 2006).

Water column NO_3^- data at sites in the Pacific were generally low ($< 1\mu M$) and not seasonally variable (Figs. 3.2B & 3.3B), suggesting these sites are not influenced by coastal upwelling. This is counter to reports by Cervantes-Duarte et al. (2013) who have worked extensively on nutrient dynamics near the entrance to Bahía Magdalena. Their research indicates upwelling from the California Current delivers NO_3^- to sites inside Bahía Magdalena annually Mar–Jun and is an important seasonal nutrient source. That we saw no increases in water column NO_3^- from Jan–Jun suggests that despite strong tidal currents in Bahía Magdalena, the reach of the California Current does not extend to mangrove channels farther north in the bay where our

sites are located or that our sampling frequency was not sufficient to detect upwelling (Zaytsev et al. 2003). It is also possible that nutrients are simply consumed by primary produces closer to the entrance of the bay and water column nutrients are depleted before arriving to our sites. Given the apparent low upwelling influence in canals of northern Bahía Magdalena reported in this study, NO_3^- available in rhodolith water samples and sediments may serve as alternate nutrient sources within the bay. Such inputs likely originate from other sources of new N via fixation and allochthonous inputs from mangrove litter which have been reported in non-rhodolith systems (Lapointe et al. 1987, Sánchez-Carrillo et al. 2009).

Role of microbes

While cryptofauna and strong winds can shape nutrient dynamics in rhodolith beds, the contribution of micro-organisms in this system must also be considered. In general, microbes can influence nutrient availability as they fix N, mineralize N & P, and oxidize NH_4^+ to produce NO_3^-, and all processes could influence nutrient dynamics at our sites. For example, although we attribute elevated NH_4^+ levels at our sites to animal excretion in rhodoliths, contributions from nitrogen fixing bacteria, diazotrophs, are also possible. This is particularly true for sites in the Pacific, where cryptofaunal biomass was lower compared to the Gulf, but NH_4^+ concentrations were still elevated. Additionally, all sites showed increased NH_4^+ in sediments relative to the water column, and sites in the Pacific occasionally had NH_4^+ levels in excess of those observed inside rhodolith samples. This is noteworthy, as all sediment cores inside and outside of beds in the Gulf and Pacific harbored an order of magnitude less infaunal biomass (Table 3.1) compared to rhodoliths of a similar size (Fig. 3.4) and would likely excrete less N waste. Mineralization of N and P could also explain these elevated nutrients in rhodoliths and sediments, where heterotrophic micro-organisms consume organic material liberating NH_4^+ and PO_4^{3-}, as is reported in marine sediments and was also suggested by Martin et al. (2007). Finally, elevated NO_3^- observed in rhodolith samples (Figs. 3.1B–3.3B) also indicate the rhodolith environment is subject to nitrifying heterotrophic bacteria which must be more abundant in rhodoliths and sediments than in the water column. Few studies have investigated microbial communities associated with rhodoliths. However, a study from Brazil suggests the bacterial composition within rhodoliths is unique compared to the water column and may play a

key part in biomineralization (Cavalcanti et al. 2014). Preliminary metagenomic work on rhodoliths from Pedregoso in the Pacific (McConnico, unpublished data) suggests microbial communities inside rhodoliths are also distinct from those in the water column and continued exploration of these microbial associations will help to clarify their no doubt important role in nutrient cycling and production in rhodolith beds.

Nutrient use by rhodoliths and community benefits

While rhodolith beds provide nutrients beyond those available in the water column, the question remains: do rhodoliths benefit from the elevated nutrient levels measured in this study? In general, low tissue nitrogen reported for rhodoliths in this study, slow growth rates in these two species [McConnico et al. 2014 (*L. muelleri*), Steller et al. 2007 (*L. margaritae*)] and limited work on other non-geniculate corallines (Björk et al. 1995, Ichiki et al. 2000) suggest rhodolith nutrient demands may be low. However, even slow growing organisms with low nutrient requirements may benefit from animal excretions. This may be especially true if nutrient availability in the environment is low or regenerated nutrients are in close proximity to the alga (Pedersen & Borum 1997, Taylor & Rees 1998). Data from our field incubations (Figs. 3.5 & 3.6) suggest rhodoliths may preferentially utilize NH_4^+, as is reported for other species (Bracken & Stachowicz 2006). However, while we attributed changes in incubation containers to assimilation by primary producers, we cannot rule out that declines in NH_4^+ and initial increases in NO_3^- could be caused by nitrifying bacteria which oxidized NH_4^+. Likewise, while rhodoliths were the largest primary producer in the incubation containers, it is possible that the microbiont community between rhodolith branches (phytoplankton, microbes and algal filaments) also contributed to changes in observed nutrient concentrations. Thus, nutrient depletion cannot be attributed solely to rhodoliths, but instead to the whole community. Rhodoliths could benefit from increased regenerated nutrients observed in this study during summer months, when growth rates for *L. muelleri* (McConnico et al. 2014) and *L. margaritae* peak (Steller et al. 2007) and N & P were high (Figs. 3.1–3.3) suggesting they likely do take advantage of cryptofaunal inputs. However, if rhodoliths do not require or use the extra nutrients, then they would presumably benefit other primary producers or microbes in close proximity (i.e. on top of rhodoliths or between their branches). An example of an alga that may benefit from these

regenerated nutrients are *Sargassum* recruits which have been observed at Los Machos after the summer (Foster et al. 2007) when water column nutrients are typically reduced (Fig. 3.1). While the specific benefit of regenerated nutrients to rhodoliths and associated species requires further study, it is clear that rhodoliths as foundation species play a role in nutrient cycling, and may be of particular importance in nutrient limited regions like the Gulf of California.

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A continuación se incluye copia del trabajo que ya ha sido publicado como producto del trabajo realizado durante el periodo de doctoral (2012–2016).

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, 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:
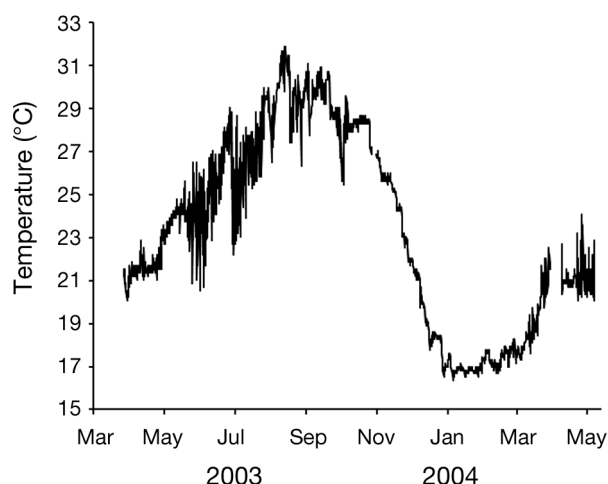
Fig. 1. Bottom temperature (~5 m) at Cabo Los Machos, March 2003 to May 2004. Data gaps during October 2003 and March 2004 occurred when logger was temporarily removed to download data

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
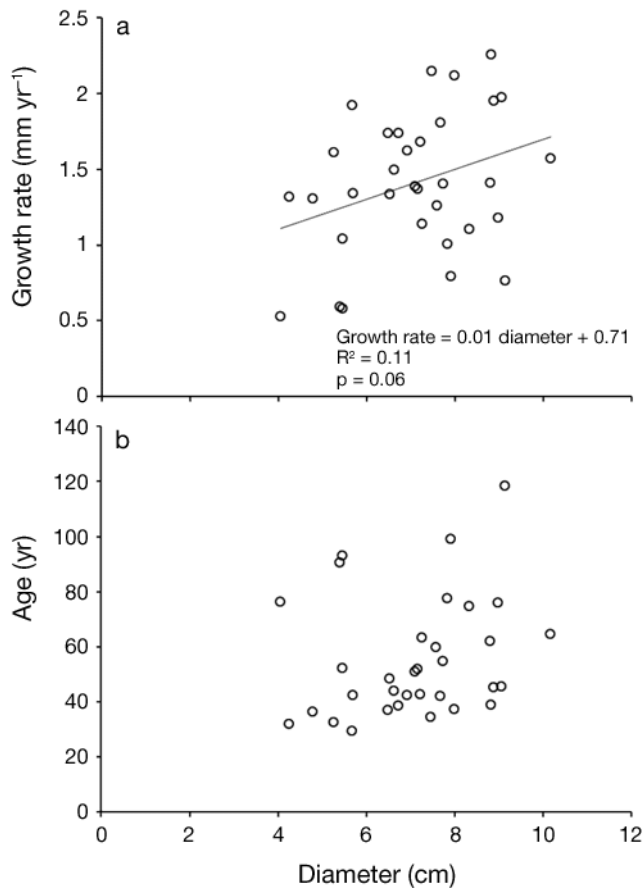
Fig. 2. *Lithothamnion muelleri* diameter vs. (a) annual growth rates (based on diametric extension); (b) age for stained rhodoliths growing in the field between October 2003 and October 2004 (n = 33 for both)
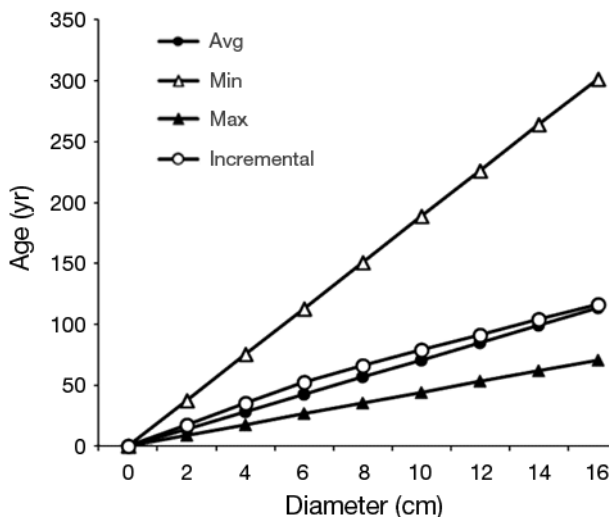

Fig. 3. Age projections for *Lithothamnion muelleri* 0–16 cm in diameter based on average (Avg), minimum (Min), maximum (Max), and incremental growth rates

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
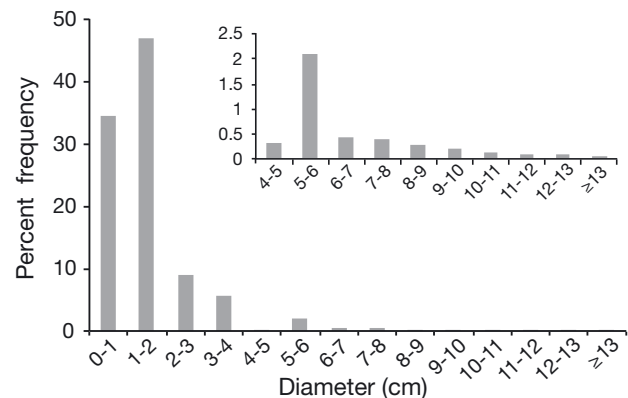

Fig. 4. Percent frequency of *Lithothamnion muelleri* (in cores and 3.14 m^2 quadrats) in March 2003 (n = 14 489 rhodoliths). Inset graph shows percent frequency of rhodoliths between 4–13 cm diameter re-plotted on a more appropriate scale
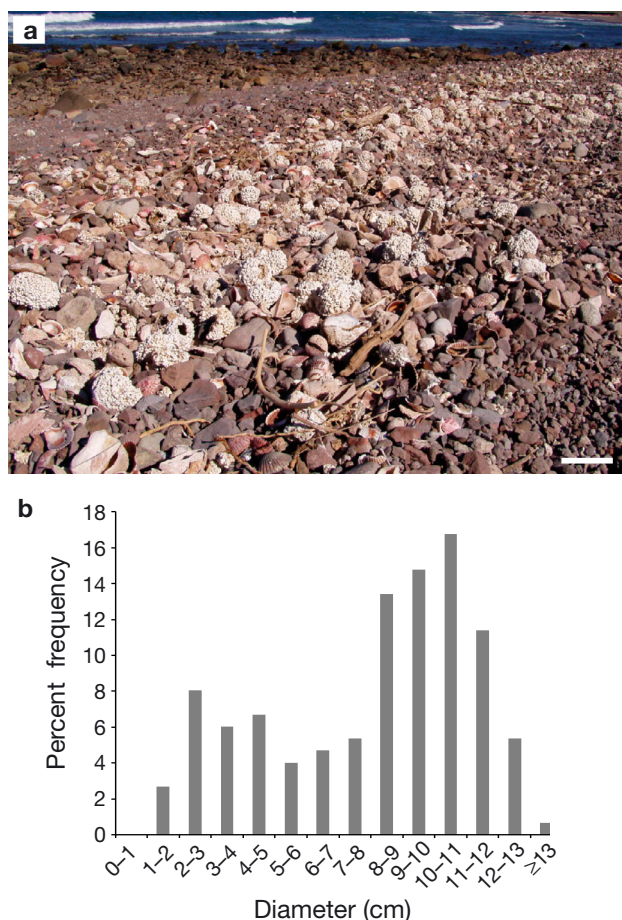
Fig. 5. *Lithothamnion muelleri*. (a) Dead, shore-cast rhodoliths (white bumpy spheres) in October 2003 after a tropical storm produced by Hurricane Marty (September 2003) passed over the study site (scale bar = ~10 cm); (b) size-frequency distribution of shore-cast rhodoliths encountered along transects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

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