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Picoplankton consumption supports the ascidian *Cnemidocarpa verrucosa* in McMurdo Sound, Antarctica

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ABSTRACT: Polar marine ecosystems commonly have a seasonal pulse of primary productivity with large diatoms or prymnesiophytes dominating. Along with benthic production (i.e. microphytobenthos), the annual phytoplankton bloom provides an essential source of food for several trophic levels, including many invertebrate communities. The oceanographic and productivity patterns in McMurdo Sound, Antarctica, result in benthic communities that include high-density assemblages of active and passive suspension feeders. For many years, it has been assumed that these benthic suspension-feeding communities went into a period of quiescence during the austral winter and spring in response to the low food and chronically low temperatures as a strategy to conserve energy. There is increasing evidence, however, that suspension feeders can feed throughout most of the year, with many using picoplankton (0.2 to 2.0 µm) as a food source. It is now recognized that picoplankton, especially heterotrophic prokaryotes, are a diverse and important component of the Southern Ocean bacterioplankton community and a dominant component of the plankton during austral winter and early austral spring in McMurdo Sound. Here, we show that the common ascidian *Cnemidocarpa verrucosa* consumes picoplankton prior to the annual spring bloom. Differences in food availability at different sites (Cape Armitage versus Cape Evans) and differences in filtration efficiencies on different fractions of the plankton community result in this ascidian acquiring significantly more carbon and energy at Cape Evans, where higher densities of *C. verrucosa* reside. This study emphasizes the importance of picoplankton as a food resource for the Antarctic benthic suspension-feeding community.

KEY WORDS: Picoplankton · McMurdo Sound · Benthic–pelagic coupling · Ascidians

INTRODUCTION

Polar marine ecosystems are often characterized as habitats where specific physical attributes vary seasonally (e.g. irradiance), but where other physical features remain relatively constant throughout the year (e.g. seawater temperature). These features define an ecosystem that is uniquely recognizable as 'polar', as does an annual pulse of primary productivity that is associated with increasing solar irradiance and a drawdown of inorganic nutrients (e.g. nitrate) in well-mixed isothermal waters (Barry 1988, Peck et al. 2006). In Antarctica, and McMurdo Sound specifically, seawater temperatures range from −1.9°C in austral winter to as warm as −0.5°C in austral summer (Hunt et al. 2003). Additionally, the attenuation of solar radiation is dominated by the optical properties of the annual sea ice combined with highly variable snow cover, with little contribution from the optically clear Case 1 water column itself (Lesser et al. 2004). In the Antarctic, development of the sea ice microbial community (SIMCO) is in turn dependent

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on the amount of snow cover and optical properties of the annual sea ice (Garrison 1991, Lizotte 2001). The austral spring is marked by the annual pulse of primary productivity that is associated with an increase in solar irradiance and melting of the annual sea ice (Lizotte 2001). For McMurdo Sound specifically, the sources of primary production include advected phytoplankton from the Ross Sea bloom (Barry 1988), macroalgal growth (Miller & Pearse 1991), and 'seeding' of the near coastal water column with the SIMCO (Lizotte 2001) that is dominated by large diatoms or prymnesiophytes and continues into shallow benthic zones as the annual sea ice melts (Clarke & Leakey 1996, Lizotte 2001). This annual pulse of planktonic production serves as an essential source of food for several trophic levels including benthic communities in the late austral spring (Dayton 1990, Grebmeier & Barry 1991, Dayton et al. 1994). Additionally, benthic primary production (i.e. microphytobenthos), which also increases as sea ice retreats and solar irradiance increases, is known to be an important source of food for benthic communities (Dayton et al. 1986). Both north-south and east-west gradients of benthic community diversity in McMurdo Sound are believed to be largely driven by differences in sea ice thickness (ranging from 1.8 to 3.1 m) and its affect on the attenuation of solar radiation, as well as a combination of benthic primary productivity and horizontal advection of plankton from the open waters of the Ross Sea along the East Sound (Dayton et al. 1986, Barry 1988, Barry & Dayton 1988, Grebmeier & Barry 1991).

The oceanographic and productivity patterns in McMurdo Sound result in benthic communities that include high-density assemblages of active and passive suspension feeders (i.e. sponges, soft corals, bivalves, and ascidians) in the East Sound (e.g. Cape Armitage and Cape Evans) compared to the lower densities and diversity of soft-bottom communities in the West Sound (e.g. Explorer's Cove) as previously described (Dayton et al. 1986, Grebmeier & Barry 1991, Slattery & McClintock 1995, Slattery et al. 1997). Given the seasonal characteristics of both planktonic and benthic productivity, it is unclear what supports these large suspension-feeding communities for the remainder of the year. For many years, it was accepted that these benthic suspension-feeding communities went into an annual period of quiescence in response to the low food, and chronically low temperatures, as a strategy to conserve energy (reviewed by Clarke 1988). However, Antarctic suspension feeders appear to cease feeding for only 2 mo, if at all, in the austral winter (June/July) and feed during the remaining portion of the year even when phytoplankton and bacterioplankton biomass is low (Barnes & Clarke 1995, Ducklow et al. 2001). Barnes & Clarke (1995) concluded, based on observations of feeding activity, that shallow-water benthic suspension-feeding communities in the Antarctic are able to feed throughout most of the year, with only short periods of non-feeding on the low concentrations of 'microplankton'. This has recently been more directly shown for deep Antarctic shelf communities in which algal blooms were indirectly related to benthic community structure and where nano- (2.0 to 20 µm) and picoplankton (0.2 to 2.0 µm) as well as sediment resuspension, lateral advection, and efficient assimilation of food all appear to play an important role in structuring these deep benthic communities (Orejas et al. 2000, Gili et al. 2001).

While it is recognized that picoplankton are a diverse and an important component of the Southern Ocean bacterioplankton community (Murray et al. 1998, 1999, Simon et al. 1999, Buitenhuis et al. 2012), they are also a dominant component of the plankton during late austral winter and early austral spring (August to November) in McMurdo Sound prior to the annual spring bloom (Rivkin 1991). This is consistent with other studies from tropical ecosystems, where work on coral reefs has shown that the picoplankton supply most of the organic nitrogen for a suite of active and passive benthic suspension feeders (Ribes et al. 2003). Additionally, at several different sites across the Caribbean basin, there is a consistent and repeatable pattern of increasing sponge size, growth and feeding rates, and food availability with increasing depth (Lesser 2006, Lesser & Slattery 2013). These patterns of larger and faster-growing sponge populations with increasing depth are driven by the availability of picoplankton, particularly heterotrophic picoplankton (Lesser 2006, Trussell et al. 2006, Lesser & Slattery 2013).

In Antarctica, the solitary ascidian *Cnemidocarpa verrucosa* is known to consume macroalgal detritus (Tatián et al. 2008), phytoplankton (Tatián et al. 2004), and bacterioplankton (Tatián et al. 2002), but no studies of picoplankton uptake have been conducted. Ascidians can filter picoplankton (Ribes et al. 2003), but the contribution of picoplankton to the carbon and energetic budgets of Antarctic ascidians is poorly understood. A recent study on the trophic structure of the benthic community in McMurdo Sound (i.e. Cape Armitage and Cape Evans) included an analysis on *C. verrucosa* (Wing et al. 2012) which showed that this ascidian utilizes organic

material originating from the SIMCO, the amount of which is location-specific and affected by the extent and persistence of sea ice cover. However, this study did not consider the potential contribution of picoplankton in the diet of this benthic ascidian. Here, we show that *C. verrucosa* consumes significant amounts of picoplankton prior to the retreat of sea ice and the onset of the annual bloom in the austral spring and acquires important carbon and energetic resources from picoplankton. Additionally, population density differences of this ascidian are correlated with the extent of the annual sea ice, the optics of the annual ice, and the availability of picoplankton.

MATERIALS AND METHODS

Target species

The target species for this study was the solitary ascidian *Cnemidocarpa verrucosa*, found in the subtidal habitats around Cape Armitage (CA: 77° 51.62′ S, 166° 40.63′ E) and Cape Evans (CE: 77° 38.09′ S, 166° 24.84′ E) on Ross Island, McMurdo Sound, Antarctica (Fig. 1), to depths in excess of 30 m (e.g. McClintock et al. 1991). Anchor ice, bare rock, sediment, and a sponge spicule mat characterize the benthic habitat of CA. The community at this site is composed of ascidians, soft corals, sea anemones, nudibranchs, infaunal bivalves, echinoderms, and diverse microphytobenthic species associated with the spicule mat. The community at CE includes crustose coralline algae-covered rocks and boulders with macrophyte (*Phyllophora antarctica*) cover that is absent at CA (Miller & Pearse 1991). The fauna of CE is similar to CA, but CE differs in the relative abundance of many of the invertebrate species (e.g. higher densities of sea urchins at CE than at CA; Brey et al. 1995). Experimentally, the collections at these 2 sites represent a natural experiment (sensu Diamond 1986).

Population density

Population densities of the solitary ascidian *C. verrucosa* were estimated between September 1993 and February 1994 on replicate (N = 5) 20 × 1 m transects. A weighted transect tape was randomly positioned parallel to shore at each of 2 depths (~6 m [shallow] and ~17 m [deep]) at both CA and CE. Divers counted all individual ascidians falling within 0.5 m of each side of the transect tape, and they collected the nearest ascidian to a randomly assigned number along the transect tape during each dive. This resulted in 5 random ascidians from each site depth that were subsequently dissected into different body tissues for proximate biochemical analyses as described by McClintock et al. (1991).

Measurements of solar radiation

In the austral spring of 2003, prior to the annual phytoplankton bloom, the downwelling spectral irradiance of both ultraviolet radiation (UVR; 300 to 400 nm) and photosynthetically active radiation (PAR; 400 to 700 nm) reaching the snow-covered (3 to 6 cm depth) ice around CA (late October) and the snow-free ice around CE (early November) was

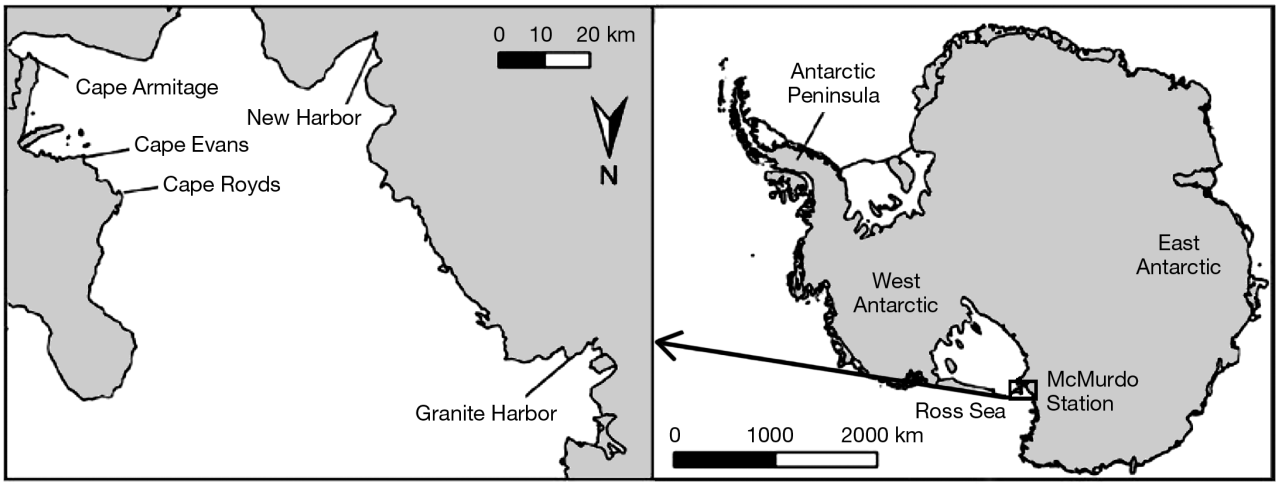

Fig. 1. Map of Antarctica with the Ross Sea expanded to show the relative locations of the study sites at Cape Armitage and Cape Evans

measured as was UVR and PAR just under the sea ice and on the seafloor (6.7 m at CA and 6.5 m at CE) for 24 h. All spectral irradiance measurements of UVR and PAR at each site were made simultaneously using multiple scanning spectroradiometers (LiCor 1800UW) that were programmed to scan 3 times every hour (total scan time ~45 s) at 2 nm intervals from 300 to 700 nm, with an hourly mean reported in units of W m^{-2} nm^{-1}. These instruments use a cosine-corrected sensor, a single monochromater, and a filter wheel to reduce stray light by isolating and measuring different portions of the spectrum and are calibrated using NIST traceable standards. The instrument sensor has a 50% detection range of ±2 nm on either side of the wavelength being measured, and minimum excitation energies on the order of 10^{-8} W cm^{-2} nm^{-1}. The temperature dependence of the detector varies from −0.1 to 0.5% over the spectral range of measurements. All spectral data were scrutinized for signals approaching the noise level of the instrument's photodiode. In all cases where low signal-to-noise was observed at a particular wavelength, all data from that wavelength and all shorter wavelengths were eliminated from the data set.

Inherent optical properties

The inherent optical properties (IOPs) of the water at CA and CE were measured using calibrated HobiLab Hydroscat (HS2) *a*-Beta and *c*-Beta profiling instruments at the same time that underwater measurements of PAR and UVR were taken. Total absorption (a) at 488 nm, the backscattering coefficient (b_b) at 488 nm, and the beam attenuation coefficient (c) at 488 nm were measured through drilled holes in the sea ice down to a depth of 10 m below the annual sea ice.

Food availability and feeding

Samples of *C. verrucosa* from both CA (6.7 m) and CE (6.5 m) were chosen for the feeding measurements. These non-destructive measurements began by confirming the pumping activity in individual ascidians by observing fluorescein dye traversing the filtration system. Dye was released near the incurrent (oral) siphon, using a syringe operated by a SCUBA diver, and observed exiting the excurrent (atrial) siphon. For the feeding studies, samples of ambient seawater were collected near the incurrent siphon of individual ascidians (N = 5; approximate size 8 to 10 cm tall for all samples at each site) from ~3 cm away. Immediately after that water collection, a water sample was collected from the excurrent flow of each individual ascidian to be paired with the ambient seawater sample. Both ambient and excurrent samples were collected with 10 ml Vacutainer® collectors. All samples were then fixed at a final concentration of 0.5% electron microscopy grade paraformaldehyde in filtered (0.2 µm) seawater and frozen at −80°C. Samples were shipped frozen and then maintained in liquid nitrogen until analysis by flow cytometry (Lesser et al. 1992, Lesser 2006) as described below.

Each sample was analyzed for cell abundances using a Becton Dickinson FACScan flow cytometer equipped with a 15 mW, 488 nm, air-cooled Argon ion laser. Simultaneous measurements of forward light scatter (FSC, relative size), 90 degree light scatter (SSC), chlorophyll fluorescence (>650 nm), and phycoerythrin fluorescence (560 to 590 nm) were made on all samples. Differentiation of cyanobacteria from prochlorophytes was based on the presence of phycoerythrin fluorescence. The photodiode (FSC) and photomultiplier (SSC) detectors were in log mode, providing 4 decades of response, and signal peak integrals were then measured. The volume of sample analyzed by the FACScan was determined gravimetrically, where the difference in milligrams is proportional to the volume of sample analyzed in milliliters. The abundance of heterotrophic bacteria was determined using PicoGreen (Molecular Probes), a dsDNA specific dye, which stains all prokaryotes and picoeukaryotes (emission fluorescence: 515 to 525 nm). Subtraction of the photosynthethic prokaryotes from the total prokaryotes provides the concentration of the heterotrophic bacterial component of the community that will also include numerous *Archaea*, and size gating allowed for the separation and enumeration of the picoeukaryotic fraction. All flow cytometry measurements included the analysis of fluorescent, calibrated beads of varying sizes to calculate the equivalent spherical diameter (ESD) of all cell populations.

The measurements described above represent instantaneous (s^{-1}) feeding as no destructive sampling was done to measure the length of the incurrent siphon, branchial basket, and excurrent siphon of individual ascidians, an essential metric required to accurately quantify pumping rates (e.g. Trussell et al. 2006). Therefore, filtration efficiency was calculated as 1 − (concentration of cells in the excurrent stream/ambient concentration of cells). All filtered cells for each individual ascidian were then converted to car-

bon equivalents using the following conversion factors: heterotrophic bacteria, 20 fg C cell^{-1} (Ducklow et al. 1993); *Synechococcus*, 470 fg C cell^{-1} (Campbell et al. 1994); and eukaryotic (phytoplankton and picoeukaryotes) cells, pg C = 0.433 × (biovolume)$^{0.863}$, where biovolume is in µm^3 cell^{-1} (Verity et al. 1992). Finally, the total carbon filtered per second was converted to J s^{-1} using a conversion factor of 1 mg C = 23.03 J, assuming a respiratory quotient (RQ) of 1.0, which is appropriate for ammonotelic animals such as ascidians (Parsons et al. 1984). The maximum potential daily intake of carbon and energy was then extrapolated assuming a constant rate of intake for all individual ascidians.

Proximate biochemical and energetic composition

The biochemical composition of *C. verrucosa* was determined from the lyophilized body tissue components of replicate ascidians (N = 5) including the tunic, body wall, endocarps, intestines, ovitestes, and branchial basket, from each site at the 2 depths described above, using techniques described by Slattery & McClintock (1995). Briefly, NaOH-soluble protein and TCA-soluble carbohydrate were determined using standard colorimetric procedures (Dubois et al. 1956, Bradford 1976), while ash and lipid were determined using standard gravimetric techniques (Freeman et al. 1953, Paine 1971). Refractory material was estimated by subtraction and, for the purposes of energetic conversion, assumed to represent insoluble protein (Lawrence 1973). The energetic composition of the tissues was calculated using specific conversion factors for each of the organic components (Gnaiger & Bitterlich 1984). The total energy content of the body tissues was then calculated as the sum of the energy values for each biochemical component.

RESULTS

The population density of *Cnemidocarpa verrucosa* at CA shallow was 0.9 ± 0.13 m^2 (mean ± SE) and at CA deep was 1.3 ± 0.09 m^2, while the population density at CE shallow was 0.3 ± 0.04 m^2 and at CE deep was 0.7 ± 0.18 m^2. The depth differences were significant (2-way ANOVA, F = 10.7, p = 0.0049) as was location (2-way ANOVA, F = 24.0, p = 0.0002), but there was no interaction of these factors (2-way ANOVA, F = 0.0001, p >> 0.05). The significant density differences between CA and CE are consistent with qualitative underwater observations made in

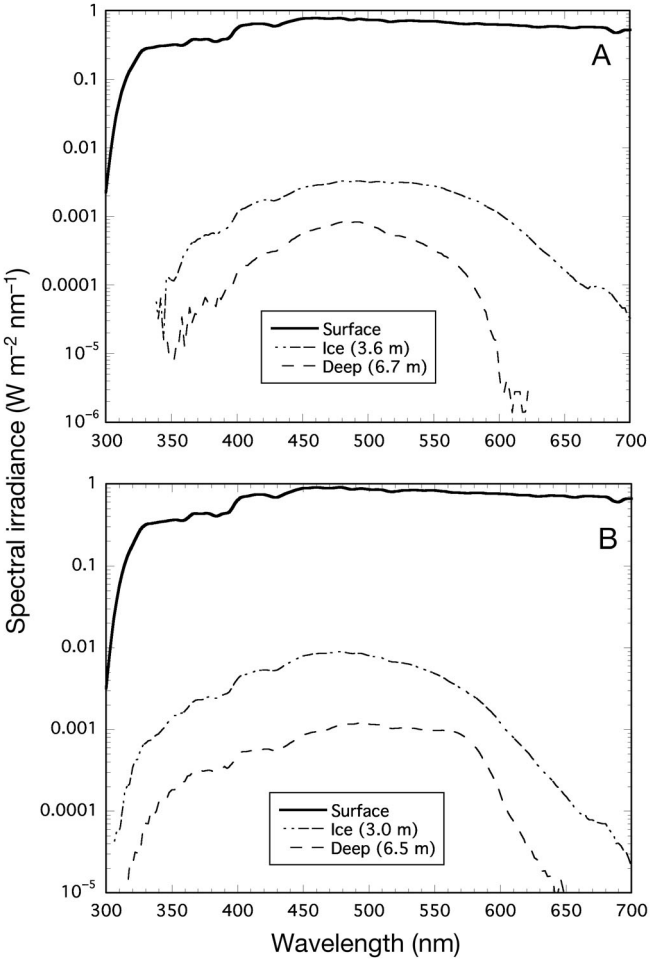

Fig. 2. Maximum spectral irradiance measurements made for (A) Cape Armitage and (B) Cape Evans. Measurements made were for surface irradiance, just under the annual ice, and on the seafloor

2003 and 2007, and the size range between CA and CE was equivocal, with individuals ranging from 2 to 10 cm in height (authors' pers. obs.).

During the timeframe of these measurements, the snow cover at CA was ~5 cm, while at CE, the ice was wind-scoured and snow-free. Both PAR and UVR were transmitted through the annual ice at CA and CE (Fig. 2). The ambient downwelling irradiance of PAR at CA was 901 µmol quanta m^{-2} s^{-1} and 1069 µmol quanta m^{-2} s^{-1} at CE, while total UVR was 28 W m^{-2} at CA and 32 W m^{-2} at CE. The attenuation of both UVR and PAR by the overlying annual ice is significant, but snow cover at Cape Armitage significantly affects both the irradiances of PAR and UVR reaching the benthos. The contribution of the water column to the attenuation of solar radiation reaching the benthos is minor. PAR at CA shallow (6.7 m depth) was ~10 µmol quanta m^{-2} s^{-1}, and UVR was

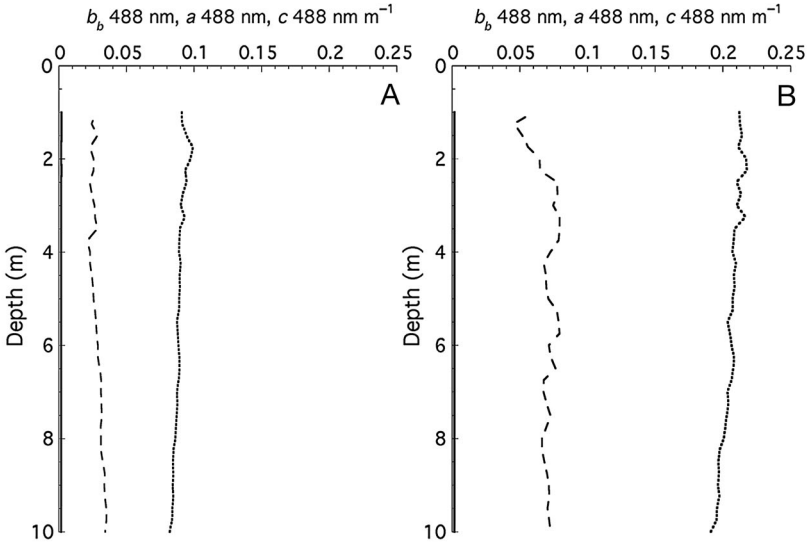

Fig. 3. Inherent optical properties (IOPs) of the water including total absorption (*a*, dashed line) at 488 nm, the backscattering coefficient (b_b, solid line) at 488 nm, and the beam attenuation coefficient (*c*, dotted line) at 488 nm for (A) Cape Armitage and (B) Cape Evans down to a depth of 10 m

0.03 W m^{-2}. At CE shallow (6.5 m depth), PAR was ~20 µmol quanta m^{-2} s^{-1}, and UVR was 0.14 W m^{-2}. Measurements of the inherent optical properties of the water column showed that the absorption (*a*), backscattering (b_b), and beam attenuation (*c*) coefficients were extremely low at both sites (Fig. 3) and dominated by the water component. The *a* and b_b values down to a depth of 10 m below the sea ice were equivalent, while the *c* values at CE were over twice those at CA throughout the measured water column.

The plankton fractions showed higher concentrations of phytoplankton (3 to 10 µm), picoeukaryotes, and picocyanobacteria at CE but greater concentrations of heterotrophic bacteria at CA (Table 1). All fractions were significantly different between locations (*t*-test, 2-tailed, $p < 0.001$ on log-transformed percentages). The filtration efficiency of phytoplankton for ascidians at CA was significantly greater (*t*-test, 2-tailed, $p = 0.004$) than for ascidians at CE (Table 1). For picoeukaryotes, the filtration efficiency between CA and CE was not significantly different (*t*-test, 2-tailed, $p > 0.05$), while the filtration efficiency of picocyanobacteria for ascidians at CE was significantly greater (*t*-test, 2-tailed, $p = 0.01$) compared to those at CA (Table 1). The filtration efficiency for heterotrophic bacteria at CA was greater than at CE (Table 1), and this difference was significant (*t*-test, 2-tailed, $p < 0.0001$). Combining the abundance of each fraction with the filtration efficiency of those fractions for each population of *C. verrucosa*, there was a significant difference between CA and CE, with ascidians at CA filtering a significantly greater proportion of the plankton (*t*-test, 2-tailed, $p < 0.007$). When the total number of cells consumed on a daily basis is converted to carbon equivalents using the unique and specific carbon-conversion efficiencies for each fraction, and with the assumption of constant pumping, the total energy intake by individual ascidians is significantly different between sites for each of these parameters (*t*-test, 2-tailed, $p < 0.0001$), with CA always having greater values than CE (Table 2).

For the proximate biochemical composition of ascidians, a 2-way ANOVA with interaction was initially run, and there were no significant independent effects of depth (ANOVA, $p > 0.05$) or the interaction of depth and location (ANOVA, $p > 0.05$). Consequently, the design was collapsed to an analysis of the effects of location with N = 10 samples in each site. The most compelling difference between sites was for the carbohydrate and lipid content of the

Table 1. Total cell abundance in each fraction of the plankton and filtration efficiency of each plankton fraction for *Cnemidocarpa verrucosa* collected from Cape Armitage (CA) and Cape Evans (CE). N = 5 individual samples (mean ± SE). *$p < 0.05$ based on *t*-test (2-tailed) between sites for each fraction

Fraction	Phytoplankton (3 to 10 µm)	Pico-eukaryotes	Picocyano-bacteria	Heterotrophic bacteria	Total
Total cell abundance (ml^{-1})					
CA	421 ± 32*	261 ± 6*	147 ± 10*	$4.2 \times 10^4 \pm 4.0 \times 10^4$*	$4.3 \times 10^4 \pm 8.6 \times 10^2$*
CE	1090 ± 44	810 ± 13	759 ± 22	$2.9 \times 10^4 \pm 2.7 \times 10^4$	$3.2 \times 10^4 \pm 7.3 \times 10^2$
Filtration efficiency (%)					
CA	84.9 ± 4.9*	51.5 ± 11.2	69.6 ± 13.9*	95.0 ± 0.7*	80.4 ± 2.5*
CE	42.8 ± 13.9	53.7 ± 16.2	94.2 ± 2.7	87.6 ± 1.7	85.3 ± 1.7

Table 2. Carbon and energy content of consumed plankton for *Cnemidocarpa verrucosa* collected from Cape Armitage (CA) and Cape Evans (CE). N = 5 individual samples (mean ± SE). *p < 0.05 based on a *t*-test (2-tailed) between sites for each fraction

	Total cells s^{-1}	Total µg C d^{-1}	Total J d^{-1}
CA	3.6×10^{4}*	267.1 ± 6.9*	6.2 ± 0.16*
CE	2.6×10^{4}	158.0 ± 29.4	3.6 ± 0.68

ovitestes, where CA exhibited significantly greater (*t*-test, 2-tailed, p < 0.05) concentrations of both biochemical constituents (Table 3).

DISCUSSION

As previously reported, the annual sea ice and the presence or absence of snow cover significantly attenuates the transmission of both UVR and PAR to the benthic communities of McMurdo Sound (Lesser et al. 2004). The water column at both CA and CE is isothermal (~−1.9°C) and isohaline (35) and best described as Case I waters, with the only differences in IOPs being the beam attenuation coefficient *c*, which indicates the presence of more particulate matter in the water column at CE compared to CA. This pattern is consistent with the greater cell abundances of large phytoplankton at CE compared to CA. Given functionally equivalent irradiances of solar radiation reaching the sea ice surface, when the generally thinner annual ice, less snow accumulation, and greater amount of ice-free time are all considered, the amount of solar irradiance reaching the benthos at CE is still greater. These underwater irradiances also influence the southernmost occurrences of macrophytes (Rhodophyta) at this site and, for the distribution of some taxa, a downward vertical extension as previously described by Miller & Pearse (1991).

During the early austral spring in McMurdo Sound, all fractions of the planktonic community were present, with typically lower abundances of phytoplankton and picoeukaryotes typical of pre-bloom conditions at both CA and CE. Low concentrations of picocyanobacteria were observed at both sites in McMurdo Sound, likely advected laterally from the open waters of the Southern Ocean where they are also reported to be at much lower concentrations in the plankton (Li 1998, Vincent 2000, Buitenhuis et al. 2012). Picocyanobacteria can occur in higher abundances in the SIMCO (Vincent 2000) and also show seasonality, with higher concentrations occurring during the austral spring and summer in coastal environments (Clarke & Leakey 1996). The largest fraction of the planktonic community in McMurdo Sound quantified by flow cytometry consisted of heterotrophic bacteria in the picoplankton size class. It is also very likely that this fraction contained *Archaea* in the picoplankton size range, which are known to be a significant component of the planktonic community of Antarctica (DeLong et al. 1994). For most of the year, the concentration of heterotrophic picoplankton in the Antarctic is low compared to lower-latitude ecosystems, but it does increase in response to the release of dissolved organic matter from the annual phytoplankton blooms in the late austral spring, with most of this new biomass entrained into the microbial loop (Rivkin 1991, Li 1998). The concentration of heterotrophic picoplankton observed during this study is consistent with quantitative observations from previous studies (Rivkin 1991). This study was undertaken prior to the annual phytoplankton bloom, after which the bacterial biomass increases in McMurdo Sound

Table 3. Proximate biochemical composition of *Cnemidocarpa verrucosa* (µg mg^{-1} tissue) collected from Cape Armitage (CA) and Cape Evans (CE). N = 10 individual samples from which each tissue type was separated and extracted (mean ± SE). *p < 0.05 in *t*-test (2-tailed)

Tissue	Carbohydrate	Lipid	Protein	Refractory	Ash
Tunic					
CA	0.6 ± 0.10	4.3 ± 0.11	7.2 ± 0.03	55.3 ± 0.34*	33.0 ± 5.94
CE	0.7 ± 0.08	4.4 ± 0.05	6.4 ± 0.13	48.2 ± 0.35	40.3 ± 7.32
Body wall					
CA	1.1 ± 0.11	10.8 ± 0.17	19.8 ± 0.08	47.1 ± 0.08*	21.6 ± 3.91
CE	0.7 ± 0.10	11.0 ± 0.05	18.6 ± 0.14	41.4 ± 0.25	28.4 ± 5.07
Endocarps					
CA	0.5 ± 0.03	5.0 ± 0.10	5.4 ± 0.13	28.3 ± 0.16	60.9 ± 11.05
CE	0.4 ± 0.03	5.8 ± 0.10	5.9 ± 0.03	29.5 ± 0.17	58.4 ± 10.69
Intestines					
CA	3.2 ± 0.21*	4.8 ± 0.05	10.6 ± 0.14	50.4 ± 0.06	30.9 ± 5.70
CE	1.4 ± 0.06	4.6 ± 0.0.5	11.0 ± 0.08	49.8 ± 0.19	33.2 ± 5.98
Ovitestes					
CA	4.6 ± 0.29*	23.5 ± 0.57*	13.4 ± 0.07	52.7 ± 0.47	5.6 ± 1.07*
CE	1.1 ± 0.08	17.0 ± 0.08	13.9 ± 0.13	52.0 ± 0.33	15.9 ± 2.82
Branchial basket					
CA	0.5 ± 0.05	7.7 ± 0.08	11.9 ± 0.26	41.8 ± 0.28	38.1 ± 6.91
CE	0.5 ± 0.03	8.3 ± 0.11	12.1 ± 0.11	41.2 ± 0.23	37.9 ± 6.77

from austral winter through austral spring and is ~35-fold greater than phytoplankton production during the same time frame (Rivkin 1991).

Antarctic ascidians are able to filter picoplankton but at lower retention efficiencies than observed for temperate species (Kowalke 1999). Here, we confirmed, using flow cytometry, that *Cnemidocarpa verrucosa* in McMurdo Sound can filter autotrophic and heterotrophic picoplankton at high efficiencies prior to the annual phytoplankton bloom. *C. verrucosa* has also been shown to feed upon phytoplankton, bacterioplankton, and macroalgal detritus depending on the habitat (Tatián et al. 2002, 2004, 2008). For this benthic invertebrate, feeding year round is essential because reproduction in *C. verrucosa* occurs during the austral winter (Sahade et al. 2004). All fractions of the planktonic assemblage assessed during this study are readily consumed by *C. verrucosa*, with the greatest efficiency in particle filtration observed for the picoplankton fractions. As a result, *C. verrucosa* at CA consumes significantly more of this resource, in terms of both carbon and energy, than conspecifics at CE, resulting in significant differences in the proximate biochemical composition of this ascidian throughout McMurdo Sound. Thus, more of these energetic resources, as carbohydrates and lipids, go into the reproductive tissues for animals from CA compared to animals from CE.

Recent studies have taken a stable isotopic approach, including the application of mixing models, to understand the trophic structure and resource dependency of benthic communities in McMurdo Sound (Norkko et al. 2007, Wing et al. 2012). Both of these studies focused on the roles of SIMCO and detritus in supporting large communities of active and passive suspension communities while also discussing the importance of trophic plasticity in a variety of taxa. Wing et al. (2012) showed that in *C. verrucosa*, the proportion of organic material coming from SIMCO is 41% (±0.07%) at CA and 16% (±0.8%) at CE during the austral spring prior to the annual phytoplankton bloom. Here, we have shown that the total carbon and energy obtained from feeding in the plankton, and specifically the heterotrophic picoplankton fraction, is almost twice as much at CA compared to CE. Unfortunately, no contemporaneous measurements and calculations of carbon and energy uptake from the SIMCO are available for comparison to the work by Wing et al. (2012). Nonetheless, we have shown here that for this member of the benthic community in McMurdo Sound, SIMCO and the annual phytoplankton bloom are not the sole sources of food that provides support for its growth and reproduction.

The coupling of water column productivity to the benthos is widely recognized as a strong determinant of community structure in many marine ecosystems (Gili & Coma 1998, Orejas et al. 2000, Witman et al. 2004). With the benthic community of Antarctica dominated by suspension feeders (Dayton et al. 1974, Orejas et al. 2000), and the fact that many of these suspension feeders likely feed throughout most of the year (Barnes & Clarke 1995), picoplankton is the most abundant food resource available to support these communities through the austral winter and spring prior to the annual phytoplankton bloom (Grebmeier & Barry 1991, Orejas et al. 2000, Gili et al. 2001). The results from this study indicate, again, that the largely unacknowledged importance of picoplankton to the benthic suspension-feeding communities of the Antarctic must be systematically examined with the results put into a new model of benthic–pelagic coupling for Antarctic benthic community structure and function.

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