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BRIEF RESEARCH REPORT
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Bacterial and Archaeal Specific-Predation in the North Atlantic Basin

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Stable isotope probing (SIP) was used to track prokaryotic and eukaryotic carbon uptake along a meridional transect (Long. 52°W) in the North Atlantic to assess if ^{13}C-resource partitioning between bacteria and archaea and ^{13}C-labeled eukaryotic predators could be detected. One-liter SIP microcosms were amended with ^{13}C-acetate or ^{13}C-urea and incubated for 48 h. Our data indicated archaea often outcompeted bacteria for ^{13}C-urea while both archaea and bacteria could incorporate ^{13}C-acetate. This ^{13}C label could also be tracked into eukaryotic microbes. The largest number of ^{13}C-labeled eukaryotic OTUs, and the greatest percentage of eukaryotic ^{13}C signal, were observed in conjunction with both archaeal and bacterial ^{13}C incorporation, suggesting that most eukaryotic predators do not distinguish between archaeal and bacterial prey. However, other ^{13}C-eukaryotic OTUs were exclusively associated with either ^{13}C-archaeal or ^{13}C-bacterial OTUs. These archaeal-specific and bacterial-specific ^{13}C-eukaryotic OTUs were related to known bactivorous predators including *Ancyromonas*, *Amastigomonas*, *Cafeteria*, and *Caecitellus*. Our SIP findings suggest both resource partitioning between bacteria and TACK (Thaumarchaeota, Aigarchaeota, Crenarchaeota, and Korarchaeota) archaea and selective predation by eukaryotic predators. Determining the equalizing mechanisms for co-existence in the marine environment can help map predator/prey interactions to better estimate carbon flow in the deep ocean.

Keywords: archaea, bacteria, predation, competition, stable isotope probing, deep ocean

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INTRODUCTION

G. E. Hutchinson confronted a major contradiction between ecological theory and the natural world in "The Paradox of the Plankton" (1961). According to the competitive exclusion principle, two species competing for the same resources cannot stably coexist. However, hundreds/thousands of phytoplankton species can be found within small volumes of water in lakes, despite limited room for niche specialization and intense competition for the same resources (Scheffer and Carpenter, 2003). Hutchinson surmised that because environmental conditions can change very rapidly in aquatic systems, no one species has the advantage long enough to exclude others (Hutchinson, 1961;

Richardson et al., 1970). Additionally, stabilizing forces may also exist that reduce intra- and inter-specific competition (Chesson and Huntley, 1997; Chesson, 2000). Multiple mechanisms have been proposed to account for this co-occurrence of highly similar species, including temporal separation of activity, resource partitioning, immigration/emigration, selective predation, and dormancy.

These ecological theories of coexistence can also be tested in deep ocean environments containing both archaea and bacteria. For many years archaea were believed to be solely extremophiles. Specifically, these microorganisms were thought to grow under conditions of very high temperature, high salinity, or extreme anaerobiosis where CO_2 is used as a terminal electron acceptor, yielding methane. Because archaea occurred in habitats that would not support the growth of eukaryotes or prokaryotes, no apparent conflict was perceived between these various life forms. However, the concept of archaea being obligate extremophiles changed when these microbes were found to inhabit coastal oceans (DeLong, 1992; Fuhrman et al., 1992). Since then, mesothermal archaeal diversity has been revealed in open ocean areas around the globe (Massana et al., 2000) and in deep-sea sediments (Vetriani et al., 1999; Teske et al., 2002; Søresnson and Teske, 2006; Biddle et al., 2008). Archaea have also been found in waters between 4 and 8°C (Massana et al., 1997), polar seas (Murray et al., 1998), soils (Birtrim et al., 1997), caves (Gonzalez et al., 2006), salt marshes (Nelson et al., 2009), and in estuarine settings (Abreu et al., 2001). The discovery of marine mesophilic archaea represents an entire clade of organisms that, up until 30 years ago, had gone completely unnoticed because of their resistance to laboratory culturing, yet are apparently ubiquitous and frequently abundant in the ocean (DeLong et al., 1994; Stein and Simon, 1996; Karner et al., 2001).

Exactly what strategies marine archaea are using to remain relatively abundant and ubiquitous remains largely unknown. Surface ocean prokaryotic communities tend to be dominated by bacteria and a small percentage of euryarchaea, but below the euphotic zone and in sediments, thaumarchaea and bathyarchaea of the TACK superphylum (Guy and Ettema, 2011) equal or outnumber bacteria in abundance (Karner et al., 2001; Herndl et al., 2005; Amano-Santo et al., 2013). Both thaumarchaea (Ouverney and Fuhrman, 2000; Seyler et al., 2014, 2018) and bathyarchaea (Seyler et al., 2014; Lazar et al., 2016) appear to be capable of organic carbon uptake, competing with bacteria for the same organic substrates. Metagenomic evidence suggests that thaumarchaea may also be capable of both autotrophy and mixotrophy (Hallam et al., 2006), and radiocarbon data has suggested that autotrophy is the dominant lifestyle of thaumarchaea below the photic zone (Ingalls et al., 2006). Thaumarchaea, however, are most frequently studied with respect to their role in ammonia oxidation in the ocean. In 2004, a unique ammonia monooxygenase (*amoA*) gene was discovered on an archaeal-associated genomic scaffold (Venter et al., 2004); a year later *amoA* genes were found in thaumarchaea (Treusch et al., 2005) and examples of archaeal *amoA* genes were observed in a variety of other marine environments (Francis et al., 2005). Currently, few thaumarchaea have been cultured, and all are ammonia oxidizers (Könneke et al., 2005; Park et al., 2012; Qin et al., 2014). However, a nitrifying lifestyle for archaea would also directly compete with nitrifying bacteria in the marine environment. It has been suggested that ammonia-oxidizing archaea are of particular importance in low-oxygen environments such as sediments and oxygen minimum zones (Francis et al., 2005; Mosier and Francis, 2008; Moin et al., 2009; Park et al., 2010). These nitrifying archaea may also be well-adapted to oligotrophic environments where the amount of available nitrogen is comparatively low (Martens-Habbena et al., 2009) which could be considered as a stabilizing force regarding preference of low rather than high ammonium concentrations.

All this conflicting potential metabolic data indicates that if the TACK-archaeota and bacteria are living in the same environment, using similar carbon and energy sources, there should be competitive exclusion and one group would eventually out-compete the other. Yet, we find both living together in the same oceanic samples. In this report, resource partitioning and selective predation were investigated as two possible mechanisms that may allow archaea and bacteria to stably coexist in the deep ocean. We chose to utilize DNA stable-isotope probing techniques (SIP; Radajewski et al., 1999) as a means to create different pools of ^{13}C-microbial prey items in marine samples (by labeling either bacteria or archaea with different ^{13}C-carbon sources). Prior research had demonstrated that archaea could successfully outcompete bacteria for ^{13}C-urea in a coastal salt marsh at low concentrations (<30 μM) during short term incubations (5 days) (Seyler et al., 2014). However, it is unclear if deep ocean archaea would also outcompete bacteria under comparable conditions to our salt marsh study. We initially set out to determine if similar resource partitioning results could also be observed in oceanic water column samples. If resource partitioning could be demonstrated, we could then test a second mechanism of co-existence (selective predation) by determining if eukaryotic predators consumed ^{13}C-archaeal or ^{13}C-bacterial prey in a specific fashion. Our findings suggested there was specific uptake of ^{13}C-urea by TACK archaea in many of our SIP experiments. Furthermore, particular ^{13}C-eukaryotes were associated exclusively with ^{13}C-archaea (archaevores), with ^{13}C-bacteria (bactivores) or detected in samples without any archaea or bacterial ^{13}C uptake (osmotrophs). This information on ^{13}C-resource partitioning and specific predation by eukaryotes provides insight into the competitive relationships between archaea and bacteria. Finally, this SIP approach also demonstrates how the deep sea can be a model system for studying competition between other microbial groups in natural settings to further our understanding of microbial ecology.

MATERIALS AND METHODS

In April 2012, water samples were collected onboard the R/V Atlantis as part of the US CLIVAR/CO_2 Repeat Hydrography program, along World Ocean Circulation Experiment (WOCE) line A20. This was a cruise of opportunity, done in conjunction with a larger effort to characterize water chemistry and marine microbial productivity. Therefore, the volumes of water available for sampling were often limited (generally <5 L at each

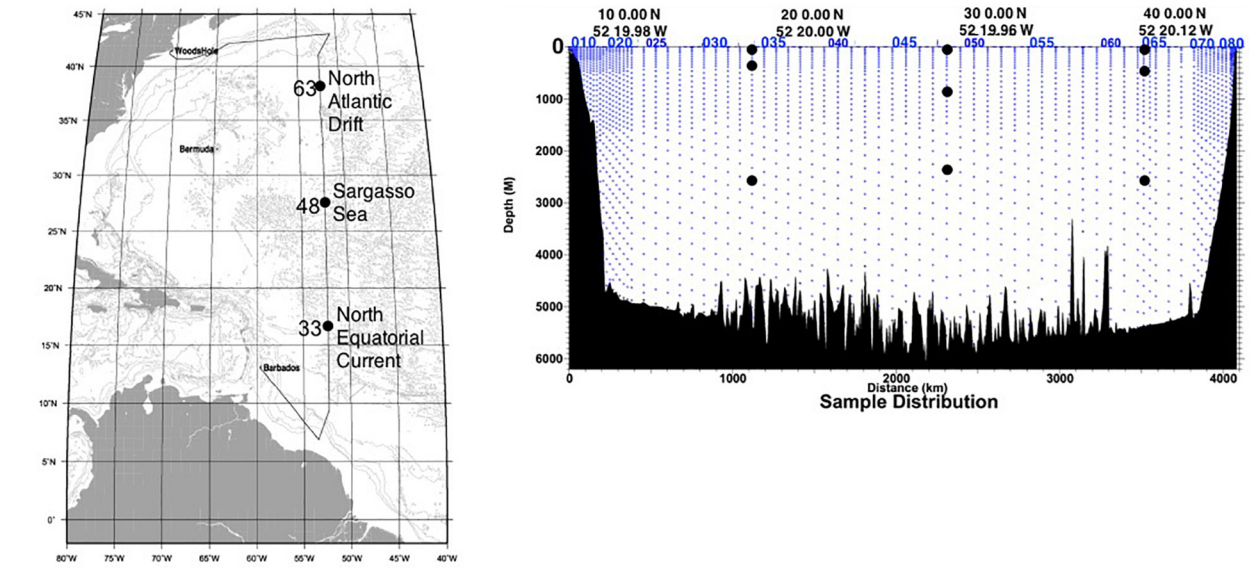

FIGURE 1 | (A) Map of the CLIVAR A20 cruise track, with each SIP sampling station indicated. **(B)** Cross section of the sampling depths of the CLIVAR 20 cruise (blue dots). The sites of the water collected for SIP microcosms are indicated (black dots). Note: Water samples were not available at all depths and stations during this cruise of opportunity. These figures are modified from the CLIVAR A20 2012 cruise report (http://cchdo.ucsd.edu, Expocode: 33AT20120419do).

station/depth per cast). As such, a total of 36 SIP microcosms were established at three stations (**Figure 1A**) from three water column zones: the mixed layer (euphotic zone, 65–115 m), the local oxygen minimum (mesopelagic zone, 365–835 m), and the bathypelagic zone (2335–2585 m; **Figure 1B**), as part of a larger effort to determine autotrophy, heterotrophy and mixotrophy in N. Atlantic waters (Seyler et al., 2018). Duplicate 1-L samples of water from each depth were amended with ^{13}C-acetate/^{12}C-urea or ^{13}C-urea/^{12}C-acetate at equimolar concentrations (20 μM), to stimulate the same populations of microbes in all microcosms from the same station/depth and maximize the number of ^{13}C-carbon sources that could be tested. Microcosms were incubated in covered containers on deck for 48 h, with a constant inflow of surface seawater to maintain stable temperature (∼ 22°C). Early in the cruise, duplicate ^{12}C-acetate and ^{13}C-acetate microcosms were established and incubated for 12–72 h to verify the minimum time necessary to obtain a positive ^{13}C-signal (Seyler et al., 2018). Negative SIP controls using ^{12}C sodium acetate were incubated for 72 h. Biomass was collected on a 0.2-μm filter using vacuum filtration.

DNA was purified using phenol-chloroform methods and ^{12}C/^{13}C-DNA was separated by isopycnic cesium chloride gradient ultracentrifugation at 200,000 × *g* for 36 h, using ^{13}C-labeled *H. salinarum* or *E. coli* DNA as a carrier (Gallagher et al., 2005). Carrier DNA produces a visible ^{13}C-lower band in the gradient, removing the need to fractionate the gradient and increasing sensitivity (Gallagher et al., 2010; Kerkhof et al., 2011; Seyler et al., 2014, 2018; Tuorto et al., 2014). Fluorescently-labeled (using ethidium bromide) ^{12}C-(upper) and ^{13}C-(lower) bands were collected by pipette. Upper and lower bands (1 μl each) were amplified using nested PCR with 5′-fluorescently- labeled, 16S rRNA archaea-specific 21F (5′-TCCGGTTGATCCYGCCGG)/958R (5′-YCCGGCGTTGAMTCCAATT) primers using the following protocol: 94°C for 5 min, 23 cycles of (94°C for 1 min, 55°C for 2 min, 72°C for 3 min). A 1 μl aliquot was then taken from this reaction and amplified using thaum/cren/bathyarchaeota-specific 7F (5′-TTCCGGTTGATCCYGCCGGACC)/518R (5′-GCTGGTWTTACCGCGGCGGCTGA) primers using the following protocol: 94°C for 5 min, 30 cycles of (94°C for 1 min, 73°C for 2 min, 72°C for 3 min), 72°C for 10 min (Perevalova et al., 2003; Ionescu et al., 2008; Seyler et al., 2018). Upper and lower bands were also amplified using bacteria-specific 27F (5′AGAGTTTGATCMTGGCTCAG)/1100R (5′-GGGTTG CGCTCGTTG) primers (Ludwig, 2007) in a 2-step process: step 1 at 94°C for 1 min 30 s, 20 cycles of (94°C for 30 s, 57°C for 30 s, 72°C for 1 min 10 s); 1 μl aliquot amplified in step 2 at 94°C for 1 min 30 s, 25 cycles of (94°C for 30 s, 57°C for 30 s, 72°C for 1 min 10 s), 72°C for 10 min. Finally, upper and lower bands were amplified for eukaryotes using 18S rRNA universal eukaryote 328F (5′-ACCTGGTTGATCCTGCCAG) (Medlin et al., 1988)/516R (5′-ACCAGACTTGCCCTCC) (Amann et al., 1990) primers in a 2-step PCR: 94°C for 1 min 30 s, 15 cycles of [94°C for 45 s, 56°C for 45 s, 72°C for 2 min], followed by 94°C for 1 min 30 s, 30 cycles of [94°C for 45 s, 56°C for 45 s, 72°C for 2 min], 72°C for 10 min. Amplicons were digested with *Mnl*I (prokaryotic amplicons) or *Hae*III (eukaryotic amplicons) in 20 μl volumes for 6 h at 37°C, then precipitated using sodium acetate and 95% ethanol (McGuinness et al., 2006). Precipitated DNA was dried and re-suspended in 19.7 μl de-ionized formamide with 0.3 μl ROX 500 size standard (Applied Biosystems). TRFLP fingerprinting

(Avaniss-Aghajani et al., 1994) was carried out on an ABI 310 genetic analyzer (Applied Biosystems, Foster City, CA, United States) using GENESCAN software. Peak detection was set at 25 arbitrary fluorescent units. Each resulting peak was considered an operational taxonomic unit (OTU).

An 18S amplicon clonal library was constructed using the Topo TA cloning kit according to the manufacturer's instructions (Invitrogen, Carlsbad, CA, United States). 192 recombinant clones from the ^{13}C-labeled bands were screened in a multiplex format (Babcock et al., 2007), to determine portions of the 18S rRNA genes which corresponded to the TRF of the ^{13}C-eukaryotic profile. Thirteen 18S rRNA genes that matched TRFs of interest were sequenced via Sanger methods using M13 primers (GENEWIZ, Inc., NJ, United States), producing 9 unique sequences (<99% similarity to each other) between 520 and 603 bp. These sequences were compared to the Silva-ARB Eukaryotic database by discontinuous MEGABLAST. Best hits were used to construct a phylogenetic tree using 460 unambiguously aligned base pairs and maximum likelihood methods (Guindon et al., 2010) in Geneious 11.1.4. Clone sequences were submitted to GenBank (accession numbers KT749976–KT749984).

^{13}C-Urea	Station 33		Station 48		Station 63	
	1	2	1	2	1	2
Mesopelagic	A B	A —	A B	A B	A —	A —
Bathypelagic	A —	——	A —	A—	— B	A —

^{13}C-Acetate	Station 33		Station 48		Station 63	
	1	2	1	2	1	2
Mesopelagic	A B	A B	A B	A B	A B	A B
Bathypelagic	A B	A B	A B	A B	— B	— B

FIGURE 2 | Patterns of ^{13}C-incorporation by archaea **(A)** and bacteria **(B)** based on ^{13}C-urea or ^{13}C-acetate additions in meso-bathypelagic samples. No incorporation of ^{13}C was detected in any microcosms established with water from the epipelagic zone.

RESULTS

A minimum incubation time of 48 h was required to unambiguously detect ^{13}C-archaeal DNA synthesis in the ^{13}C-carrier band (Seyler et al., 2018). In 7 microcosms (6 epipelagic, 1 bathypelagic), no signal could be detected in the ^{13}C-band (no PCR amplicon could be detected by electrophoresis gel, and the resulting digests produced no TRFLP peaks). In 7 microcosms from mesopelagic or bathypelagic samples, signal from ^{13}C-urea was only detected in archaea. In one bathypelagic microcosm (Station 63), signal from ^{13}C-urea was only detected in bacteria. Three mesopelagic microcosms had both archaea and bacteria ^{13}C signals resulting from ^{13}C-urea amendments. In all twelve ^{13}C-acetate mesopelagic and bathypelagic microcosms, both archaea and bacteria incorporated ^{13}C, except bathypelagic microcosms at Station 63, where only bacterial uptake of ^{13}C-acetate was detected (**Figure 2**). No ^{13}C uptake was detected in ^{12}C controls.

TRFLP analysis detected 37 eukaryotic OTUs, grouped based on whether the ^{13}C signal was also detected in the ^{13}C-archaea and ^{13}C-bacteria, in the ^{13}C-archaea alone, in the ^{13}C-bacteria alone, or without a ^{13}C signal from either prokaryotic group (**Figure 3**). Seventeen eukaryotic OTUs were detected in SIP microcosms with both bacterial and archaeal ^{13}C uptake. Ten eukaryotic OTUs were associated exclusively with ^{13}C-archaea (archaevores), and 7 eukaryotic OTUs were only observed with ^{13}C-bacteria (bacterivores). Three eukaryotic OTUs were detected in samples without any archaea or bacterial ^{13}C uptake (osmotrophs). The total number of observed archaeal-specific predator OTUs was higher than that of bacterial-specific predators, however, if the total adjusted TRFLP peak area was considered a proxy for relative abundance, the non-specific predators tended to constitute a greater percentage of the overall ^{13}C-eukaryotic community profile (**Figure 3**).

Nine rRNA genes with ^{13}C-eukaryotic TRF peaks were identified in the clonal library. Of these, three were found exclusively in microcosms where bacteria incorporated ^{13}C signal (TRFs 182, 201, 269), three were found only in microcosms where archaea incorporated ^{13}C signal (TRFs 329, 333, 339), two were found in both (TRFs 273, 305), and one was found in the microcosm where neither bacteria nor archaea incorporated ^{13}C signal (TRF 293). An 18S phylogenetic tree (**Figure 4**) indicated bacterial uptake-associated eukaryotes were associated with relatives of the parasitic dinoflagellate *Syndiniales* group, a flagellate (*Ancyromonas* sp.), and an apuzoan (*Amastigomonas* sp.). The archaea uptake-associated eukaryotes were associated with radiolarians or a dinoflagellate group (*Heterocapsa* sp.). Non-specific prokaryotic predators were related to a bicosoecida group (*Cafeteria* sp.) and a marine fungus (*Paraphysoderma sedebokerense*). The 18S rRNA gene from the eukaryote believed to be osmotrophic aligned to another flagellate group (*Caecitellus paraparvulus)*.

DISCUSSION

Interactions between prokaryotes, protist predators, and dissolved organic carbon pools in the world's oceans may have far-reaching effects on global biogeochemical cycles (Kujawinski, 2011). Deep ocean waters represent the largest pool of dissolved organic carbon (Hansel and Carlson, 1998), the respiration of which accounts for up to one third of oceanic biological CO_2 production (Del Giorgio and Duarte, 2002; Arístegui et al., 2005). The factors which control microbial community dynamics, carbon respiration, and mortality in the deep ocean are therefore of great importance to the global carbon cycle. Archaea, particularly thaumarchaea belonging to the TACK superphylum, have been found to dominate prokaryotic communities in the deep ocean (Herndl et al., 2005; Varela et al., 2008). Yet, archaeal

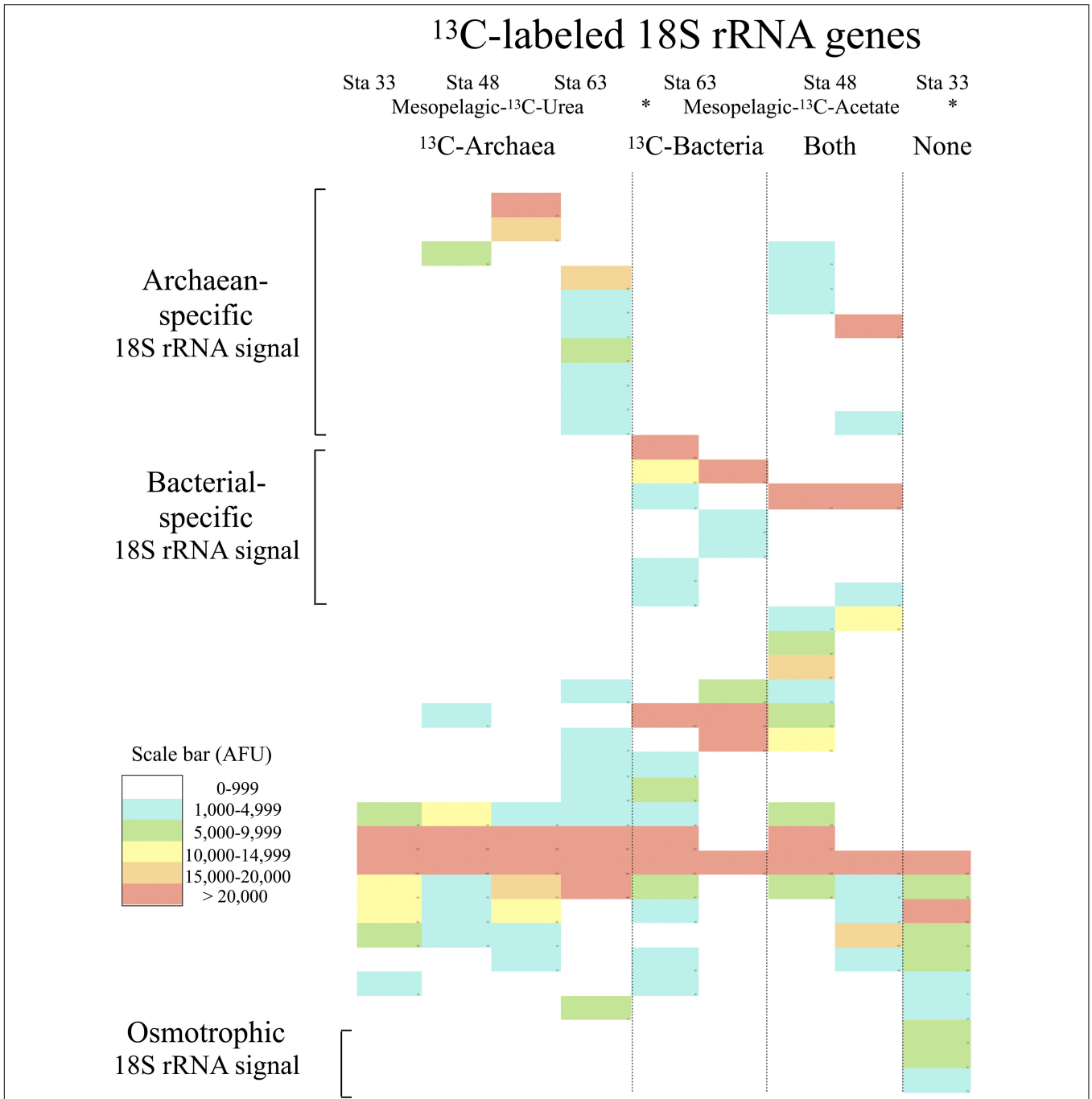

FIGURE 3 | Heat map of TRFLP peaks from ^{13}C-labeled 18S rRNA genes detected in SIP microcosms after 48 h. The station numbers and the ^{13}C substrates used for labeling the archaea or bacteria in the microcosms are indicated on top. TRFLP peaks are grouped by predation pattern (i.e., only ^{13}C-archaea, only ^{13}C-bacteria, both ^{13}C-archaea and ^{13}C-bacteria, and neither the ^{13}C-archaea nor ^{13}C-bacteria). Intensity of cell shading corresponds to the normalized TRFLP peak area for the overall community profiles in arbitrary fluorescence units (scale bar-AFUs).

utilization of dissolved and particulate organic matter in the deep sea remains poorly constrained, and even less is known about the relationship of predator grazing to archaeal function in the deep sea.

"Bottom-up" controls such as the availability of nutrients (Wilkins et al., 2012) and the character of dissolved organic matter (Smriga et al., 2016) may have significant effects on the community structure of prokaryotes. Past studies demonstrated that archaea take up certain carbon sources at an equal or higher rate than bacteria in deep ocean waters (e.g., Ouverney and Fuhrman, 2000; Teira et al., 2006; Kirchman et al., 2007). Thaumarchaea are known to incorporate urea as a carbon source

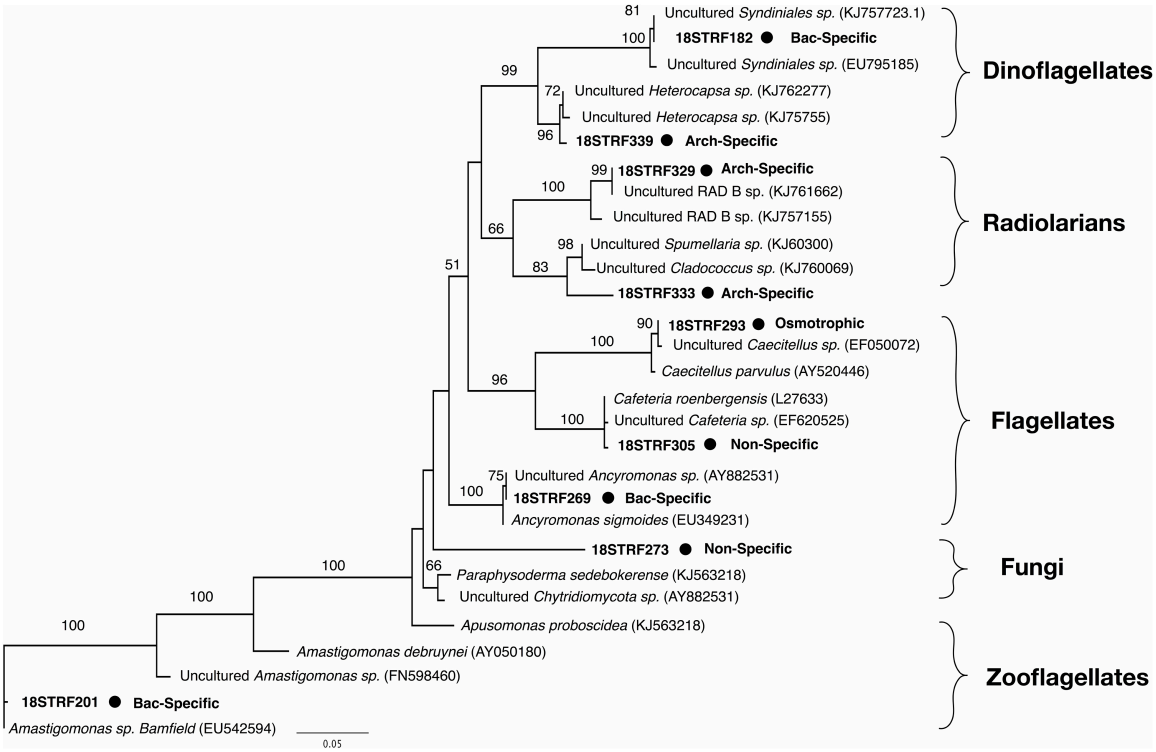

FIGURE 4 | Maximum likelihood phylogenetic tree of ^{13}C-labeled 18S rRNA genes corresponding with nine of the TRFLP peaks shown in **Figure 3**. The tree is based on 460 unambiguously aligned base pairs. The size of the TRFLP peak, the ^{13}C-predation pattern, and the bootstrap values for 100 iterations are all indicated.

(Seyler et al., 2014, 2018) and they may use it as an alternative nitrogen source to ammonium to fuel nitrification (Alonso-Sáez et al., 2012). In many of our mesopelagic and bathypelagic microcosms, ^{13}C-urea uptake was detected in archaea but not bacteria, suggesting that archaea can outcompete bacteria for urea at those particular samples, at the concentration tested here. Competition for substrates in oligotrophic environments where nutrients and energy are limiting seems to favor archaea over bacteria (Jardillier et al., 2005; Vuillemin et al., 2019). Additionally, PCR amplification of key genes in the Thaumarchaeota suggest that ecological functioning of this group may shift with depth (Hu et al., 2011). One possibility of our observed resource partitioning for ^{13}C-urea by archaea may be our SIP incubation conditions. That is, by conducting the SIP incubations at sea surface temperature, rather than at *in situ* mesopelagic and bathypelagic temperatures, we may have stimulated or accelerated activity in some clades. However, an increase in temperature cannot bestow metabolic capability where none had previously existed; we therefore feel confident in stating that archaea are capable of outcompeting bacteria for urea under the conditions provided in our microcosms [For further discussion, see Seyler et al. (2018)].

In addition to resource partitioning, our SIP experiment indicated that selective predation may partly account for archaeal/bacterial co-existence. The main causes of mortality in marine microorganisms are viruses and grazing by phagotrophic protists (Jardillier et al., 2005; Arístegui et al., 2009). Phagotrophic grazing- "top-down" population control- can structure the microbial community, activity, and physiology of prokaryotic prey (Šimek et al., 1997; Lin et al., 2007; Saleem et al., 2012), including shifts in community assemblages as a result of the prey preferences of protists (Jardillier et al., 2005; Jezbera et al., 2006). Protistan species can act as bacterivore, herbivore, carnivore of other protozoa and/or metazoans (e.g., nauplii, copepodite, and metazoan larvae), and can even consume dissolved organic matter through saprotrophy or osmotrophy (Swanberg and Caron, 1991; Caron et al., 2009; Worden et al., 2015). Specific predation of archaea has been addressed in very few studies, e.g., at marine oxic-anoxic interfaces (Anderson et al., 2012) and in freshwater (Ballen-Segura et al., 2017). Here, we demonstrate both archaeal and bacterial-specific predation by a subset of eukaryotic predators in the mesopelagic and bathypelagic water column. However, our data suggest the archaea-specific predators represent a small percentage of the overall the eukaryotic predatory community compared to non-specific microbial predators.

This study demonstrates that certain ^{13}C-eukaryotic OTUs are associated with either ^{13}C-archaeal or ^{13}C-bacterial signals. This transfer of ^{13}C-carbon from prokaryote to eukaryote could result from predation or by exudation/episymbiosis. Often ciliates or flagellates have surface associations with bacteria for detoxification or defense (Petroni et al., 2000; Edgcomb et al., 2011). Although we did not test for the presence of prokaryotes in food vacuoles or on the external surfaces of deep-sea eukaryotes

by microscopy, an assessment of whether predation or symbiosis is the predominant mechanism for carbon transfer can be made using the SIP results directly. To a first order, if predation is the dominant mechanism, we can presume that in many microcosms, the ^{13}C-carbon will pass directly from substrate to prokaryote to eukaryote predator. Therefore, a much higher ^{13}C-eukaryotic signal compared to a ^{13}C-prokaryotic signal will be observed in the PCR product from the ^{13}C-labeled DNA. On the other hand, if growth of the eukaryote is predicated on growth of an epibiont, there should always be a comparable PCR signal from both prokaryote and eukaryote within the ^{13}C-band. All of our SIP microcosms had significantly higher eukaryotic signal than prokaryotic signal in the ^{13}C-band (**Supplementary Figure S1**), suggesting a tight coupling between these groups that is likely a predation signal.

If differential predation influences the coexistence of archaea and bacteria, the mechanisms used by predators to discern between the archaea and bacteria are largely unexplored. It is known that prey item size, surface properties, concentration, and particle attachment can be major controlling elements selecting for prey items by eukaryotic grazers (Lampert, 1987; Gonzalez et al., 1990, 1993; Jürgens and Matz, 2002; Thurman et al., 2010; Tuorto and Taghon, 2014). Recent studies suggest that marine archaea are significantly smaller than bacteria on average (Stepanauskas et al., 2017; Santoro et al., 2018). Aggregation on detrital particles, as observed in euryarchaea (Orsi et al., 2015), may provide refuge from predation (Langenheder and Jürgens, 2001; Šimek et al., 2001), as well as a host of biochemical interactions, exopolymers, and toxicity (Jürgens and Matz, 2002). Further studies will be necessary to explore the mechanisms of selective predation in deep ocean settings.

Predation by protists is also a key mechanism for the transfer of dissolved organic carbon to higher trophic levels in the microbial loop (Azam et al., 1983; Jürgens and Massana, 2008; Worden et al., 2015). The structure of the marine microbial food web and efficiency of carbon transfer are major determinants in the rate of oceanic carbon sequestration and the type/amount of higher consumers in the ecosystem (Limardo and Worden, 2015). Although prokaryotes mobilize dissolved carbon into biomass, it is the heterotrophic strategies of small eukaryotic consumers that determine whether the net flow of organic matter will ultimately end up as a trophic "link" (i.e., trophic transfer to top predators and export) versus a trophic "sink" (i.e., be remineralized as dissolved organic matter or CO_2). The archaeal contribution to the microbial loop is still poorly understood and, consequently, often easy to ignore. SIP studies such as described here can map trophic interactions between microbial predators and prey to predict the fate of organic carbon in marine ecosystems.

DATA AVAILABILITY

The datasets generated for this study can be found in GenBank, KT749976–KT749984.

AUTHOR CONTRIBUTIONS

LS and LK wrote the original manuscript. LS, LM, and LK designed the SIP experiments. LS set up microcosms and performed all the laboratory work. ST and LM performed the data analysis and interpretation of data. DG was co-chief scientist on R/V Atlantis during CLIVAR leg A20 and supervised all onboard research. LK conceived the original idea, oversaw all laboratory work, and provided data analysis.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2019.00555/full#supplementary-material

FIGURE S1 | Top half of gel showing amplification of 18S rRNA genes from either the ^{12}C-band or the ^{13}C-band within the SIP microcosms indicated. Lanes are **(A)** empty; **(B)** lambda HinDIII ladder; **(C)** negative PCR control; **(D)** ^{13}C-*Halobacterium* carrier; **(E)** station 63–2585 m, ^{13}C-acetate amended, ^{12}C-band; **(F)** station 63–2585 m, ^{13}C-acetate amended, ^{13}C-band; **(G)** station 48–2335 m, ^{13}C-acetate amended, ^{12}C-band; **(H)** station 48–2335 m, ^{13}C-acetate amended, ^{13}C-band; **(I)** station 48–2335 m, ^{13}C acetate-amended, ^{13}C-band (duplicate Niskin cast); **(J)** empty; **(K)** positive control; **(L)** empty. Bottom half gel of indicates amplification of 16S rRNA genes from the identical samples as the 18S rRNA amplification above with the exception that the ^{12}C-bands (Lanes **E, G**) were diluted 1:10 prior to amplification of the 16S rRNA genes. All ^{13}C-bands were all amplified for 16S rRNA genes without dilution as above. The concentration of PCR product from each amplification is indicated above the band.

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