Nutrient production in rhodolith beds: impact of a foundation species and its associates

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ABSTRACT: Foundation species harboring associated fauna and micro-organisms provide an opportunity to explore nutrient contributions from excretion and decomposition (recycled nutrients) relative to new inputs. Rhodoliths, free-living non-geniculate coralline algae, support diverse cryptofaunal and microbial assemblages which could supply regenerated nutrients to their hosts, but studies of such nutrient dynamics are limited. We assessed temporal variability in concentrations of dissolved inorganic nutrients (ammonium: NH_4^+, nitrate + nitrite: NO_x^-, and orthophosphate: PO_4^{3-}) associated with rhodolith beds on the Gulf of California and Pacific sides of Baja California Sur, Mexico, and considered potential sources of nutrient enrichment from cryptofauna, microbes and allochthonous inputs. Data suggest rhodoliths and/or sediments provide NH_4^+, NO_x^- and PO_4^{3-} in excess of water column availability, regardless of season or year. Cryptofaunal biomass was positively correlated with rhodolith diameter at all sites, and in some cases so was nutrient concentration. Ammonium and PO_4^{3-} enrichment in rhodoliths may be attributed to cryptofaunal excretion or decomposition by micro-organisms. While seasonal delivery of new nutrients (NO_x^-) via wind-induced water motion occurred in the Gulf, NO_x^- in the Pacific was likely impacted by microbial-mediated nitrification. Light and dark incubations showed that rhodolith assemblages may initially take up NH_4^+ over NO_x^-, but all nutrients were consumed in the presence and absence of light. This study highlights the importance of rhodoliths in coastal and estuarine environments not only as foundation species, but also for their role in nutrient cycling, especially in areas of seasonal nutrient limitation.

KEY WORDS: Rhodolith · Cryptofauna · Microbes · Nutrient recycling · Nitrogen · Phosphorus · Upwelling · Gulf of California · Bahía Magdalena · Bahía Concepción

INTRODUCTION

Foundation species provide many direct and indirect ecosystem services, including their potential to influence nutrient availability (Jones et al. 1994). Producers and consumers acting as foundation species can enrich the local nutrient supply via their own decomposition and excretion or by trapping nutrients from the surrounding environment as reported for kelps (Krumhansl & Scheibling 2012), terrestrial forests (Ellison et al. 2005), seagrass habitats (Hemminga et al. 1991) and/or mussel beds (Bracken 2004). Increases in recycled nitrogen or phosphorus from such sources, along with new nutrients via upwelling, fixation and/or weathering (Dugdale & Goering 1967, Paytan & McLaughlin 2007), in turn fuel primary/secondary production, shaping ecosystems from the bottom up.

Rhodoliths, non-geniculate coralline algae, are foundation species with a global distribution (Weber-

Van Bosse & Foslie 1904, Foster 2001) and the potential to influence nutrient dynamics in areas of high abundance. Aggregations, or beds, of the free-living algae provide habitat for numerous cryptofauna (macro- and microscopic species hidden within and among their branches), epiphytes and microbial organisms. Studies worldwide cite high biodiversity, unique species associations and the importance of rhodolith beds to fisheries (e.g. Bosence 1979, Steller et al. 2003, Kamenos et al. 2004, Neill et al. 2015). As with other foundation species harboring animals (Meyer et al. 1983, Taylor & Rees 1998, Bracken et al. 2007, Lapointe et al. 2014), it could be predicted that rhodolith associates may provide additional nitrogen and phosphorus to their hosts and the surrounding community. Such regenerated nutrients may be of importance in the tropics and subtropics, where rhodoliths are abundant and new nutrient inputs via upwelling or from land can be limited. However, detailed studies on nutrient production or fluxes from rhodolith beds are limited (Martin et al. 2007) despite their importance to understanding the high productivity associated with rhodolith communities.

Rhodolith communities are abundant on the Gulf of California and Pacific coasts of Baja California, Mexico, and provide model systems to examine nutrient cycling under seasonal nutrient limitation (Gulf) and in nutrient-rich estuarine environments (Pacific). Evaluation of nutrient availability associated with rhodoliths and the ambient environment would provide the first direct measure of nutrient production in rhodolith beds from this region. Comparisons of dissolved inorganic nutrients from not only between individual rhodolith branches, but also between the water column and surface sediments would allow for determination of the relative contribution of nutrients from specific sources. Sediments associated with rhodolith beds may be important given the high organic content supplied by mangroves in the Pacific (Chávez Rosales 2006) compared to carbonate sediments in the Gulf. Additionally, rhodoliths sit in and on top of sediments, at times partially buried, which may influence nutrient fluxes associated with rhodolith interstitial water. Such data sets coupled with information on the relationship between cryptofaunal biomass and nutrient availability in rhodoliths, as well as field incubations of rhodoliths, would allow for a preliminary contrast of the relative contribution of new vs. regenerated nutrients in rhodolith systems and their potential utilization by rhodoliths and their associates. These findings might be widely applicable and at present, largely unknown for rhodolith ecosystems globally.

Thus, the specific objective of this study was to determine temporal variability in dissolved inorganic nutrient concentrations (ammonium: NH_4^+, nitrate + nitrite: NO_x^-, and orthophosphate: 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 and sediments, and from between rhodolith branches to assess if regenerated nutrients associated with rhodoliths were greater than surrounding nutrient pools. Additionally, sediments were experimentally removed from rhodoliths to determine if they impacted rhodolith nutrient content. We further investigated the relationship between nutrient availability, rhodolith size and cryptofaunal biomass to determine if larger rhodoliths harbor more cryptofauna and possibly have access to more regenerated nutrients. Rhodolith branch tips were analyzed for total nitrogen content to assess their nitrogen status, and field incubations were done to determine potential nutrient uptake by rhodoliths and contributions by microbial organisms.

MATERIALS AND METHODS

Study sites

Research was done from January 2013 to April 2015 at 2 sites (Pedregoso and Comisión Federal de Electricidad [CFE]) within Bahía Magdalena on the Pacific coast of Baja California Sur, Mexico (between 24° 54′– 24° 48′ N and 112° 05′–112° 06′ W) and 1 site (Los Machos) at the mouth of Bahía Concepción in the Gulf of California (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 are lined by mangroves on 1 or both sides. Sediments here are fine grain (<500 µm), composed of sand and silt or mud. This lagoon complex represents a nutrient-rich 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 (usually closer to the lagoon entrance). Nutrients near the sediment–water interface fall within these concentrations, except that NH_4^+ and PO_4^{3-} can reach up to 12.2 and 2.08 µM, respectively, near the lagoon entrance (Cervantes-Duarte et al. 2013).

The Gulf rhodolith bed (Los Machos) ranges from 2–8 m depth and is a mixture of the rhodolith *Lithothamnion muelleri* and the brown alga *Sargassum*

horridum. Sediments here are coarse, composed of rhodolith fragments and siliciclastic sand, intermixed with larger boulders. The central Gulf of California 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 and the Gulf study site, water column nutrients can be seasonally limited (~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 (Murillo Murillo 2005).

Detailed site descriptions, including a map of the study sites, temperature data and temporal variation in rhodolith communities at all sites (during 2013–2015), are reported in McConnico et al. (2017). Foster et al. (2007), Avila & Riosmena-Rodríguez (2011) and McConnico et al. (2014) also provided additional quantitative assessments of these same beds. Although sites on the 2 sides of the Baja California peninsula are composed of different rhodolith species, their morphology and size are similar, and both species harbor many cryptofauna. Rhodolith beds were accessed using small boats and a combination of SCUBA or snorkel depending on tidal height. Bottom water temperature was monitored during the study using HOBO Pendant® data loggers (model UA-002-08; 1 $site^{-1}$) and digital thermometers (from scuba consoles). Average monthly temperatures ranged from ~17.5–20°C in January to 28–31°C during August and September, with 2013 generally cooler than 2014/2015 (McConnico et al. 2017).

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

Variation in nutrient availability was determined from water samples collected inside and outside of all rhodolith beds approximately seasonally, every 3–5 mo. Water column, sediment and interstitial water from rhodolith samples were collected within each bed (10 replicates each taken at random locations along a 30 m transect placed in the middle of the bed). Only sediment samples were collected outside of the bed (10 replicates were distributed 50–100 m from the bed edge and obtained using a random number 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. All were sampled with 50 ml sterile syringes. To obtain water samples from between rhodolith branches, a flexible plastic sheet was gently wrapped over the surface of the alga and secured with a small piece of wire to retain interstitial water. This collection technique allowed for the plastic to snugly cover the entire rhodolith, minimizing dilution or escape of interstitial water. Rhodoliths were brought to the surface, placed in a funnel, the plastic punctured and contents drained into a sterile container. Total sample volume extracted typically varied from ~30–100 ml depending on rhodolith size (~3–13 cm diameter), but nutrient estimates from all sample types are reported based on the sample volume analyzed so they could be directly comparable. When <30 ml of sample was available, nutrient analysis was prioritized as follows: NH_4^+, NO_x^- 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 the Gulf site in October 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_x^- and PO_4^{3-} within approximately 1 wk of collection. Samples not immediately analyzed were frozen, and all were analyzed using standard analytical techniques for seawater (Strickland & Parsons 1972). Nutrient detection limits were 0.5 µM for NH_4^+, and 0.1 µM for NO_x^- and PO_4^{3-}. When nutrient concentrations were below detectable levels, 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 beds, which represented the lowest concentrations observed in the study. This approach was more conservative than using 0 µM and did not unfairly bias data interpretation. Nutrient data are reported as average µM concentration for each nutrient and sample type, at each site. Parametric and non-parametric data analyses were not done, as data violated the assumptions of such tests (Underwood 1997), but patterns were clear and compared as trends.

Temperature and nutrient concentration

Average NH_4^+, NO_x^- and PO_4^{3-} concentrations from water column samples (taken at 1 m above the

rhodolith beds) were plotted against average monthly water temperature at a similar depth to determine if the relationship was significant and corresponded to upwelling or seasonal wind events. As field temperature data were unavailable at the Gulf site in 2013, average temperature for sites in the Pacific were used in analyses and considered comparable (McConnico et al. 2017). Analyses were done for all 3 sites and nutrient types, but only significant linear regressions are reported.

Sediment effects on rhodolith nutrient concentration

Field experiments at the Gulf site and in the Pacific (Pedregoso) were done in October 2014 to determine if sediment trapped between rhodolith branches impacted observed nutrient concentrations in rhodolith interstitial water. Five rhodoliths (5–8 cm diameter with <10% epiphyte cover) were haphazardly collected from each site and lightly shaken underwater (and over collection containers) to remove interstitial sediments. Once sediments were removed, rhodoliths were attached with elastic straps on top of plastic tubs affixed to metal posts, raised 30 cm above the rhodolith beds (see Fig. A1 in the Appendix). This mounting technique allowed for unobstructed water flow well above the sediment influence and enabled us to capture cryptofauna that fled rhodoliths during the experiment. Experimental units were placed at random points along a 30 m transect in the middle of each bed. After 48 h, fauna that had fled rhodoliths and landed in collection containers were preserved in 70% EtOH for biomass determination, and rhodolith interstitial water was collected using the same technique previously described for seasonal sampling. These water samples were compared to those collected from 5 unmanipulated rhodoliths (randomly occurring along the same 30 m transect at each site) on the same day, at the same time. All samples were GF/F filtered and stored on ice in the dark until analyzed for NH_4^+, NO_x^- and PO_4^{3-}. Data were analyzed using separate t-tests for each site and nutrient type, except that a Welch's t-test was used to compare NH_4^+ data at Pedregoso as variances were unequal (Ruxton 2006). Additionally, only 4 samples were included in the analyses at Pedregoso. Experiments were repeated there in April 2015 with an increased sample size (n = 9), but the results were similar to those in October 2014 and are not reported herein.

Fauna in rhodoliths and sediments

To determine the relationship between rhodolith diameter, cryptofaunal biomass and nutrient production, water samples were collected (using the previously described technique) from 15 rhodoliths of varying sizes (~3–8 cm diameter) at the 2 Pacific sites and 20 rhodoliths (~3–13 cm diameter) from the Gulf site during January 2013. After extracting interstitial water, rhodoliths were fixed in formalin (~10%) and 24 h later preserved in 70% EtOH until they could be broken, and fauna sorted. Rhodolith diameter was determined to the nearest mm based on average x, y, z axial measurements using Vernier calipers, and fauna retained on a 500 µm sieve were identified to phylum and counted. Biomass estimates were based on wet weights taken after blotting specimens dry on filter paper and then re-suspending them in distilled water of a known mass. Regression analysis was used to determine the relationship between rhodolith diameter and cryptofauna biomass, and between rhodolith diameter and nutrient (NH_4^+, NO_x^- and PO_4^{3-}) concentration of rhodolith interstitial water. The latter comparison was not made at CFE, as nutrient data for rhodoliths were not available at this site/date.

To determine if sediments inside and outside of the bed also harbored organisms which could impact nutrient effluxes, infaunal invertebrates were sampled in sediments at each site during June and July 2014. Five ~7 cm diameter cores, pushed to 6 cm depth, were taken at random locations along a 30 m transect inside of beds, and 5 were taken outside of beds using a random number 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.

Light and dark incubations

Field incubations were done at the Gulf site (October 2014) and Pedregoso in the Pacific (April 2015) to determine nutrient uptake by rhodoliths in the light and dark. Twelve rhodoliths (~6–8 cm diameter, with <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 (~11:00–14:00 h). Six experimental units

were exposed to ambient light (covered by a grey mesh screen to mimic subtidal light levels), and 6 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 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_x^- 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 per experimental container.

Rhodolith nitrogen content

Tissue nitrogen was quantified to determine nutrient status of rhodoliths at all sites. Branch tips (n = 10, ~1–2 mm pieces) were removed from 5 rhodoliths at each site during June and July 2014. Care was taken to remove pigmented surfaces of the rhodoliths and minimize addition of extra inorganic biomass. Samples were air dried and % nitrogen based on total dry tissue determined using an ECS 410 Elemental Analyzer at San Diego State University's analytical facility.

RESULTS

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

Average NH_4^+ concentrations at the Gulf site ranged from ~0.5–15 µM during 2013–2014 (Fig. 1A). Rhodolith samples had the highest NH_4^+ content throughout much of the study, except during June/July 2013 when high NH_4^+ was also detected in sediments outside the bed. Intermediate concentrations were often seen in sediment samples inside and outside the bed and lowest concentrations were observed in the water column (1 m and 10 cm above the bed). Rhodolith and sediment samples showed strong seasonal nutrient cycles, with highest levels in summer or late spring. Seasonal NH_4^+ patterns were absent in water column samples (Fig. 1A).

Nitrate + nitrite (NO_x^-) concentration was ~0.1–8.0 µM at the Gulf site (Fig. 1B). Nitrate + nitrite (NO_x^-) was always greatest in rhodoliths, followed by sediments inside the bed, while sediments outside

the bed and water column samples were typically lowest throughout the study. Nitrate + nitrite (NO_x^-) concentration was seasonally higher in January (2013 and 2014) for all sample types (Fig. 1B).

Phosphorus concentrations at the Gulf site ranged from ~0.7–5.4 µM (Fig. 1C). The highest concentrations were typically observed in rhodoliths except during June/July 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-} concentrations in sediments outside the bed were reduced (compared to rhodoliths) and/or were similar to water column samples (Fig. 1C).

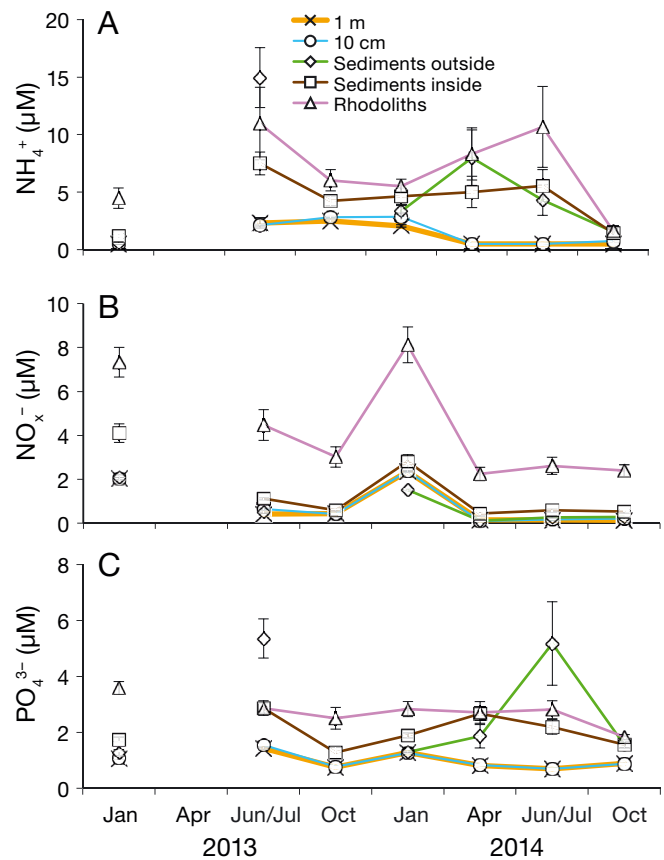At the Pacific sites, NH_4^+ ranged from 0.5–23.4 µM at Pedregoso and 0.5–16.4 µM at CFE

Fig. 1. Nutrient concentrations (mean ± SE) at the Gulf of California site: (A) NH_4^+, (B) NO_x^- and (C) PO_4^{3-}. In the key, '1 m' and '10 cm' are distances above rhodoliths in the water column, 'outside' and 'inside' sediments refer to samples taken from the top layer of sediments outside and inside of rhodolith beds, respectively, and 'rhodolith' refers to water samples collected from in between rhodolith branches. For all sample types n = 10 except that no samples were taken for sediments outside of the bed in October 2013
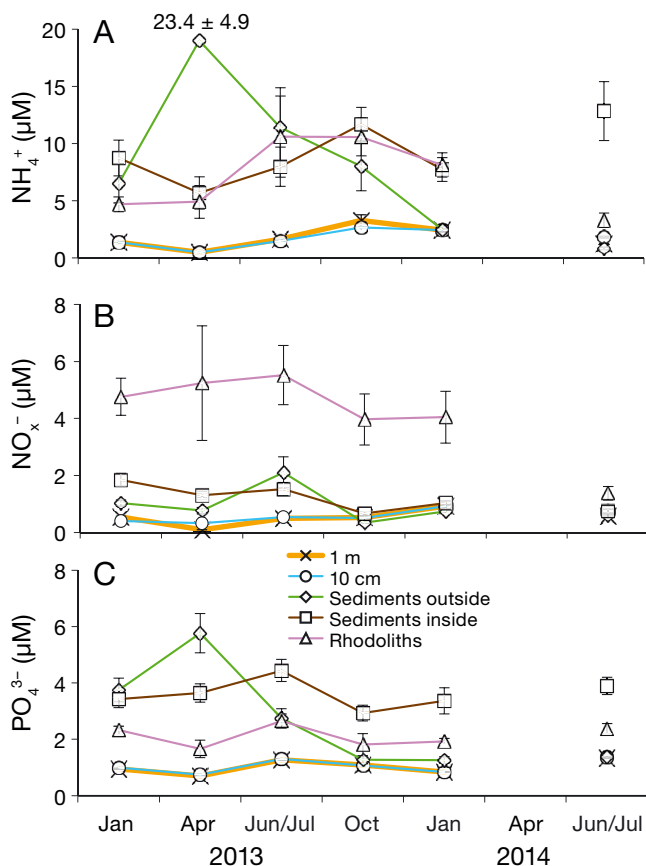
Fig. 2. Nutrient concentrations (mean ± SE) at a Pacific site (Pedregoso): (A) NH_4^+, (B) NO_x^- and (C) PO_4^{3-}. Definitions as in Fig. 1. For all sample types n = 10 except n = 9 for NO_x^- and n = 7 for PO_4^{3-} in rhodoliths in April 2013, and n = 8 for NO_x^- in water samples from '10 cm' June/July 2014

Fig. 3. Nutrient concentrations (mean ± SE) at a Pacific site (Comisión Federal de Electricidad, CFE): (A) NH_4^+, (B) NO_x^- and (C) PO_4^{3-}. Definitions as in Fig. 1. For all sample types n = 10 except n = 0 for sediments and rhodoliths in January 2013, and n = 8 for PO_4^{3-} in rhodoliths in April 2013

(Figs. 2A & 3A). Sediments inside and outside the bed, as well as rhodoliths often had the highest NH_4^+ content at both sites, while lowest NH_4^+ concentrations were detected in water column samples. Ammonium concentrations in sediments outside the bed were similar to low levels observed in the water column at Pedregoso in January and June/July 2014 and October 2013 through June/July 2014 at CFE (Figs. 2A & 3A).

Nitrate + nitrite ranged from ~0.1–5.5 µM at Pedregoso and was usually higher than observed at CFE (~0.1–3.0 µM; Figs. 2B & 3B). Nitrate + nitrite concentrations were highest in rhodoliths from both sites throughout the study, except during June/July 2013 when high levels were also detected in sediments inside the bed at CFE. Rhodolith samples at Pedregoso contained more NO_x^- than at CFE during all sampling dates. Sediments inside of the bed were usually higher in NO_x^- than sediments outside of beds, and the lowest concentrations were seen in
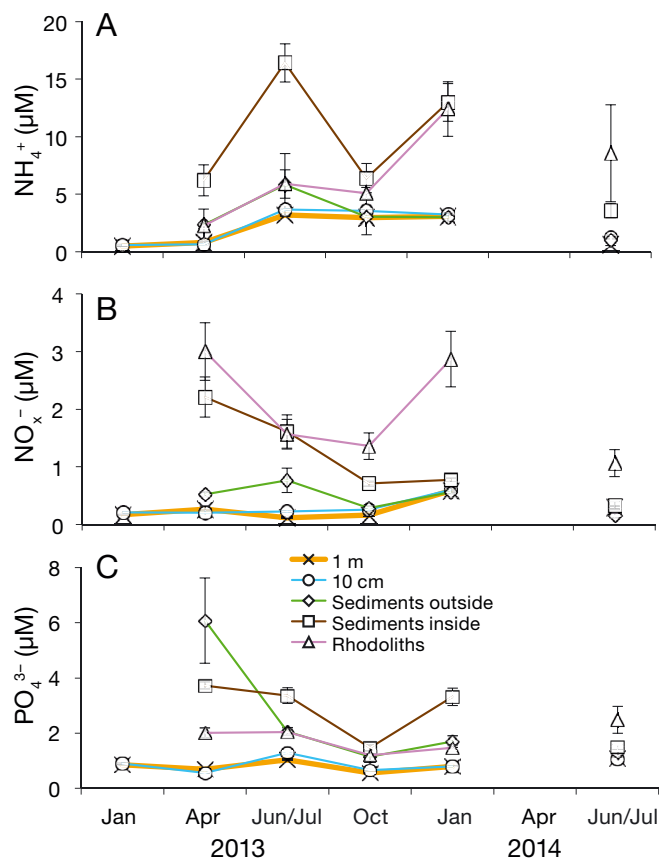
water column samples at both sites. Nutrient concentration throughout the study was more variable from sampling date to sampling date at CFE compared to Pedregoso, especially for rhodolith interstitial water (Figs. 2B & 3B)

Phosphorus concentrations ranged from 0.7–5.8 µM at Pedregoso and 0.6–6.1 µM at CFE (Figs. 2C & 3C). The highest concentrations were frequently associated with sediments inside the bed at both sites, except in April 2013 when PO_4^{3-} levels peaked in sediments outside of both beds and were high in rhodoliths at CFE during June/July 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 that rhodolith samples contained the greatest PO_4^{3-} concentration during June/July 2014. Phosphorus concentrations were lowest in water column samples at both sites throughout the study (Figs. 2C & 3C).

Temperature and nutrient concentration

Nitrate + nitrite (NO_x^-) was negatively correlated to water temperature at the Gulf site ($R^2 = 0.77$, $F_{1,6} = 17.10$, $p = 0.01$). No other nutrient vs. temperature regressions were significant.

Sediment effects on rhodolith nutrient concentration

Sediment removal from rhodoliths had no effect on nutrient concentrations in rhodolith interstitial water at the Gulf site (NH_4^+: $t_8 = -0.96$, $p = 0.36$; NO_x^-: $t_8 = -1.55$, $p = 0.16$; PO_4^{3-}: $t_8 = 0.84$, $p = 0.43$; Fig. 4A). Experimental results were also not significant at Pedregoso (Pacific site) (NH_4^+; Welch's $t_3 = -1.49$, $p = 0.23$; NO_x^-: $t_6 = -0.50$, $p = 0.63$; PO_4^{3-}: $t_6 = 0.58$, $p = 0.58$; Fig. 4B). However, average NH_4^+ concentration was 1.5 µM greater in samples from unmanipulated controls compared to samples where sedimen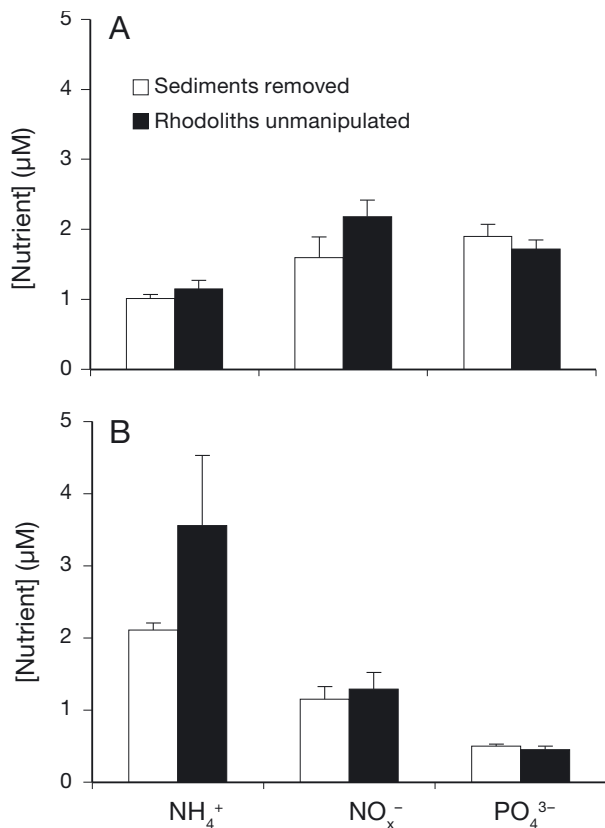ts were removed from rhodoliths. Unequal variance and small sample size may have prevented detection of significant differences. Biomasses of organisms that fled rhodoliths at the Gulf and Pacific sites were 0.02 ± 0.01 g and 0.13 ± 0.05 g, respectively, and were considered negligible.

Fauna in rhodoliths and sediments

Faunal biomass ranged from 0.1–16.9 g at the Gulf site, 0.3–12.1 g at Pedregoso and 0.4–14.0 g at CFE in the Pacific, with rhodoliths ~6–8 cm in diameter averaging ~3–4 g biomass ind.$^{-1}$. Cryptofaunal biomass increased with rhodolith diameter, and the relationship was significant at all sites (Fig. 5). Cryptofauna were generally more numerous at the Gulf site (118–3447 ind. rhodolith^{-1}) than in the

Fig. 4. Nutrient concentrations (mean ± SE) for rhodoliths with 'sediments removed' and 'rhodoliths unmanipulated' with sediments in place from (A) the Gulf of California site and (B) a Pacific site (Pedregoso); n = 5 for each sample type at the Gulf site and n = 4 at Pedregoso
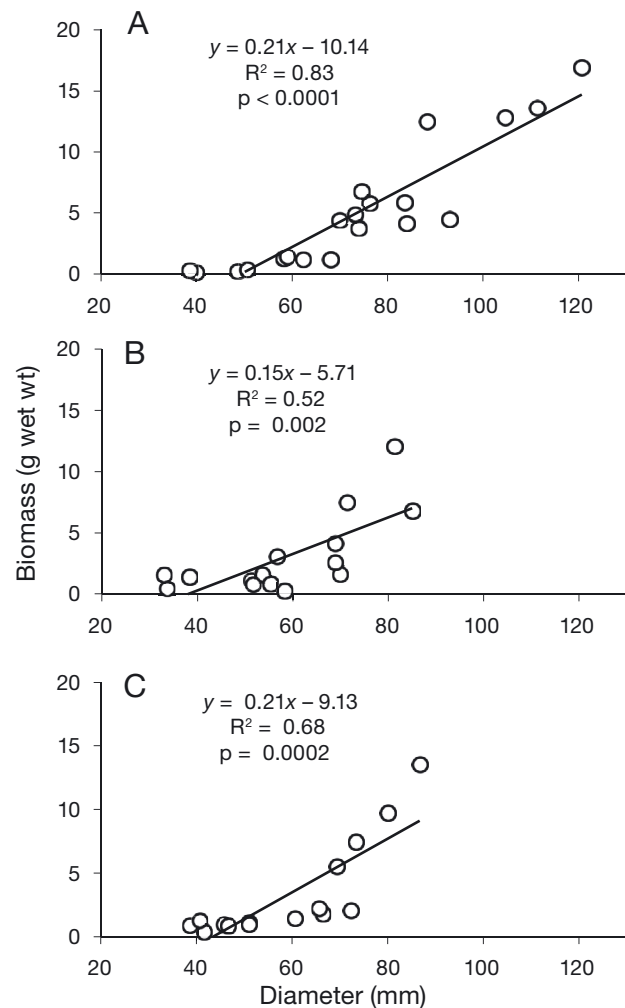
Fig. 5. Total cryptofaunal biomass vs. rhodolith diameter (January 2013) at (A) the Gulf of California site (n = 20) and in the Pacific at (B) Pedregoso (n = 15) and (C) Comisión Federal de Electricidad (CFE, n = 15)

Table 1. Biomass (mean ± SE wet wt in g) and % relative biomass of cryptofaunal taxa and macroalgae per rhodolith collected at the Gulf of California site (Los Machos) and in the Pacific (Pedregoso and Comisión Federal de Electricidad [CFE]) during January 2013. 'Non-annelid worms' include Platyhelminthes, Nematoda and Nemertea

Taxon	Los Machos		Pedregoso		CFE	
	Biomass (n = 20)	% Relative biomass	Biomass (n = 15)	% Relative biomass	Biomass (n = 15)	% Relative biomass
Annelida	0.93 ± 0.19	18.18	0.42 ± 0.09	13.63	0.61 ± 0.13	18.60
Arthropoda	0.35 ± 0.07	6.84	0.11 ± 0.02	3.45	0.05 ± 0.01	1.62
Bryozoa	0.70 ± 0.28	13.70	0	0	0	0
Chordata (tunicates)	0.98 ± 0.26	19.16	0.02 ± 0.01	0.58	0.21 ± 0.08	6.39
Chordata (fishes)	0	0	0	0	0.02 ± 0.003	0.55
Cnidaria	0.06 ± 0.03	1.11	0.43 ± 0.10	14.17	0.10 ± 0.03	3.11
Echinodermata	1.25 ± 0.37	24.56	0.13 ± 0.04	4.16	0.14 ± 0.04	4.25
Mollusca	0.37 ± 0.11	7.33	0.36 ± 0.13	11.79	0.68 ± 0.26	20.88
Non-annelid worms	0.08 ± 0.02	1.65	0.001 ± 0.000	0.02	0.01 ± 0.01	0.18
Porifera	0.01 ± 0.00	0.10	1.55 ± 0.69	50.74	1.45 ± 0.62	44.42
Unknown 1 (possible tunicates)	0.23 ± 0.05	4.54	0	0	0	0
Unknown 2 (unidentified taxa)	0.01 ± 0.01	0.24	0.0001 ± 0.0001	0	0	0
Macroalgae	0.13 ± 0.04	2.59	0.04 ± 0.03	1.44	0.0003 ± 0.0002	0.01

Pacific: Pedregoso (57–1729 ind. rhodolith^{-1}) and CFE (154–829 ind. rhodolith^{-1}). Annelids, arthropods, mollusks and echinoderms accounted for much of the biomass or abundance at all 3 sites. In addition to these taxa, biomass of tunicates and epiphytic bryozoans was also particularly high at the Gulf site, and at Pacific sites cnidarians and/or sponges (Porifera) accounted for much of the biomass (Table 1). Interestingly, rhodoliths at CFE occasionally harbored solitary tunicates (~3 cm diameter) and fish (~3 cm long) inside thalli, and larger gastropods (2–3 cm long) on top of thalli. This was not typical of other sites.

Infaunal biomass was low in sediment cores taken inside and outside of rhodolith beds (Table 2). Average biomass was <0.2 g core^{-1} for all sites and sample types. At the Gulf site and CFE (Pacific), biomass was slightly greater from cores inside the bed compared to outside, but at Pedregoso (Pacific), biomass was similar in- and outside of the bed. In general, core samples were dominated by nematodes, tanaids, annelids, and occasionally, small gastropods.

Table 2. Infaunal biomass (mean ± SE wet wt in g) from sediment cores inside and outside of rhodolith beds at the Gulf of California site (Los Machos) and in the Pacific (Pedregoso and Comisión Federal de Electricidad [CFE]) during June/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 concentration was positively correlated with rhodolith diameter at the Gulf site (Fig. 6A–C). The relationship was not significant at Pedregoso in the Pacific (Fig. 6D–F). Data outliers, which could not be justifiably removed, partially impacted these results.

Light and dark incubations

Changes in nutrient concentrations during the 2 h incubation were similar in light and dark containers at the Gulf site (Fig. 7A–C). Ammonium concentrations declined by ~1–2 µmol rhodolith^{-1} over the 2 h experiment, while PO_4^{3-} was reduced only slightly. Nitrate + nitrite increased during the first hour and then declined in the second hour. Based on the difference between average nutrient concentration for light and dark treatments at time 0 and 60 min, the ratio of NH_4^+ depletion to NO_x^- production after the first hour of incubation was 1.5:1.

Nutrient depletion was similar in light and dark containers at Pedregoso in the Pacific (Fig. 7D–F). 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_x^- 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. Based on the difference between average nutrient concentration for light and dark treatments at time 0 and 30 min, the ratio of NH_4^+ depletion to NO_x^- production after 30 min of incubation was ~8:1.
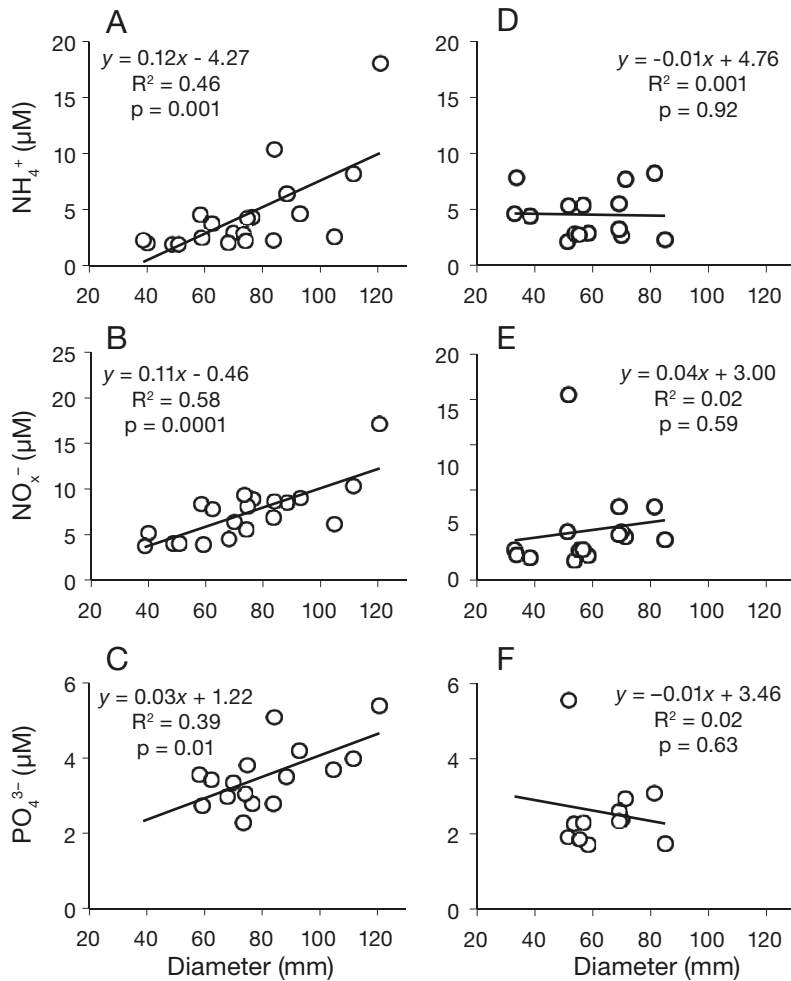
Fig. 6. Nutrient concentrations (NH_4^+, NO_x^- and PO_4^{3-}) of rhodolith interstitial water vs. rhodolith diameter (January 2013) (A–C) at the Gulf of California site and (D–F) in the Pacific (Pedregoso)

Rhodolith nitrogen content

Average % nitrogen in rhodoliths from the Gulf was 0.14 ± 0.01, while in the Pacific, % nitrogen was 0.26 ± 0.02 at Pedregoso and 0.21± 0.01 at CFE.

DISCUSSION

Our data show that rhodolith beds on both the Gulf and Pacific sides of Baja California modify their local environment, creating nutrient hotspots throughout much of the year. Elevated nutrient concentrations between rhodolith branches and sediments compared to water column samples were consistent at all 3 sites and were 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). The precise mechanism for nutrient enrichment was not identified, but investigations of cryptofaunal biomass in relation to rhodolith size, high nutrient content in sediments, as well as field incubations, suggest that cryptofauna along with microbial activity may account for increased nutrient availability. Temporal trends in water column nutrient availability indicate that 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

Organismal excretion and decomposition (i.e. recycled nutrients) may account for increases in NH_4^+ and PO_4^{3-} observed in rhodoliths. The large number and high biomass of cryptofauna present in rhodoliths supports this, as does the positive correlation between rhodolith size and nutrient concentration observed in the Gulf. Interestingly, while cryptofaunal biomass was also high and positively correlated with rhodolith size in the Pacific, there was no significant relationship between rhodolith diameter and nutrient concentration. This may indicate that distinct faunal communities associated with each site, and especially differences between the Gulf and Pacific sites, have differential impacts on local nutrient recycling. This can be partially attributed to differences in excretion rates among the dominant taxa at each site. Additionally, sponges which accounted for nearly half the biomass inside rhodoliths at Pacific sites were negligible at the Gulf site and may harbor species-specific microbes which can influence nitrogen cycling (Fiore et al. 2010, Perea-Blázquez et al. 2012). Alternatively, it is also possible that the varying availability and sources of new nutrients (see below) in each ecosystem may influence cryptofaunal composition and in turn species composition may also impact local nutrient recycling, as proposed by Cardinale et al. (2009) for stream systems. As sediment removal experiments were not significant in the Gulf or Pacific, it does not appear that fine sediments trapped
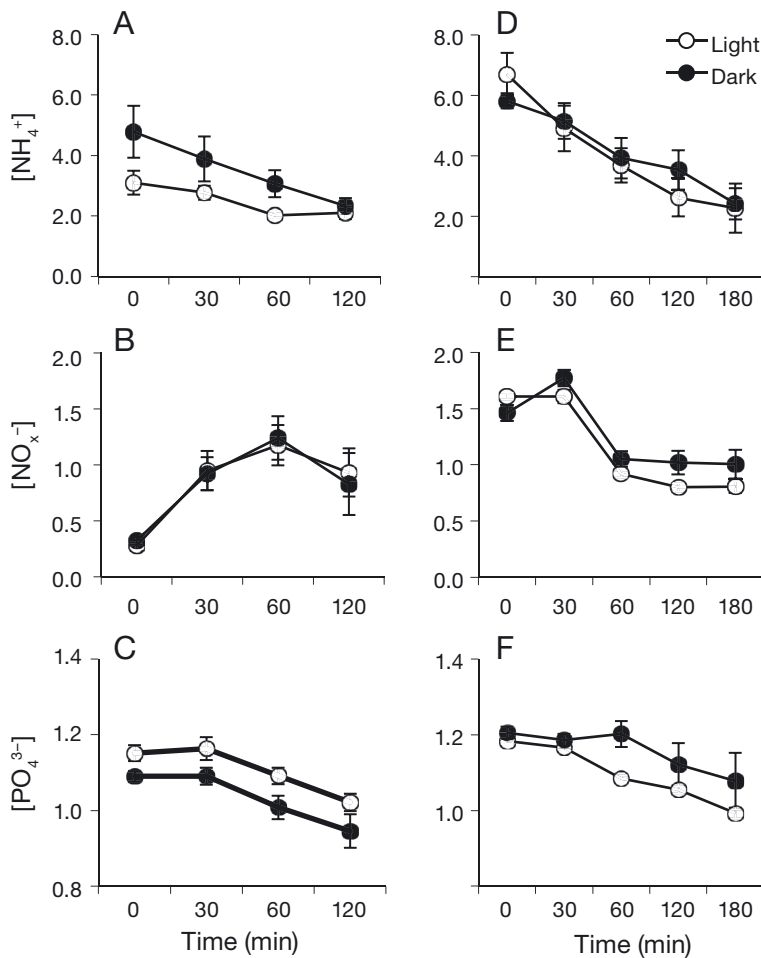
Fig. 7. Nutrient concentrations (NH_4^+, NO_x^- and PO_4^{3-}, mean ± SE µmol rhodolith^{-1}) for incubations under 'light' and 'dark' conditions (A–C) at the Gulf of California site in October 2014 and (D–F) in the Pacific (Pedregoso). Note that n = 6 per treatment, and at time '0,' nutrient concentrations are reported as µmol container^{-1}

a larger study, Halfar et al. (2006) also examined water column nutrients associated with 2 rhodolith-dominated areas in the Gulf of California. They did not measure NH_4^+ and cited the importance of upwelling to nutrient delivery in the Gulf. Martin et al. (2007) quantified nutrient fluxes (NH_4^+, nitrate, nitrite, PO_4^{3-} and silica) from sediments to the water column in a rhodolith bed from France. Net community increases in nitrogen and phosphorus 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 and those working on nutrient enrichment by organisms in other systems (e.g. corals: Meyer et al. 1983, Shantz & Burkepile 2014; mussels/seagrasses: Peterson & Heck 2001; algae: Bracken 2004, Bracken et al. 2007, Pfister 2007, Aquilino et al. 2009, Lapointe et al. 2014).

New nutrients

Despite prior characterization of the Bahía Magdalena Lagoon Complex as an upwelling influenced area, only the Gulf site followed strong seasonal cycles in NO_x^- availability, suggesting that new nitrogen may be delivered to each site via distinct allochthonous sources. Increased NO_x^- in January 2013 and 2014 coincided with strong northwest winter winds reported for the Gulf (Alvarez-Borrego 1983) which may seasonally push cold water and nutrients from the Gulf of California into the mouth of Bahía Concepción and could account for new nitrogen within this rhodolith bed. This is supported by the negative correlation between water temperature and NO_x^- concentration observed at this site and reports by others (Martínez-López & Gárate-Lizárraga 1994, 1997, Lechuga-Devéze et al. 2000, Palomares-García et al. 2002, Murillo Murillo 2005). Additionally, 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 given its timing, does not likely contribute much of the NO_x^- measured in the present study. Terrestrial nitrogen and phospho-

between rhodolith branches impacted nutrient content in rhodolith interstitial water, and would not account for observed site differences. The extent to which each of these factors influences nutrient pools or nitrogen cycling within rhodoliths requires further study and has interesting implications regarding controls of productivity and stability within rhodolith ecosystems.

While the exact mechanism of nutrient enrichment is unclear, comparative data on nutrient dynamics or sources in rhodolith beds are sparse. Ballesteros (1989) 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 that study were within the range or lower than those we report for beds in Baja. As a part of

rus are also unlikely new nutrient sources, as fresh-water input is limited and does not correspond to winter NO_x^- nor early summer PO_4^{3-} peaks, and anthropogenic influences are also limited in this remote area of Baja (Mendoza-Salgado et al. 2006).

Water column NO_x^- concentrations at Pacific sites were low (<1 µM) and not seasonally variable, suggesting they are not influenced by coastal upwelling. This is counter to previous reports of seasonal upwelling (March to June) inside the entrance of Bahía Magdalena (Cervantes-Duarte et al. 2013). That we saw no increases in water column NO_x^- from January to June suggests that despite strong tidal currents in Bahía Magdalena, the reach of the California Current does not extend into northern mangrove channels where our study sites are located or that sampling frequency was insufficient to detect upwelling (Zaytsev et al. 2003). Given the low upwelling influence reported in the present study, NH_4^+ 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 nitrogen via fixation and allochthonous inputs from mangrove leaf litter, which are important contributors of organic material in Bahía Magdalena (Chávez Rosales 2006) and have been reported for non-rhodolith systems (Lapointe et al. 1987, Sánchez-Carrillo et al. 2009).

Role of microbes

While cryptofaunal inputs and strong winds may partially shape nutrient dynamics in rhodolith beds, micro-organisms likely contributed as well. Specifically, nitrogen fixation and mineralization of nitrogen and phosphorus in rhodoliths and sediments could have contributed to elevated NH_4^+ and/or PO_4^{3-} at study sites, as previously reported for coral reef sediments (Capone et al. 1992) and rhodoliths (Martin et al. 2007). This would account for elevated NH_4^+ concentrations in sediments from Pacific sites compared to rhodoliths even though all sediment cores harbored an order of magnitude less infaunal biomass and would likely excrete less waste. These effects were more pronounced at Pacific sites, where sediments are fine grained and enriched by mangrove litter. The resulting high organic content in sediments would support increased microbial activity and ultimate availability for use by higher trophic levels as was also suggested in Bahía Magdalena by Chávez Rosales (2006). Finally, elevated NO_x^- observed in rhodolith samples indicated that the rhodolith envi-

ronment is subject to nitrifying bacteria, which could be more abundant in rhodoliths and sediments than in the water column. While nitrite was not monitored continuously in the present study, it was greater in rhodoliths compared to water column and sediment samples at the Gulf site when assessed in October 2014 (L. McConnico unpubl. data). This further supports increased nitrification within rhodolith interstitial spaces. Research on microbial communities associated with rhodoliths is limited, but they may play a key role in biomineralization (Cavalcanti et al. 2014). Preliminary metagenomic work on rhodoliths from Pedregoso in the Pacific (L. McConnico unpubl. data) suggests that rhodolith microbial communities are distinct from those in the water column. Continued exploration of these microbial associations will help clarify their role in nutrient cycling within rhodolith beds.

Nutrient use by rhodoliths and potential community benefits

While rhodolith beds provide nutrients beyond those available in the water column, the question remains: Can rhodoliths or their associated community benefit from increased nutrient concentrations? In general, low nitrogen content reported for rhodoliths in the present study, slow growth rates (McConnico et al. 2014) and limited work on other non-geniculate corallines (Björk et al. 1995, Ichiki et al. 2000) indicate that rhodolith nutrient demands may be low. However, even slow-growing organisms with low nutrient requirements may benefit from recycled nutrients (Pedersen & Borum 1997, Taylor & Rees 1998). While field incubations indicate that nitrification accounted for some of the observed NH_4^+ depletion, ratios of NH_4^+ removal to NO_x^- production suggest at least some of the NH_4^+ was used within experimental units. It is possible that rhodoliths preferentially assimilated NH_4^+, as has been reported for other species (Bracken & Stachowicz 2006), or that the microbiont community between rhodolith branches (phytoplankton, microbes and algal filaments) also contributed to changes in observed nutrient concentrations. Rhodoliths could benefit from increased regenerated nutrients during summer months, when growth rates for *Lithothamnion* (McConnico et al. 2014) and *Lithophyllum* peak (Steller et al. 2007) and nitrogen and phosphorus were high, suggesting they may take advantage of localized nutrient enrichment. However, if rhodoliths do not require or use the extra nutrients, they would

presumably benefit other primary producers or microbes in close proximity (i.e. on top of rhodoliths or between their branches). *Sargassum* recruits present after the summer senescence of adult thalli (Foster et al. 2007), when water column nutrients are reduced, may be one alga to benefit from these regenerated nutrients at the Gulf site. While the specific benefit to rhodoliths and associated species requires further study, rhodoliths as foundation species play a role in nutrient cycling, and may be of particular importance in seasonally nutrient-limited regions like the Gulf of California.

CONCLUSIONS

Rhodoliths acting as foundation species influence local nutrient availability. More detailed experiments are necessary to determine the relative contribution of nutrient enrichment from microbial vs. cryptofaunal activities, but preliminary work suggests that both influence nutrient dynamics in Baja California and may be seasonally more important than new nutrients via upwelling. Additional nutrients associated with rhodoliths may facilitate primary and secondary production in seasonally nutrient-limited environments like the Gulf of California, but perhaps are less essential on the Pacific coast of Baja where sediments inside and outside of rhodolith beds are also nutrient rich and potentially influenced by mangroves. Given the global distribution and ecological importance of rhodolith systems, their contribution to nutrient cycling warrants further study, as rhodoliths and their associates are vulnerable to climate change, ocean acidification and other anthropogenic disturbances.

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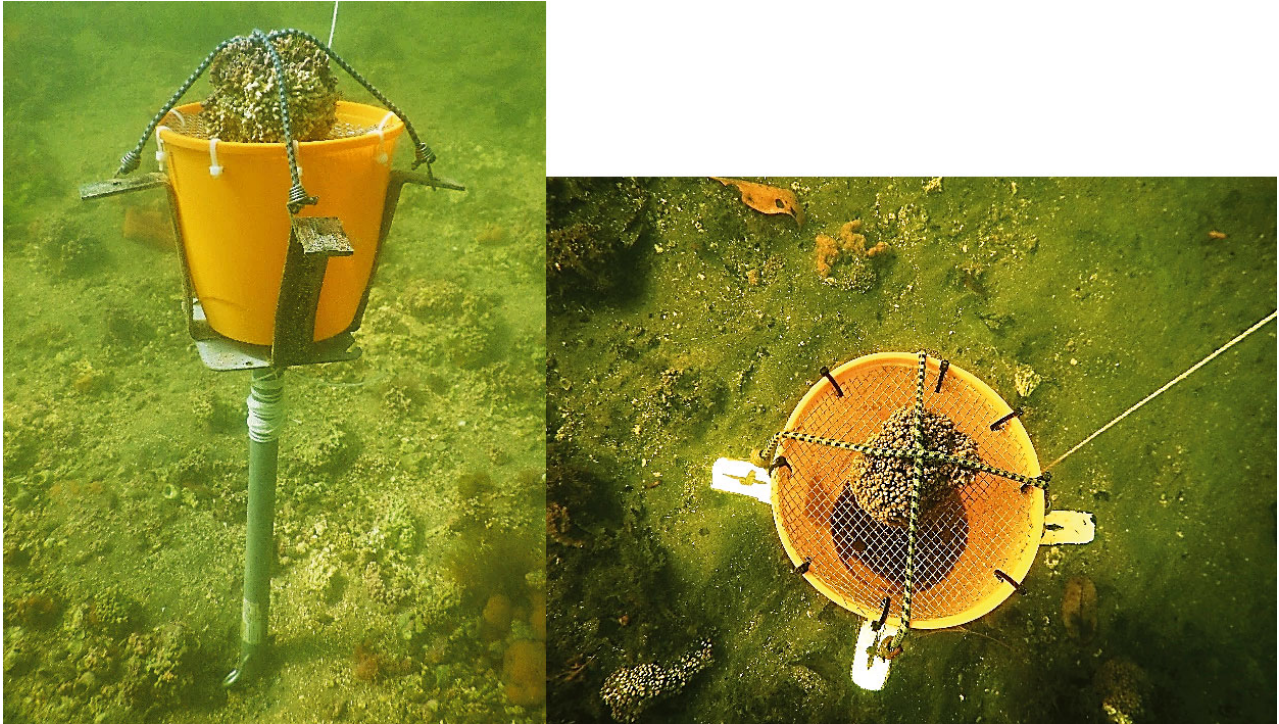shelf of the Baja California Peninsula. J Oceanogr 59:
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Appendix

Fig. A1. Equipment and techniques used to raise rhodoliths above the bed in the sedimental removal experiments