VIMS Articles   Virginia Institute of Marine Science

2016

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Recommended Citation

Contribution to the Themed Section: 'The Role of Zooplankton in Marine Biogeochemical Cycles: From Fine Scale to Global Theories'

Copepod summer grazing and fecal pellet production along the Western Antarctic Peninsula

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Copepods are important grazers on phytoplankton and contributors to carbon export, but their role is poorly understood in the Western Antarctic Peninsula (WAP), a region of high productivity and rapid climate warming. We conducted grazing and egestion experiments with large, dominant copepods each January from 2012 to 2014. We found higher gut evacuation rates (k), initial gut pigment and ingestion rates (I) for *Calanus propinquus* and *Rhincalanus gigas* compared with *Calanoides acutus*. Since k and I linearly increased with chlorophyll a for most species, ingestion rates were 4−70 times greater in more productive coastal regions than offshore, slope waters. Copepods have a low grazing impact on phytoplankton biomass (<1%) and productivity (1%, up to 11%) compared with the dominant WAP macro- and microzooplankton. Egestion rates were high (0.8−37.3 µgC ind.$^{-1}$ day^{-1}); however, ~58% of fecal pellets are retained in the upper water column. Daily carbon rations of ~1% indicated feeding on other carbon sources (protozoans and metazoans) to meet metabolic demands. However, during a coastal phytoplankton bloom, daily C rations increased to up to 13%, indicating increased reliance on phytoplankton. Future changes in the WAP plankton community may affect food web carbon flow and export.

KEYWORDS: copepod; grazing; Antarctic Peninsula; egestion; fecal pellets; carbon; biogeochemistry

INTRODUCTION

In the Southern Ocean, copepods are the most abundant mesozooplankton, and are important grazers of phytoplankton, with daily carbon (C) ingestion up to 50% of primary production (Schnack-Schiel *et al.*, 1985; Conover and Huntley, 1991; Atkinson and Shreeve, 1995; Atkinson *et al.*, 1996a; Dubischar and Bathmann, 1997; Cabal and Alvarez-Marqués, 2002). The dominant copepods employ

feeding modes ranging from carnivorous (*Paraeuchaeta antarctica*), to omnivorous (*Calanus propinquus*), to mostly herbivorous (*Calanoides acutus*) (Yen, 1991; Atkinson, 1998; Pasternak and Schnack-Schiel, 2001), but most have flexible feeding behaviors depending on food availability (Metz and Schnack-Schiel, 1995; Froneman *et al.*, 1996; Calbet *et al.*, 2006). Furthermore, larger copepods produce carbon-rich fecal pellets with sinking rates of 100's m day^{-1} that can be an important source of C export from the euphotic zone (Turner, 2015). In a 5-year time-series analysis of sediment trap collections over the continental shelf of the Western Antarctic Peninsula (WAP), copepods had the second highest contribution to C flux from fecal pellets by taxon (after krill), contributing an annual average of 22% of total fecal pellet particulate organic C flux (compared with 72% for krill fecal pellets; Gleiber *et al.*, 2012). Thus, copepods are both critical grazers in the ecosystem and mediators of C flux.

The WAP has some of the highest seasonal productivity in the Southern Ocean, and is experiencing one of the most rapid rates of warming on Earth (Vaughan *et al.*, 2003). A large summer phytoplankton bloom (>600 mg Chl a m^{-2}) supports an ecosystem with high abundance of krill that are food for upper trophic levels, such as seabirds and marine mammals (Ducklow *et al.*, 2012). Changes due to warming in the northern WAP over the last few decades have led to a latitudinal "climate gradient," affecting food web dynamics with significant changes at all trophic levels from plankton to top predators (Montes-Hugo *et al.*, 2008; Stammerjohn *et al.*, 2008; Ducklow *et al.*, 2012).

Krill and other macrozooplankton in summer in the WAP have a low average grazing impact ($<1\%$ of daily primary production, PP), although localized krill swarms and ephemeral salp blooms can consume $>100\%$ of PP (Bernard *et al.*, 2012). A recent study by Garzio *et al.* (Garzio *et al.*, 2013) found microzooplankton (<200 μm, mostly single-celled protozoa) are important grazers in the WAP, consuming 32 to $>100\%$ of PP. Yet, microzooplankton exert higher grazing pressure on bacterioplankton, picoautotrophs and nanophytoplankton than on the large diatoms (>20 μm) that dominate summer blooms (Montes-Hugo *et al.*, 2008, 2010). An inverse model for the WAP food web further indicates a shift over the last decade in the northern WAP from an herbivorous system, with krill as the dominant grazers, to a microbial system with microzooplankton as dominant grazers (Sailley *et al.*, 2013). With their flexible feeding strategies, copepods are a direct link between these two systems, as grazers of both large diatoms and microzooplankton. The role of copepods in affecting the fate of the WAP summer phytoplankton bloom, however, is unknown.

Time-series analyses indicate changes are occurring in WAP zooplankton (Ross *et al.*, 2008, 2014; Steinberg *et al.*, 2015), including increasing copepod abundance over the past two decades (Gleiber, 2015). Long-term changes in zooplankton can lead to changes in the efficiency of the biological pump and impact higher trophic levels (Steinberg *et al.*, 2012). This study investigates the role of copepods in grazing phytoplankton and in fecal pellet production (FPP) in the WAP to better understand pelagic food web energy transfer, biogeochemical cycling and effects of climate change in this region.

METHOD

Study area and copepod collection

We conducted experiments to examine grazing and egestion (FPP) rates for large, dominant copepod species in the WAP in January 2012, 2013 and 2014 aboard the "ARSV Laurence M. Gould" as part of the Palmer Antarctica Long-Term Ecological Research (PAL LTER) program. Copepods for experiments were collected at stations encompassing the north–south, and cross-shelf (coastal, shelf, slope) gradients of the WAP (Fig. 1) with double oblique net tows within the upper 200 m using a 2×2 m rectangular frame net with 700-μm mesh and non-filtering cod end (Steinberg *et al.*, 2015). Precautions were taken to limit gut evacuation during sampling, including low tow speed and short (<20 min) tow duration (Båmstedt *et al.*, 2000). See Supplementary data, Tables SI and SII, for sampling location details.

We focus on the larger (>1 mm) adults of *C. acutus*, *C. propinquus*, *Rhincalanus gigas* and *P. antarctica*. Small copepods (e.g. *Metridia gerlachei*, *Oithona* spp., Clausocalanidae, *Oncaea* spp.) are also abundant in the region (Gleiber, 2015). Thus, in our calculation of total copepod integrated grazing, we include impact of other species using literature values for their grazing parameters. Abundance of all copepod species was determined from 1×1 m, 333-μm mesh net, 0- to 300-m double oblique tows collected on PAL LTER cruises over 21 years (1993–2013; Gleiber, 2015). Copepod abundance includes later copepodite and adult stages, with the exception of *P. antarctica* which includes adults only.

Phytoplankton biomass and PP were determined at each station at discrete depths (Vernet *et al.*, 2008) and integrated (Bernard *et al.*, 2012). Phytoplankton biomass (mg Chl a m^{-2}) was integrated over the upper 100 m of the water column and PP (mgC m^{-2}day^{-1}) integrated to the bottom of the euphotic zone (30–70 m).

Grazing rate

Grazing rates were estimated using the gut fluorescence technique described by Båmstedt *et al.* (Båmstedt *et al.*,
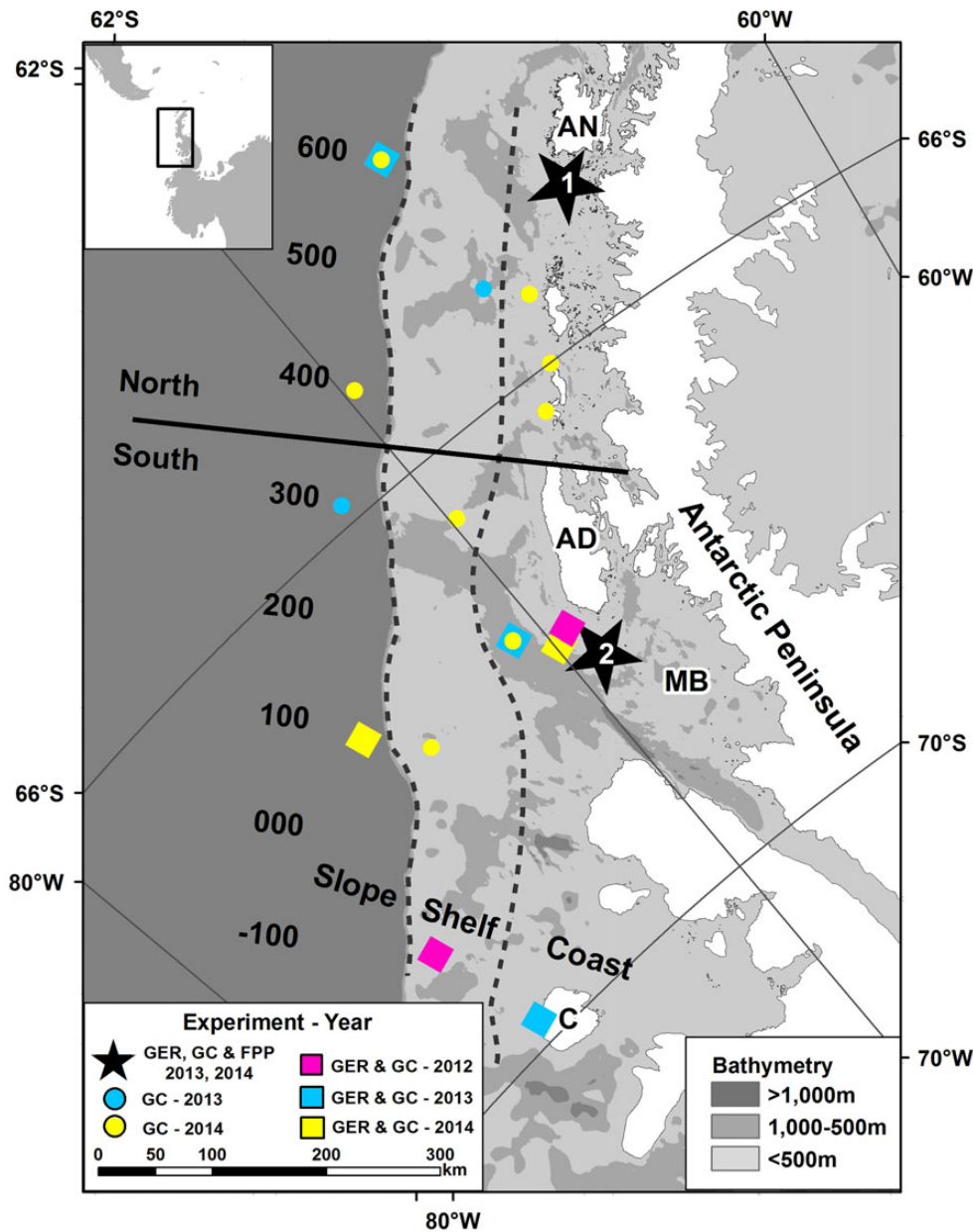
Fig. 1. Stations sampled during January 2012, 2013 and 2014 off the Western Antarctic Peninsula. Black stars indicate "process study" sites where gut content (GC) samples were collected, and fecal pellet production (FPP) and gut evacuation rate (GER) experiments were conducted in 2013 and 2014. Additional locations of GER experiments and GC sample collection in 2012, 2013 and 2014 are indicated. AN, Anvers Island; AD, Adelaide Island; MB, Marguerite Bay; C, Charcot Island. Palmer Station is located on Anvers Island. LTER grid lines are numbered (600 to −100). Solid lines separate the "north" and "south" gradients. Coast, shelf and slope regions are separated by a dashed line. All region divisions are based on hydrographic and sea ice conditions (Martinson *et al.*, 2008; Stammerjohn *et al.*, 2008).

2000). Ingestion (grazing) rates were calculated for each species using equations derived in Båmstedt *et al.* (Båmstedt *et al.*, 2000): $I = k \times G$; where I is ingestion rate [ng(Chl *a* equiv.)ind.$^{-1}$day^{-1}], G is instantaneous gut pigment content [ng(Chl *a* equiv.)ind.$^{-1}$] and k is daily gut evacuation rate (GER) (day^{-1}). We did not measure gut pigment degradation, thus omitted a pigment degradation correction on the recommendation of Durbin and Campbell

(Durbin and Campbell, 2007). While gut pigment disappearance is taken into account in the exponential evacuation rate curve (Durbin and Campbell, 2007; Landry *et al.*, 2009; Bernard *et al.*, 2012), G could be underestimated due to pigment destruction occurring in the time between collection and net tow retrieval.

For measurement of G, copepods were collected at stations throughout the study area (Fig. 1, Supplementary

data, Table SI). Copepods were removed from the cod end and immediately anesthetized with soda water to prevent gut clearance (Kleppel *et al.*, 1988; Båmstedt *et al.*, 2000), identified to species, frozen in liquid nitrogen, and stored at $-80°C$ for gut fluorescence analysis.

For GER experiments, contents of the cod end were gently transferred to a 20-L bucket containing surface seawater through a submerged 5-mm mesh sieve to remove larger zooplankton while minimizing damage to copepods. Copepods were immediately transferred with a 0.5-mm mesh sieve (to exclude large phytoplankton) to replicate 20-L buckets containing particle-free seawater (0.2 μm filtered). Buckets were kept in a flow-through aquarium maintained at $\pm 1.0°C$ ambient temperature. The first time point ($t = 0$) was taken $3-10$ min after the cod end was recovered. Subsequent samples were taken at $t = 5, 10, 15, 20, 25, 30, 40, 50, 60, 90, 120$ and 180 min. At each time point, copepod subsamples were removed from each replicate bucket using a 0.5-mm mesh sieve, anesthetized, and sorted to species within $5-10$ min of collection under dim light (Båmstedt *et al.*, 2000). Groups of the same species were transferred to cryovials, frozen in liquid nitrogen and stored at $-80°C$ for gut fluorescence analysis. Two replicate GER experiments were conducted at each site (Fig. 1, Supplementary data, Table SI).

GER constants (k, h^{-1}) are the slope of the exponential decrease of gut pigments G (Chl a + phaeopigments) over time (Båmstedt *et al.*, 2000). We compared GERs calculated with both exponential and linear models with variability in the ending time ($t = 1.0, 1.5, 2.0, 3.0$ h) (Schnetzer and Steinberg, 2002). An exponential model with experiments conducted over 3-h best fit (i.e., highest r^2) the decline of gut pigments during the GER experiments. Gut passage times were calculated from $1/k$ (h). Hourly GERs were multiplied by 24 to convert to daily rates, and used in the above ingestion rate equation.

Daily, integrated grazing rates for each species were estimated using their measured abundances over the 21-year PAL LTER time series (Gleiber, 2015). Integrated grazing rates [μg(Chl a equiv.) m^{-2}day^{-1}] for each species is the product of ingestion rate [ng(Chl a equiv.)ind.$^{-1}$day^{-1}] and integrated abundance (ind. m^{-2}) (Båmstedt *et al.*, 2000). Total copepod integrated grazing rate is the sum of all individual species integrated grazing rates, converted to C using a C:Chl a ratio of 63:1 (Bernard *et al.*, 2012). These values were used to estimate copepod grazing impact on phytoplankton biomass (mgChl a m^{-2}) and PP (mgC m^{-2}day^{-1}) by species, and for the whole copepod community.

Gut fluorescence analysis

Gut contents of copepods were determined fluorometrically (Båmstedt *et al.*, 2000). For analysis of January 2012 gut pigments, one to two replicate groups of copepods of each species ($25-75$ for *C. acutus*, $5-25$ for *C. propinquus*, and $1-2$ for *R. gigas* and *P. antarctica*) were homogenized with a Misonix XL-2000 sonicator in 10 mL of 90% acetone. Gut pigments were extracted in a freezer for $2-24$ h and centrifuged at 3000 rpm for 5 min. Sonicating animals before extraction reduces the normal extraction time from 24 to 2 h (Båmstedt *et al.*, 2000). Fluorescence was measured before and after acidification with 10% HCl with a TD-700 fluorometer. For analysis of January 2013 and 2014 gut pigment samples, we used a reduced extraction volume and minicuvette method (Takatsuji and Hamasaki, 1997; Schnetzer and Steinberg, 2002). Individuals, or groups of two to three copepods, of each species were homogenized in 1.0 mL of 90% acetone and analyzed with a Turner Designs Trilogy with minicell insert. We analyzed $1-30$ subsamples of the same species per time point. Concentrations of chlorophyll a and phaeopigment were calculated using the equations in Parsons *et al.* (Parsons *et al.*, 1984) and Båmstedt *et al.* (Båmstedt *et al.*, 2000).

Egestion rate

To measure egestion rate, we conducted FPP experiments at coastal process study sites (Fig. 1, Supplementary data, Table SII). Cod end contents were gently transferred to a 60-L tub containing surface seawater. Groups of each locally abundant copepod species were gently transferred to FPP chambers (fecatrons; Juul-Pedersen *et al.*, 2006). Fecatrons were two nested 1-L plastic containers, one with a 1-mm mesh bottom suspended inside the other, and filled with water collected below the chlorophyll maximum (to minimize addition of large diatom chains inseparable from fecal pellets). The design allows pellets to fall through, preventing coprophagy or fragmentation of pellets by copepods (Urban-Rich *et al.*, 1999; Wexels Riser *et al.*, 2002, 2007). Each experiment comprised $1-5$ replicate fecatrons, each containing $5-50$ copepods, depending on species. Incubations lasted $12-18$ h, and were kept within $\pm 1.0°C$ of ambient surface seawater and in dim light. We incubated three control fecatrons without copepods at each location.

Following incubations copepods were removed, counted, assessed if alive (replicates with dead animals were discounted), and frozen at $-80°C$ for CN analysis. Contents of the 1-L fecatrons were filtered through a 64-μm sieve, rinsed onto combusted GF/F filters with 0.2-μm FSW, and frozen at $-80°C$. Three replicate 0.2-μm FSW blanks were analyzed using the same method, to account for C and N in the combusted GF/Fs and FSW. Three replicate initial and final water samples were collected in each experiment, filtered, stored at $-80°C$ and analyzed for Chl a and phaeopigments.

Total organic C and N concentrations were determined using a method modified from Ruck et al. (Ruck et al., 2014). Pellets, controls and animals were dried in an oven at 60°C for 72 h, and total animal dry weight measured. Pellets and controls (on combusted GF/Fs) and animals were transferred to combusted glassware (525°C for 2 h), placed in a dessicator with a small beaker of concentrated HCl for 12–14 h to remove inorganic C, and returned to the oven until dry. Subsamples of homogenized animal tissue (1–4 copepods) were weighed using a Sartorius XP1000P microbalance. The acidified, dried GF/Fs and animal subsamples were packed into tin capsules and processed using a Costech ECS 4010 CHNSO analyzer for flash combustion with acetanilide or atropine as the standard. Mean C and N concentrations from seawater controls were subtracted from fecal pellet C and N to account for organic particles from the seawater filtered onto GF/Fs along with fecal pellets.

Fecal pellet C content was used to calculate egestion rates as follows: $E = [FPC/\text{no. ind.}/t] \times 24$ h; where E is egestion rate (μgC ind.$^{-1}$day^{-1}), FPC is fecal pellet carbon (μgC), "no. ind." is the number of copepods in the incubation, and t is incubation time (h). Integrated egestion rate (μgC m^{-2}day^{-1}) for each species is the product of mean egestion rate (μgC ind.$^{-1}$day^{-1}) and species integrated abundance (ind. m^{-2}) using abundances for each species over the 21-year PAL LTER time series. Total copepod integrated egestion rate is the sum of individual species integrated egestion rates.

Daily rations

Daily C ration, expressed as a percentage of body C ingested or egested per day, was calculated for each species from C content (mgC ind.$^{-1}$) and applied to daily C specific ingestion (grazing) and egestion rates.

Data analysis

Regression analyses were used to test for significant correlations between station integrated Chl a versus k, I and egestion rate for each species. One-way ANOVA was used to compare G, I, egestion rate, body dry weight and C content and elemental ratios between different species. One- and two-way ANOVA was used to compare integrated Chl a, k, G and I for copepods between four subregions encompassing the variation in WAP hydrographic and sea ice conditions: North-Coast, South-Coast, North-Slope, South-Slope (see "Study area"; Fig. 1). We excluded the shelf region, which was a transition between the coast and slope. Results of grazing and egestion experiments conducted at coastal stations in 2013 and 2014 were also compared using ANOVA. Data were rank transformed to meet normality and equal variance assumptions. Analyses were conducted using SigmaPlot 11.0. Only statistically significant ANOVA results ($P < 0.05$) are described in Results unless otherwise noted.

RESULTS

Hydrographic setting

Sea surface temperature (SST) ranged from -1.8 to $2.8°C$ and sea surface salinity ranged from 32.1 to 33.8 at stations sampled. Integrated Chl a ranged from 18.1 to 579 mg m^{-2} and integrated PP ranged from 255 to 8979 mgC m^{-2}day^{-1}. See Supplementary data, Tables SI and SII.

Copepod grazing

Gut evacuation rate constant (k)

Hourly GER constants (k) were lowest on average for *C. acutus* [0.37 ± 0.22 h^{-1}; mean $\pm$ standard deviation (SD)], compared with *C. propinquus* (0.61 ± 0.57 h^{-1}) and *R. gigas* (0.63 ± 0.48 h^{-1}). Values of k and $1/k$ for all GER experiments are given in Supplementary data, Table SIII.

The positive linear relationships between water column Chl a and k for *C. acutus* and *C. propinquus* were significant (Fig. 2a and b). We therefore used this relationship to estimate k applied in ingestion rate calculations (see below) at stations where GER experiments were not conducted. The relationship between Chl a and *R. gigas* GER was not significant (Fig. 2c), so we used the *R. gigas* average GER (0.63 h^{-1}) in ingestion rate calculations. Since we did not conduct GER experiments with *M. gerlachei*, we applied an average GER from the literature of 1.0 h^{-1} (Froneman *et al.*, 2000; Li *et al.*, 2001; Pakhomov and Froneman, 2004).

Individual gut content (G) and ingestion rates (I)

The average initial gut contents for *R. gigas* and *C. propinquus* were 2–10 times higher, and ingestion rates over three times higher, than those of *C. acutus* and *M. gerlachei* (Table I). *Calanoides acutus* and *R. gigas* had lower gut contents in higher Chl a conditions (>400 mg m^{-2}) (Fig. 3). We did not sample *C. propinquus* at stations with high Chl a.

Ingestion rate of *C. acutus*, *C. propinquus* and *R. gigas* increased with Chl a (Fig. 2d–f). We used these significant positive linear relationships, and the average ingestion rate of *M. gerlachei* [24.0 ng(Chl a equiv.)ind.$^{-1}$day^{-1}] (Table I) to determine the ingestion rate used in integrated grazing rate calculations (see below). Note the right-skewed distribution of ingestion rates (Fig. 2d–f), thus median ingestion rates [*C. acutus* = 18.7, *C. propinquus* = 53.2, *R. gigas* = 84.7, *M. gerlachei* = 16.6 ng(Chl a equiv.)ind.$^{-1}$day^{-1}] are lower than mean values (Table I).

For Clausocalanidae and *Oithona* spp., we applied an ingestion rate from the lower end of literature values of 38
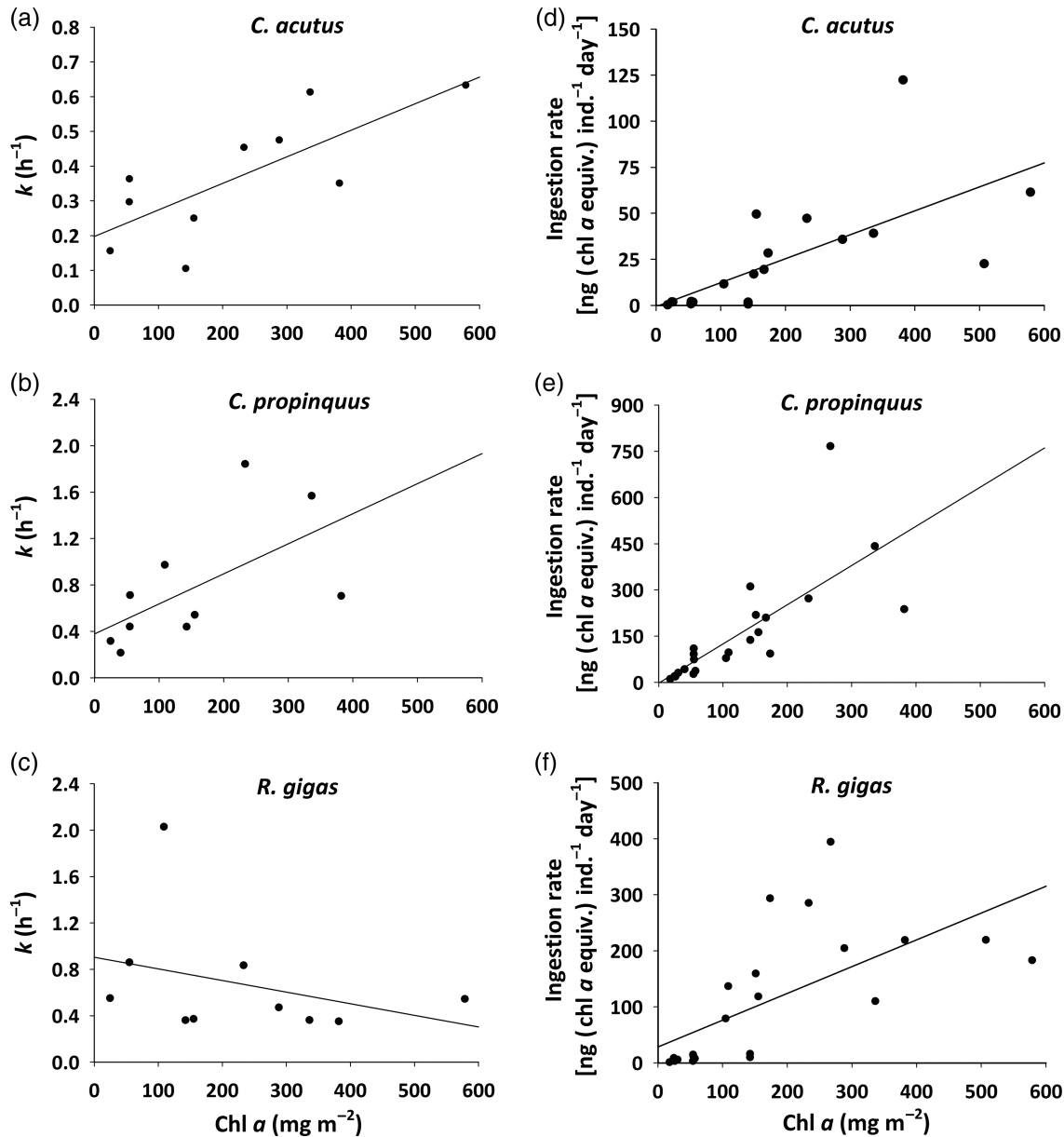
Fig. 2. Relationship between integrated (0–100 m) Chl *a* and (**a**–**c**) copepod gut evacuation rate constants (*k*, h^{-1}) and (**d**–**f**) copepod daily ingestion rates [*I*, ng(Chl *a* equiv.) ind.$^{-1}$day^{-1}]. Gut evacuation rate experiments were conducted in January 2012, 2013 and 2014. Values of *k* (h^{-1}) are an average from replicate experiments (if available) at each location. Ingestion rates are an average of replicates at each location (*n* = 1–53). Regression equations and statistics are as follows: (a) *Calanoides acutus* [*k* = (7.65e^{-4} × Chl *a*) + 0.197, r^2 = 0.57, *P* = 0.011, *n* = 10], (b) *Calanus propinquus* [*k* = (2.59e^{-3} × Chl *a*) + 0.378, r^2 = 0.37, *P* = 0.05, *n* = 10], (c) *Rhincalanus gigas* [*k* = −(1.00e^{-3} × Chl *a*) + 0.904, r^2 = 0.11, *P* = 0.348, *n* = 10], (d) *C. acutus* [*I* = (0.130 × Chl *a*) − 0.658, r^2 = 0.48, *P* = 0.001, *n* = 21], (e) *C. propinquus* [*I* = (1.27 × Chl *a*) − 2.06, r^2 = 0.55, *P* < 0.001, *n* = 22] and (f) *R. gigas* [*I* = (0.478 × Chl *a*) + 28.4, r^2 = 0.41, *P* < 0.001, *n* = 22].

and 16 ng(Chl *a* equiv.)ind.$^{-1}$day^{-1}, respectively (Atkinson, 1996; Bernard and Froneman, 2003, 2005; Pakhomov and Froneman, 2004).

Integrated grazing rates and grazing impact
The six copepod species used in our total copepod integrated grazing calculations represent an average of 95% (range 77–100%) of the abundance of non-carnivorous

WAP copepods (Gleiber, 2015). *Metridia gerlachei* had the highest average integrated grazing rate [15.1 μg(Chl *a* equiv.)m^{-2}day^{-1}] and contributed to an average of 43% of the total copepod grazing (Table II). While the average grazing rate for *C. acutus* [14.3 μg(Chl *a* equiv.)m^{-2}day^{-1}] was similar to *M. gerlachei*, this value is influenced by one station (−100 000 in 2011) with a record abundance of *C. acutus* (44 378 ind. m^{-2}), yielding a rate of 1459 μg(Chl

Table I: Average individual initial gut content and daily ingestion rates

Copepod species	Initial gut content (G) [ng(Chl a equiv.) ind.$^{-1}$]	Ingestion rate (I) [ng(Chl a equiv.) ind.$^{-1}$day^{-1}]	n
C. acutus	4.3 ± 6.2 (<0.1–41.2)	37.4 ± 53.7 (<0.1–364)	329
C. propinquus	8.4 ± 10.0 (0.2–55.2)	133 ± 208 (2.2–1430)	193
R. gigas	10.7 ± 12.3 (<0.1–58.6)	133 ± 161 (0.5–865)	219
M. gerlachei	1.0 ± 1.0 (<0.1–3.2)	24.0 ± 23.1 (2.1–76.4)	31

Data are from January 2012, 2013 and 2014 gut content analyses ($n = 4$, 247, and 522, respectively, for all four species combined). Copepod species are: *Calanoides acutus, Calanus propinquus, Rhincalanus gigas,* and *Metridia gerlachei*. $I = k \times G \times 24$ (see "Results: Gut evacuation rate constant (k)" for explanation of k value applied in calculations). Values are mean ± standard deviation; range in parentheses. n = number of gut content samples per species.

a equiv.)m^{-2}day^{-1} (Table II). Excluding this outlier, the average integrated grazing rate for *C. acutus* was 6.72 μg(Chl a equiv.)m^{-2}day^{-1}.

The combined daily grazing impact of the six copepod species was low, removing <1% of both phytoplankton biomass and PP daily, on average (Table II). Grazing impact ranged from 0.1 to 1% of phytoplankton biomass and <1 to 11% of PP.

Regional comparison

Integrated Chl a was an order of magnitude higher at stations along the coast than the slope ($P = 0.02$), but there was no significant difference between north and south within either coast or slope (Fig. 4a). Differences between subregions for GER, initial gut content and daily ingestion rate for *C. acutus*, *C. propinquus* and *R. gigas* (Fig. 4b–d) follow trends in Chl a, with some exceptions. GERs do not vary greatly among locations for each species; the only significant regional difference is between the North-Coast and South-Slope (higher and lower, respectively) for all species combined ($P = 0.04$). While *R. gigas* shows little regional variation in GER, gut content and ingestion rates were 30–70 times higher on the coast than the slope with no significant latitudinal differences (Fig. 4b–d). *Calanoides acutus* and *C. propinquus* gut contents and ingestion rates were also significantly greater on the coast than the slope (Fig. 4c). Significant differences in gut contents and ingestion rates between species existed in each region for the North-Coast and South-Coast, but not on the slope (Fig. 4c and d).

Copepod egestion

Egestion rates ranged from 0.82–37.3 μgC ind.$^{-1}$day^{-1}, with average rates by species of 3.66 (*C. acutus*), 6.98

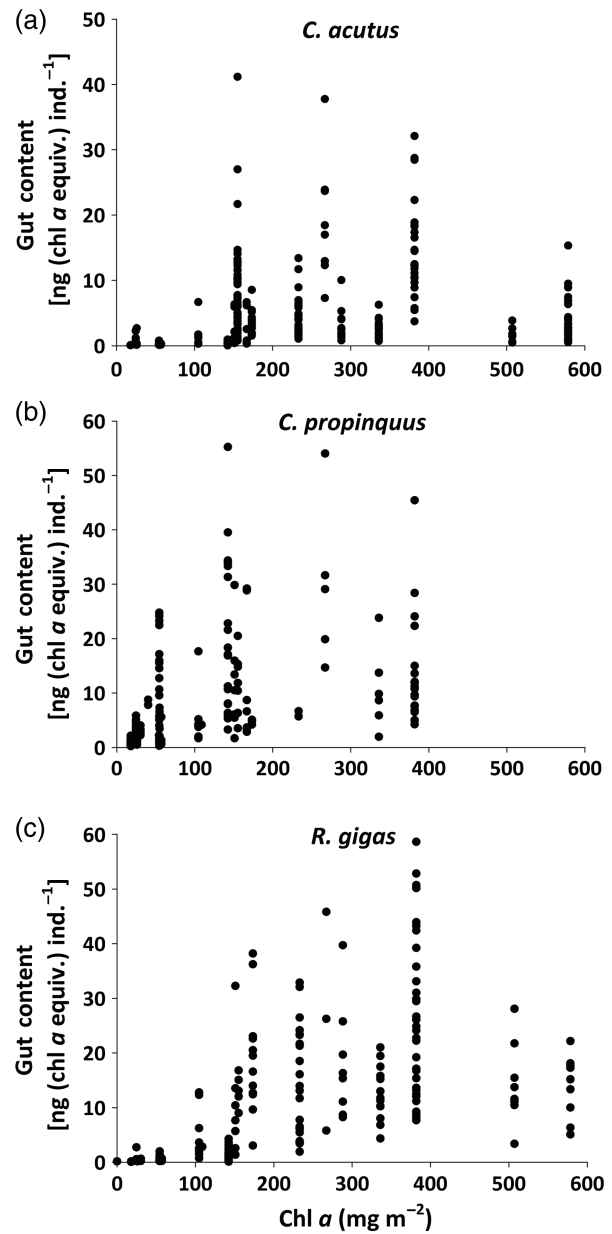**Fig. 3.** Variation in individual copepod gut content [ng(Chl a equiv.) ind.$^{-1}$] with Chl a for (**a**) *Calanoides acutus* ($n = 321$), (**b**) *Calanus propinquus* ($n = 176$) and (**c**) *Rhincalanus gigas* ($n = 219$). Chl a integrated to 0–100 m.

(*C. propinquus*), 2.95 (*R. gigas*), and 15.4 (*P. antarctica*) μgC ind.$^{-1}$day^{-1} (Table III). *Calanus propinquus* had the highest egestion rate of the herbivorous and omnivorous copepods, which was significantly higher than *R. gigas* ($P = 0.007$). Chl a was not depleted at the end of experiments, thus herbivorous animals were not starved during the incubation. The carnivorous copepod *P. antarctica* however was not fed additional prey, but had significantly higher egestion rates (Table III). Fecal pellet C:N

Table II: Total abundance, daily integrated grazing rates, grazing contribution and grazing impact of herbivorous copepods in the WAP

| Copepod species | Abundance (ind. m^{-2}) | Daily integrated grazing rates | | Grazing contribution (%) | Grazing impact | |
		[μg(Chl *a* equiv.) m^{-2}day^{-1}]	(mgC m^{-2}day^{-1})		% Chl *a*	% PP
*C. acutus**	638 ± 3337 (<1–44 378)	14.3 ± 118.0 (<0.1–1459.0)	0.92 ± 7.43 (<0.1–91.92)	7.8 ± 12.6 (0.3–88.6)	<0.01 ± 0.04 (0–0.57)	0.07 ± 0.38 (0–4.68)
C. propinquus	12 ± 37 (0–376)	1.7 ± 9.5 (0–122.9)	0.11 ± 0.60 (0–7.72)	3.3 ± 7.6 (0–67.8)	<0.01 ± <0.01 (0–0.05)	0.01 ± 0.03 (0–0.39)
R. gigas	36 ± 76 (0–727)	2.2 ± 3.8 (0–25.1)	0.12 ± 0.24 (0–1.58)	9.0 ± 12.3 (0–70.2)	<0.01 ± 0.01 (0–0.19)	0.04 ± 0.10 (0–1.01)
M. gerlachei	622 ± 799 (<1–5281)	15.1 ± 19.3 (<0.1–126.7)	0.95 ± 1.22 (<0.1–7.98)	43.2 ± 24.8 (1.4–95.9)	0.03 ± 0.03 (0–0.19)	0.19 ± 0.34 (0–2.27)
Clausocalanidae	228 ± 456 (<1–3349)	8.8 ± 17.7 (<0.1–127.3)	0.55 ± 1.11 (<0.1–8.02)	22.5 ± 15.7 (0.2–89.4)	0.02 ± 0.06 (0–0.50)	0.18 ± 0.71 (0–8.04)
Oithona spp.	482 ± 1306 (0–14 584)	7.4 ± 20.1 (0–218.8)	0.47 ± 1.26 (0–13.78)	14.2 ± 13.7 (0–75.6)	0.02 ± 0.06 (0–0.48)	0.16 ± 0.56 (0–5.82)
Total	2019 ± 4481 (13–53 550)	49.3 ± 145.8 (0.3–1782.6)	3.10 ± 9.18 (<0.1–112.31)		0.08 ± 0.14 (<0.1–1.06)	0.65 ± 1.49 (0.3–11.39)

Copepod species are: *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas*, and *Metridia gerlachei*, Clausocalanidae and *Oithona* spp. Abundance (ind. m^{-2}) is integrated from 0–300 m. Grazing impact is presented as percentage of phytoplankton biomass (% Chl *a*) and primary productivity (% PP) consumed per day. Values are mean ± standard deviation, with range in parentheses, for the 21-year time series ($n = 202$). The mean ± standard deviation and range of phytoplankton biomass (Chl *a*) integrated 0–100 m and primary productivity (PP) integrated to the bottom of the photic zone in January 1993–2013 were: Chl *a* (mg m^{-2}) = 84.0 ± 112.9 (12.8–1009.5), PP (gC m^{-2}day^{-1}) = 1.18 ± 1.65 (0.04–13.88).
*Mean includes one station (−100 000 in 2011) with an abundance of (44 378 ind. m^{-2}), over three times the next highest *Calanoides acutus* abundance.

elemental ratios ranged from 1.7 to 28.5, with a mean of ∼7 for all species (Table III). Since egestion rates were not significantly correlated with Chl *a* or SST, we used the average egestion rate for each species (see above) to calculate integrated rates. See Supplementary data, Table SIV, for egestion rates and fecal pellet C:N ratios for each location, with corresponding station Chl *a* and SST.

Calanoides acutus had the highest integrated egestion rate, with average FPP of 2.3 mgC m^{-2}day^{-1} over the 21-year time series, and up to 162 mgC m^{-2}day^{-1} at one station with high *C. acutus* abundance (Table IV). Even excluding this outlier, average *C. acutus* integrated egestion rate is an order of magnitude higher than all other species. Integrated egestion rates were lowest for the less abundant *P. antarctica*, despite this species having the highest individual rate.

Copepod daily rations

Copepod dry weight and C content differed significantly among species ($P < 0.001$); *P. antarctica* was the largest with both dry weight (4.4 mg) and C content (3.1 mgC) on average three to five times greater than other species (0.8–1.5 mg dry wt. and 0.4–0.7 mgC) (Table V). *Rhincalanus gigas* had significantly lower C content (∼33%) than all other species examined (44–48%; Table V). We

used mean C content (mgC) for each species to calculate body rations.

The proportion of body C ingested daily as phytoplankton was low (∼1%) for *C. acutus*, *C. propinquus* and *R. gigas* (Table V). Among these three species, *C. propinquus* and *R. gigas* had slightly higher daily rations, consuming up to 13% of their body C per day as phytoplankton. The proportion of body C egested daily was also low: ∼1% for all species, with *C. propinquus* (copepod with highest body C) egesting a slightly higher proportion (up to 3.6%; Table V). We did not use these data to determine egestion:ingestion ratios since GER and FPP experiments were not always conducted with animals from the same location.

Ingestion and egestion during a phytoplankton bloom

We compared copepod ingestion and egestion rates from experiments conducted on the coast in 2013 during post-bloom conditions, and in 2014 during peak bloom, as determined by November–March Chl *a* at Palmer Station (Fig. 1). Stations sampled in January 2014 had extremely high Chl *a* in the coastal regions due to late seasonal ice retreat, and a delayed spring bloom in January (compared with November/December in 2013). Average (± SD) integrated Chl *a* for coastal stations in 2014 was 335 ± 152 mg m^{-2} ($n = 10$), with surface Chl *a* up to 23 mg m^{-3}. In the
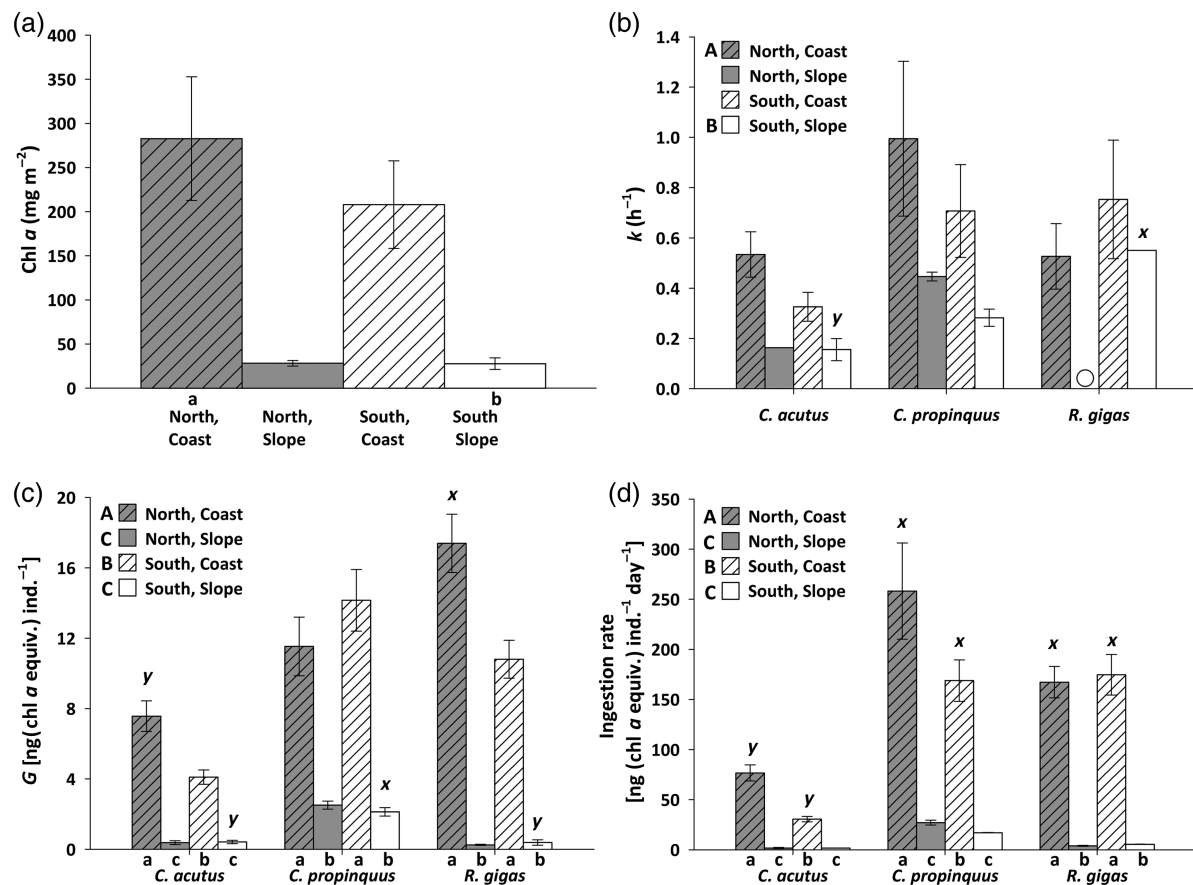
Fig. 4. Regional comparison of water column Chl *a* and copepod grazing parameters from experiments conducted in January 2012, 2013 and 2014. (**a**) Chl *a* integrated 0–100 m; (**b**) gut evacuation rate constant, (**c**) initial gut content and (**d**) daily ingestion rate for the copepods *Calanoides acutus*, *Calanus propinquus* and *Rhincalanus gigas*. Error bars are standard error, letters indicate statistically significant ($P < 0.001$, two-way ANOVA) differences in grazing parameters among regions for each species (lower case, a > b > c) or all for species combined (upper case, A > B > C). Regions designated with the same letter, or no letter, are not significantly different ($P > 0.05$). Significant difference in Chl *a* between regions is labeled as described above; there are no significant differences in gut evacuation rates between regions for any species. Species significantly different from each other within a region are indicated with a different letter ($x > y$; $P < 0.05$, one-way ANOVA). Open circle indicates no experiment for species at that location.

austral summer of 2012/2013, sea ice retreat occurred 44 days earlier (S. Stammerjohn, personal communication), with peak bloom (surface Chl $a = 30$ mg m^{-3} near Palmer Station) in late November; by January 2013 coastal Chl *a* was on average 92.9 ± 51.3 mg m^{-2}, significantly lower than in January 2014 ($P = 0.005$).

In higher phytoplankton biomass conditions in January 2014, *C. acutus* and *C. propinquus* GERs were, on average, twice as fast (higher k) as in 2013 (for *C. propinquus*, $P = 0.002$), whereas initial gut contents for both species were similar in both years (Fig. 5a and b). Ingestion rates were significantly greater for both species in 2014 (*C. acutus*, $P = 0.032$; *C. propinquus*, $P < 0.001$) (Fig. 5c). However, GERs were similar in both years for *R. gigas*, but gut content over six times greater ($P < 0.001$) in 2014, resulting in ingestion rates 10-fold higher in 2014 (Fig. 5a–c).

The daily body rations (% bodyC ingested day^{-1}) for *C. acutus* and *R. gigas* were also significantly higher in 2014, with *C. acutus* increasing from 0.3 to 1.2% (2013 to 2014, respectively; $P = 0.001$), and *R. gigas* from 0.3% to 3.3% ($P < 0.001$). *Calanus propinquus* daily body ration increased from 1.6 to 2.5% ($P > 0.05$). Daily egestion rates, fecal pellet C:N ratio and egestion body ration were not significantly different between years.

DISCUSSION

Species-specific grazing

Gut evacuation rates

GERs (*k*) for copepods and other mesozooplankton are highly variable as they can depend upon temperature, phytoplankton biomass and quality, as well as zooplankton vertical migration, diel periodicity and feeding

Table III: Average daily copepod egestion rates and fecal pellet C:N ratios

Copepod species	Egestion rate (μgC ind.$^{-1}$day^{-1})	Fecal pellet C:N (μgC:μg N)	n
C. acutus	3.66 ± 2.33 (0.82–7.69)	6.49 ± 2.0 (4.07–9.68)	11
C. propinquus	6.98 ± 6.27 (1.26–24.2)	6.94 ± 5.13 (1.71–17.7)	11
R. gigas	2.95 ± 2.91 (0.60–13.2)	8.20 ± 8.43 (1.73–28.5)	16
P. antarctica	15.4 ± 12.9 (6.36–37.3)	7.39 ± 2.42 (5.03–10.2)	5

Data are from January 2013 and 2014 fecal pellet production experiments ($n = 16$ and 27, respectively, for all four species combined). Results are shown for *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas*, and *Paraeuchaeta antarctica*. Values are mean ± standard deviation; range in parentheses. n = number of fecatron incubations.

Table IV: Total integrated abundance and daily egestion rates

Taxon	Abundance (ind. m^{-2})	Daily integrated egestion (mgC m^{-2}day^{-1})
*C. acutus**	638 ± 3337 (<1–44 378)	2.34 ± 12.21 (<0.01–162.35)
C. propinquus	12 ± 37 (0–376)	0.09 ± 0.25 (0–2.62)
R. gigas	36 ± 76 (0–727)	0.11 ± 0.22 (0–2.14)
P. antarctica	622 ± 799 (<1–5281)	0.02 ± 0.04 (0–0.42)
Total	2019 ± 4481 (13–53 550)	2.54 ± 12.41 (<0.01–165.07)

Integrated abundance (0–300 m) is from stations sampled in January 1993–2013 ($n = 202$). Integrated egestion is the product of mean egestion rate for each species (see Table III) and integrated abundance. Copepods are: *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas*, and *Paraeuchaeta antarctica*. Values are mean ± standard deviation; range in parentheses.
*Mean includes one station (−100 000 in 2011) with an abundance of (44 378 ind. m^{-2}), over three times the next highest *Calanoides acutus* abundance.

strategy (Dam and Peterson, 1988; Atkinson *et al.*, 1992, 1996a; Schnetzer and Steinberg, 2002). The range in phytoplankton biomass (18−579 mg Chl *a* m^{-2}) and temperature (−1.5 to 2.1°C) in our study is the widest among copepod grazing studies south of the Antarctic Polar Front (APF) (Table VI). Thus, it is not surprising that we found a wide range in k (h^{-1}) for each species (*C. propinquus*, 0.2−2.5; *R. gigas*, 0.3−2.0; *C. acutus*, 0.1−0.8). GERs for *C. propinquus* spanned the literature range, those for *R. gigas* and *C. acutus* were at the low end or below literature values (Table VI). This trend is expected

as previous studies of *C. propinquus* occurred in more polar regions (SST ≤0°C), while those of *R. gigas* and *C. acutus* include warmer regions near the APF (sub-Antarctic). Since k increases with temperature (Dam and Peterson, 1988), due to higher metabolic rate in warmer regions, a lower k for *R. gigas* and *C. acutus* is expected for our higher latitude, colder region. Furthermore, k increased with increasing Chl *a* for *C. acutus* and *C. propinquus*. A similar trend has been reported for high latitude regions (Dagg and Walser, 1987; Atkinson *et al.*, 1996b), while in temperate regions (with higher variation in temperature) k trends positively with SST (Dam and Peterson, 1988) as long as food is not limiting.

We calculate k as the slope of the exponential decrease in gut pigments over 3 h, similar to the methods used in other Southern Ocean copepod grazing studies (Table VI, and references therein). However, a recent study on *in vivo* individual copepod gut fluorescence with laser imaging found k was significantly higher during feeding than non-feeding, suggesting conventional estimates of copepod ingestion using the GER method can be underestimated by 15−70% (Karaköylü and Franks, 2012). Thus, *in situ* gut passage times may be shorter (higher k) than calculated using our method, making our ingestion and grazing rates conservative.

Individual gut content

Average gut contents for *R. gigas*, *C. propinquus* and *C. acutus* were at the high end of literature values for the Southern Ocean (Atkinson *et al.*, 1996a; Table VI references), with maximum values over 30 ng(Chl *a* equiv.)ind.$^{-1}$. One explanation for the high gut Chl *a* content and low GERs of copepods in our study is that copepod feeding can saturate or decrease at high Chl *a* concentrations. At stations with the highest Chl *a* (integrated, >400 mg m^{-2}; surface, up to 23 mg m^{-3}), *C. acutus* and *R. gigas* gut contents averaged 64% (as low as 8%) and 84% (as low as 54%), respectively, of those at stations with lower Chl *a* (155−382 mg m^{-2}; surface, 1−14 mg m^{-3}) (Fig. 3). Similarly, Atkinson *et al.* (Atkinson *et al.*, 1996a) found little difference in gut contents of *C. acutus*, *R. gigas* and *C. propinquus* during a bloom (surface Chl *a* 6.5−19 mg m^{-3}) compared with those collected during a moderate bloom (integrated, Chl *a* 223 mg m^{-2}; surface Chl *a* 1−4 mg m^{-3}; Atkinson *et al.*, 1992), suggesting saturation.

As we usually conducted tows during daylight hours, we did not capture possible diel variability in GER and gut content (Atkinson *et al.*, 1992; Li *et al.*, 2001; Bernard and Froneman, 2003); however, this variability is reduced at high latitudes in summer due to reduced hours of darkness (Conover and Huntley, 1991).

Table V: Individual copepod elemental composition and daily rations

	C. acutus	C. propinquus	R. gigas	P. antarctica
Copepod elemental composition				
mgC	0.37 ± 0.14	0.67 ± 0.19	0.42 ± 0.18	2.13 ± 0.76
Dry Wt. (mg)	0.83 ± 0.40	1.53 ± 0.32	1.27 ± 0.36	4.41 ± 1.45
% Carbon	47.8 ± 14.9	44.3 ± 12.5	32.8 ± 8.25	48.1 ± 2.85
C:N (µgC:µgN)	7.30 ± 1.84	5.07 ± 1.49	4.71 ± 1.25	7.66 ± 1.44
n	24	21	24	10
Copepod daily ingestion				
Ingestion rate (µgC ind.$^{-1}$day^{-1})	2.36 (0–22.9)	8.36 (<0.1–90.1)	8.40 (<0.1–54.5)	
Body ration (% C ingested ind.$^{-1}$day^{-1})	0.64 (0–6.3)	1.25 (<0.1–13.5)	1.99 (<0.1–12.9)	
Copepod daily egestion				
Egestion rate (µgC ind.$^{-1}$day^{-1})	3.66 (0.8–7.7)	6.98 (1.3–24.2)	2.95 (0.6–13.3)	15.4 (6.4–37.3)
Body ration (% C egested ind.$^{-1}$day^{-1})	1.08 (0.27–2.03)	0.89 (0.45–2.02)	1.58 (0.33–3.21)	0.69 (0.50–0.84)

Copepods for elemental composition were collected in January 2013 and 2014; differences in carbon content, dry weight, C:N & % carbon (proportion of dry weight that is carbon) among species are significant ($P < 0.001$, one-way ANOVA). Values are mean ± standard deviation; n = number of animals analyzed. Individual copepod daily rations expressed as a percentage of body carbon ingested or egested daily. Copepod species are: *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas*, and *Paraeuchaeta antarctica*. Ingestion for *P. antarctica* is excluded because it is a carnivorous copepod for which we did not conduct ingestion experiments. Average ingestion and egestion rate for each species are listed for comparison. Values are mean; range in parentheses.

Daily ingestion rates and rations

Average daily ingestion rates for *C. acutus*, *C. propinquus*, *R. gigas*, and *M. gerlachei* are similar to those reported in literature (Table VI); this is consistent with the comparably lower *k* and higher gut pigment in our study, as ingestion is calculated as the product of *k* and initial gut content. Maximum ingestion rates for all (except *M. gerlachei*) are among the highest for Southern Ocean copepods (Atkinson *et al.*, 1992, 1996a).

Calanus propinquus and *R. gigas* ingestion rates were on average four to five times higher than *C. acutus* and *M. gerlachei*, which is not surprising as the former are larger copepods with higher gut pigment contents. Individual ingestion rates for *C. propinquus* and *R. gigas* [mean = 133 ng(Chl *a* equiv.)ind.$^{-1}$day^{-1} for both] were higher than for the abundant small euphausiid *Thysanoessa macrura* [10–120 ng(Chl *a* equiv.)ind.$^{-1}$day^{-1}], but generally lower than the pteropod *Limacina helicina*, and euphausiids *Euphausia crystallorophias* and juvenile *E. superba* in the WAP [920–6620 ng(Chl *a* equiv.)ind.$^{-1}$day^{-1}; Bernard *et al.*, 2012]. Ingestion rates for large adult *E. superba* [up to 8950 ng(Chl *a* equiv.)ind.$^{-1}$day^{-1}] were an order of magnitude higher than those of copepods in our study (Bernard *et al.*, 2012).

Despite the high copepod gut pigment/C content and ingestion rates relative to larger animals, mean daily rations of ∼1% indicate that phytoplankton contribution to the diet of the copepods was low. Copepod daily rations in our study were within range of most previous summer studies (Table VII). While copepods could meet their metabolic requirements (3.4–3.8% for respiration and an additional 1.6–4.5% for egg production; Dagg *et al.*, 1982; Conover and Huntley, 1991; Schnack-Schiel *et al.*, 1991; Atkinson *et al.*, 2012b) feeding on phytoplankton alone, average daily rations are below those needed

to satisfy metabolic costs and would not fuel reproduction (Huntley *et al.*, 1991). This is common for Southern Ocean copepods (Atkinson and Shreeve, 1995; Mayzaud *et al.*, 2002; Calbet *et al.*, 2006; Lee *et al.*, 2013) and indicates protozoans and metazoans may be an important food source. *Calanus propinquus* is a known omnivore, even during spring and summer blooms when phytoplankton is abundant (Schnack-Schiel *et al.*, 1991; Bathmann *et al.*, 1993; Atkinson, 1995, 1998; Atkinson *et al.*, 1996a). *Rhincalanus gigas* and *C. acutus* have often been considered mostly herbivorous during the austral spring and summer, feeding indiscriminately on phytoplankton (Atkinson and Shreeve, 1995; Atkinson, 1995, 1998). A more recent study in the northern WAP suggests these copepods feed selectively based on size, motility and quality of prey. Calbet *et al.* (Calbet *et al.*, 2006) found *C. acutus*, *R. gigas* and *C. propinquus* had high clearance rates and a preference for motile cells (e.g. ciliates and *Gyrodinium* spp.), although autotrophs were the largest C source for these copepods.

Low C intake from phytoplankton is also evident for other mesozooplankton in the WAP during summer. Bernard *et al.* (Bernard *et al.*, 2012) examined daily rations of euphausiids using the same methods, and found a low contribution of phytoplankton (*E. superba* daily rations on average 0.3%, up to 3%), suggesting protozoans or copepods are also important in their diet. Furthermore, salp (*Salpa thompsoni*) and *L. helicina* larger daily rations (15 and 1–27%, respectively) also indicate consumption of other sources of C at times (Bernard *et al.*, 2012). There are no studies of predation on protozoans (or other metazoans) in the WAP by copepods, and few by krill or other macrozooplankton (e.g. Atkinson and Snyder, 1997; Martin *et al.*, 2006; Reiss *et al.*, 2015). These studies are needed to discern the importance of non-phytoplankton prey.
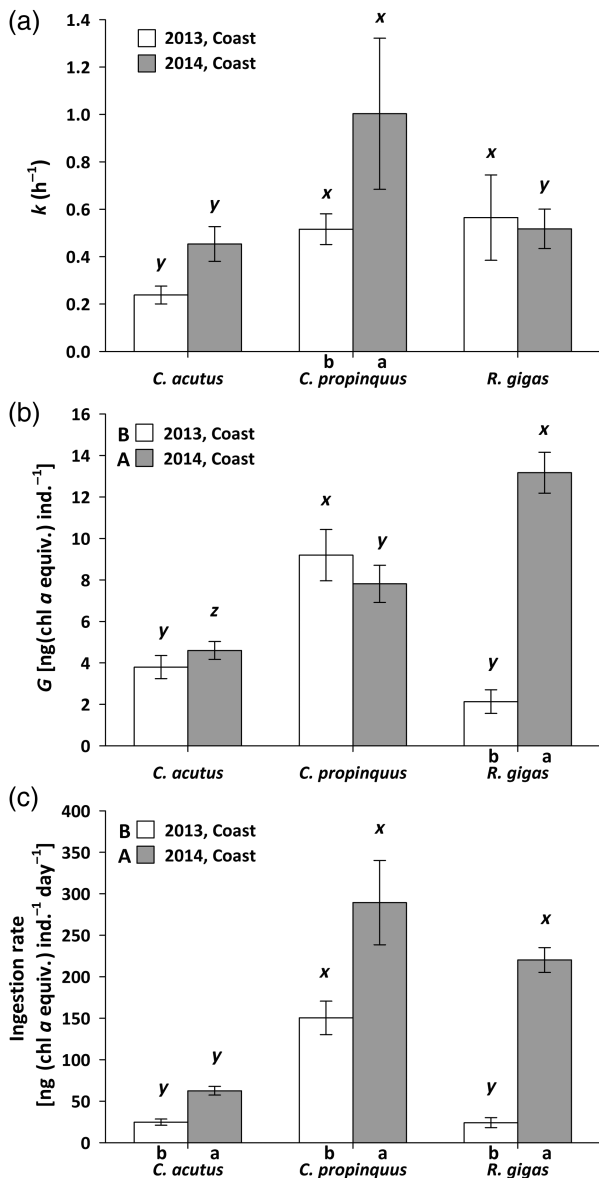
Fig. 5. Comparison of (**a**) gut evacuation rates (k), (**b**) gut content (G) and (**c**) ingestion rates measured in the coastal region of the WAP in January 2013 (Chl $a = 92.9 \pm 51.3$ mg m^{-2}; mean $\pm$ standard deviation) and 2014 (Chl $a = 335 \pm 152$ mg m^{-2}) for the copepods *Calanoides acutus*, *Calanus propinquus*, and *Rhincalanus gigas*. Error bars are standard error, labels indicate statistically significant ($P < 0.05$, two-way ANOVA) differences in ingestion rate between years for each species (lower case letters) or all species combined (capital letters): a > b (A > B). Species significantly different from each other within a year are indicated with a different letter ($x > y > z$; $P < 0.05$, one-way ANOVA).

Regional comparison

Phytoplankton biomass and composition in the WAP varies both along a coast-shelf-slope gradient (Vernet *et al.*, 2008), and a latitudinal gradient (Montes-Hugo *et al.*, 2008). Mean Chl a was highest near the coast (245 mg m^{-2}), and sharply decreased offshore (shelf:

93 mg m^{-2}, slope: 20 mg m^{-2}). WAP phytoplankton in summer are mostly large (>20 μm) diatoms, but due to warming, over the last three decades regional differences have developed with a shift toward smaller cells north of our study region (Montes-Hugo *et al.*, 2008, 2009; Vernet *et al.*, 2008). Considering these gradients, we examined how regional changes associated with the climate gradient might impact copepod grazing.

Copepod grazing generally follows regional differences in Chl a, with higher gut content and ingestion rates on the coast than slope. This is consistent with previous studies comparing phytoplankton blooms to oceanic conditions, with similar differences in phytoplankton biomass (Atkinson *et al.*, 1992, 1996a; Li *et al.*, 2001). GER varied less with Chl a, which further suggests saturation of feeding at higher Chl a concentrations on the coast (Atkinson *et al.*, 1996a). However, we conducted fewer GER experiments on the slope than coast, so k is not as well constrained for the slope.

Since daily rations are calculated from the ingestion rate applied to mean body C content of each species, relative regional differences in rations reflect that of ingestion rate. *Calanus propinquus* and *R. gigas* had significantly higher average rations on the coast (2.0 and 2.6%, respectively) than slope (0.2 and <0.1%), suggesting they are primarily herbivorous on the coast and more detritivorous or carnivorous on the slope (Atkinson and Shreeve, 1995; Calbet *et al.*, 2006; Lee *et al.*, 2013). Bernard *et al.* (Bernard *et al.*, 2012) showed similar differences in *E. superba* diet between the coast and slope. Thus, if a shift towards decreased phytoplankton biomass and smaller phytoplankton continues farther south in the WAP (Montes-Hugo *et al.*, 2009), copepods and other zooplankton will need to further supplement their diet with microzooplankton (Garzio and Steinberg, 2013) or smaller phytoplankton.

The only significant difference with latitude was for *C. acutus* gut content and ingestion rate along the coast, where *C. acutus* followed the trend in phytoplankton biomass most strongly. *Calanoides acutus* body ration was also significantly higher in the North, Coast (1.5%), than South, Coast (0.5%). While *C. acutus* daily rations are low, this could be enough to support their metabolism as *C. acutus* can use excess lipid stores from winter diapause into the next season (Calbet *et al.*, 2006). Daily rations on the slope for *C. acutus* (<0.3%) are well below metabolic requirements (Dagg *et al.*, 1982; Conover and Huntley, 1991; Schnack-Schiel *et al.*, 1991; Atkinson *et al.*, 2012b). *Calanoides acutus* can rapidly consume large motile cells (i.e. ciliates and dinoflagellates), but they are primarily herbivores with a preference for large diatoms important in building their lipid stores (Atkinson, 1998; Calbet *et al.*, 2006; Pasternak *et al.*, 2009). Thus, the predicted shift to

Table VI: Comparison of gut evacuation and daily ingestion rates for dominant copepods in different regions of the Southern Ocean

Copepod species	Gut evacuation rate (k) (h^{-1})	Ingestion rate (I) [ng(Chl a equiv.) ind.$^{-1}$day^{-1}]	Region	Season	Reference
C. acutus	**0.4 (0.1–0.8)**	**37 (<1–364)**	**Western Antarctic Peninsula**	**Summer**	**This study**
	0.7–1.0	28–60	APF of the Lazarev Sea; SIZ of the Indian Sector	Spring	Dubischar and Bathmann (1997), Tirelli and Mayzaud (1999)
	0.8	50–83	Prydz Bay (pack-ice)	Summer	Li *et al.* (2001)
	1.2–1.9	34–51	APF; Spring ice edge and MIZ of the Lazarev Sea	Summer	Froneman *et al.* (2000), Pakhomov and Froneman (2004)
	1.7	326	Prydz Bay (polynya)	Summer	Li *et al.* (2001)
	2.1–5.1	82–775	South Georgia	Summer	Atkinson *et al.* (1992)
	2.8	–	Winter ice edge of the Lazarev Sea	Summer	Froneman *et al.* (2000)
C. propinquus	**0.7 (0.2–2.5)**	**133 (2–1429)**	**Western Antarctic Peninsula**	**Summer**	**This study**
	0.2–3.2	3–461	Spring and Winter ice edge of the Lazarev Sea; SIZ of the Indian Sector	Spring	Dubischar and Bathmann (1997), Tirelli and Mayzaud (1999)
	0.9–2.7	75–205	Spring and Winter ice edge of the Lazarev Sea	Summer	Froneman *et al.* (2000), Pakhomov and Froneman (2004)
R. gigas	**0.6 (0.3–2.0)**	**133 (<1–865)**	**Western Antarctic Peninsula**	**Summer**	**This study**
	0.3–1.0	21–230	APF of the Lazarev Sea; SIZ of the Indian Sector	Spring	Dubischar and Bathmann (1997), Tirelli and Mayzaud (1999)
	0.5–1.7	182–549	South Georgia	Summer	Atkinson *et al.* (1992)
	0.5–2.9	46–145	APF; Spring ice edge and MIZ of the Lazarev Sea	Summer	Froneman *et al.* (2000), Pakhomov and Froneman (2004)
M. gerlachei	**1.0***	**24 (2–76)**	**Western Antarctic Peninsula**	**Summer**	**This study**
	0.4–1.8	26–95	MIZ, Spring and Winter ice edge of the Lazarev Sea	Summer	Froneman *et al.* (2000), Pakhomov and Froneman (2004)
	0.6–0.7	13–132	Prydz Bay	Summer	Li *et al.* (2001)
	1.75	–	Prince Edward Archipelago	Autumn	Perissinotto (1992)
Clausocalanidae	0.4	39–285	APF near Prince Edward Islands	Autumn	Bernard and Froneman (2003), Bernard and Froneman (2005)
	0.9	–	South Georgia	Summer	Atkinson (1996)
	1.41	–	Prince Edward Archipelago	Autumn	Perissinotto (1992)
	–	76	Spring ice edge of the Lazarev Sea	Summer	Pakhomov and Froneman (2004)
Oithona spp.	0.4–0.6	16–111	APF near Prince Edward Islands	Autumn	Bernard and Froneman (2003), Bernard and Froneman (2005)
	1.5	–	South Georgia	Summer	Atkinson (1996)
	–	16	Spring ice edge of the Lazarev Sea	Summer	Pakhomov and Froneman (2004)

Copepods are: *Calanoides acutus, Calanus propinquus, Rhincalanus gigas, Metridia gerlachei, Clausocalanidae*, and *Oithona* spp. Values are calculated using the gut fluorescence technique, and ingestion rates are de-corrected for pigment destruction (if necessary). Values from the present study (bolded) are included for comparison.
*Gut evacuation rate for *M. gerlchei* was not measured in this study, an average value from literature is used.
APF, Antarctic Polar Front; MIZ, Marginal Ice Zone; SIZ, Seasonal Ice Zone.

smaller phytoplankton in the WAP could remove a critical source of nutrition for *C. acutus*.

Total copepod integrated grazing rates and grazing impact

Mean daily integrated grazing rate for all copepods combined (3.1 mgC m^{-2}day^{-1}) was within the wide range found previously in the Southern Ocean in spring and summer (<0.1–94 mgC m^{-2}day^{-1}; Schnack-Schiel *et al.*, 1985; Atkinson, 1996; Razouls *et al.*, 1998; Cabal and Alvarez-Marqués, 2002; Mayzaud *et al.*, 2002; Bernard and Froneman, 2003, 2005; Tanimura *et al.*,

2008) and high abundance of one species (*C. acutus* in 2011) resulted in grazing rates up to 92 mgC m^{-2}day^{-1}. We note that total integrated grazing rate as calculated (applying ingestion rates in this 3-year study to species abundances 1993–2013) is subject to error resulting from interannual differences in environmental conditions (e.g. temperature, phytoplankton biomass). For example, ingestion rates for *C. acutus*, *C. propinquus* and *R. gigas* were applied to net tow abundance based on a linear relationship with Chl *a*; if these copepods become food saturated, this relationship would overestimate grazing rate at high Chl *a* concentrations. Conversely, total copepod integrated grazing rate could be underestimated as it does

Table VII: Comparison of individual daily body ration (% carbon) ingested as phytoplankton for dominant copepods in different regions of the Southern Ocean

Copepod species	Body ration (%C ingested ind.$^{-1}$day^{-1})	Region	Season	Reference
C. acutus	**0.6 (<0.1–6.2)**	**Western Antarctic Peninsula**	**Summer**	**This study**
	0.2–1.1	Amundsen Sea	Summer	Lee *et al.* (2013)
	0–7	Gerlache and Bellingshausen Sea	Summer	Atkinson and Shreeve (1995), Calbet *et al.* (2006)
	5.6–27	South Georgia	Summer	Atkinson *et al.* (1992)
	3.2–28.0	Antarctic Peninsula	Summer	Schnack-Schiel *et al.* (1985)
C. propinquus	**1.3 (<0.1–13.5)**	**Western Antarctic Peninsula**	**Summer**	**This study**
	0–15	Bellingshausen Sea	Summer	Atkinson and Shreeve (1995), Metz and Schnack-Schiel (1995)
	5.3–23.1	Antarctic Peninsula	Summer	Schnack-Schiel *et al.* (1985)
R. gigas	**2.0 (<0.1–12.9)**	**Western Antarctic Peninsula**	**Summer**	**This study**
	0.1–0.3	Amundsen Sea	Summer	Lee *et al.* (2013)
	0.8–2.8	Bellingshausen Sea	Summer	Atkinson and Shreeve (1995)
	1.5–3.0	South Georgia	Summer	Atkinson *et al.* (1992), Atkinson *et al.* (1996a)
	1.3–9.6	Antarctic Peninsula	Summer	Schnack-Schiel *et al.* (1985)
M. gerlachei	0.5–10.4	Bellingshausen and Amundsen Sea	Summer	Lee *et al.* (2013), Atkinson and Shreeve (1995), Metz and Schnack-Schiel (1995)
	6.4–35.2	Antarctic Peninsula	Summer	Schnack-Schiel *et al.* (1985)
Oithona spp.	0.5–3.5	Bellingshausen Sea	Summer	Atkinson and Shreeve (1995)

Copepods are: *Calanoides acutus, Calanus propinquus, Rhincalanus gigas, Metridia gerlachei, Oithona* spp. Values from the present study (bolded) are included for comparison.

not include *Oncaea* spp. and earlier stage copepodites, which are important grazers (Schnack-Schiel *et al.*, 1985; Atkinson *et al.*, 1996a; Bernard and Froneman, 2005).

WAP copepods had low impact on phytoplankton standing stock (<0.1–1%) and PP (<1–11%). This is comparable to previous studies of the same copepod species, with grazing impact from <1 to 4% of Chl *a* and <1 to 55% of PP (Schnack-Schiel *et al.*, 1985; Atkinson, 1995; Atkinson and Shreeve, 1995; Atkinson *et al.*, 1996a; Razouls *et al.*, 1998; Cabal and Alvarez-Marqués, 2002; Tanimura *et al.*, 2008; Lee *et al.*, 2013). We note that we integrated copepod biomass in the top 300 m, whereas primary production was integrated through the euphotic zone, under the assumption that these copepods are largely capable of migrating into the top layer to feed. As some of these species are stronger vertical migrators (e.g. *M. gerlachei*) than others (Atkinson, 1998), it is possible not all deeper copepods fed in the upper layers, resulting in an even lower grazing impact.

Combined grazing of euphausiids, pteropods and salps in the WAP in summer (excluding regions with salp blooms where grazing impact is up to 30% phytoplankton standing stock) was <0.3% of phytoplankton standing stock and <0.6% of productivity (Bernard *et al.*, 2012). Combining our results with those of Bernard *et al.* (Bernard *et al.*, 2012) for macrozooplankton, we estimate mean meso- plus macrozooplankton community grazing impact of ~0.5% phytoplankton standing stock and ~1.2% of PP. This is relatively low compared with summer microzooplankton grazing in the WAP, which was on average 55–85% of PP (Garzio *et al.*, 2013). Although microzooplankton are the most important grazers of phytoplankton in the WAP, krill swarms, salp blooms or copepod aggregations would result in higher localized mesozooplankton grazing contribution.

Copepod egestion

Herbivorous copepod (*C. acutus, R. gigas* and *C. propinquus*) average daily egestion rate was 5.5 µgC ind.$^{-1}$day^{-1}, higher than most previous report at high latitudes (Table VIII). This is not surprising since the WAP is a productive continental shelf with a high contribution of zooplankton fecal pellets to POC export, especially in summer (67%, up to 100%; Gleiber *et al.*, 2012), compared with other high-latitude regions (Wassmann *et al.*, 1999; Dagg *et al.*, 2003; Wexels Riser *et al.*, 2008; Smith *et al.*, 2011). To our knowledge, these are the first reported egestion rates for the carnivore *P. antarctica*, which were high compared with herbivorous copepods, despite that we did not add prey to their incubations. We suggest that either *P. antarctica* were feeding on protozoans or small metazoans, or as these are the largest of the species we examined, a full gut upon capture would result in comparatively higher FPP.

Daily individual egestion rates differed significantly among species, with *R. gigas* and *C. acutus* having lower, and *C. propinquus* and *P. antarctica* higher average rates. Few previous studies in the Southern Ocean quantify copepod FPP (Table VIII), and of these only Dagg *et al.* (Dagg *et al.*, 2003) report species-specific rates. Their results indicate egestion rates generally lower than in our

Table VIII: Comparison of daily individual egestion and integrated egestion rates for copepods, and other mesozooplankton at high latitudes

Taxon	Egestion rate (μgC ind.$^{-1}$day^{-1})	Daily integrated egestion (mgC m^{-2}day^{-1})	Region	Reference
Copepods	**5.5 (0.9–24.2)**	**2.5 (0–165)**	**Western Antarctic Peninsula**	**This study**
	0.2–0.8	–	APF at 170°W	Dagg *et al.* (2003)
	0.4–3.8	–	Norwegian Shelf	Urban-Rich *et al.* (1999)
	0.9–9.3	20–60	Barents Sea	Wexels Riser *et al.* (2007)
	1.7	0.4–1.7	Central Arctic	Olli *et al.* (2007)
	–	44–122	Baffin Bay	Sampei *et al.* (2004)
	–	0.2–20	Southern Indian Ocean	Møller *et al.* (2011)
Mesozooplankton	–	0.2–0.6	ACC and APF of the Lazarev Sea	Dubischar and Bathmann (2002)
	–	12.4	MIZ of the Lazarev Sea	Dubischar and Bathmann (2002)
Krill	0–745	–	South Georgia	Atkinson *et al.* (2012a)
Salp blooms	–	20	Antarctic Peninsula	Phillips *et al.* (2009)

Values from the present study (bolded) are included for comparison.
ACC, Antarctic Circumpolar Current; APF, Antarctic Polar Front; MIZ, Marginal Ice Zone.

study (Table VIII). This discrepancy is likely due to regional or temporal differences in phytoplankton assemblage. Dagg *et al.* (Dagg *et al.*, 2003) sampled near the APF with smaller phytoplankton cells (Urban-Rich *et al.*, 2001), and our study was at higher latitudes with large diatoms dominant.

Fecal pellet C:N elemental ratios ranged from 3.9 to 22.2, with average pellet C:N ratios of 7–8, similar to that reported for copepod fecal pellets at high latitudes (Morales, 1987; Urban-Rich *et al.*, 1999). Fecal pellet C:N ratios were on average slightly higher than copepod body elemental ratios (4.7–7.7), consistent with reports of fecal pellets of copepods and other zooplankton being N-depleted as zooplankton assimilate N more efficiently than C (Morales, 1987; Mayor *et al.*, 2011; Atkinson *et al.*, 2012a).

Mean total copepod integrated egestion rate ($\sim$2.5 mgC m^{-2}day^{-1}) was lower than in most other high-latitude studies (Table VIII), although maximum rates associated with high copepod densities were on the high end of those previously reported. Total copepod integrated egestion rate calculated in our study is an underestimate as we only included four species, excluding about 75% of other copepods by number (Gleiber, 2015). However, many of the abundant copepods are small (e.g. *Oithona* spp., Clausocalanidae, *Oncaea* spp.; Gleiber, 2015), and would produce smaller, slower sinking fecal pellets that are attenuated more rapidly in the water column than larger pellets (Dagg *et al.*, 2003; Steinberg *et al.*, 2008) due to microbial degradation, horizontal transport, destruction from turbulence, and zooplankton fragmentation or ingestion (González and Smetacek, 1994; Dagg *et al.*, 2003; Wexels Riser *et al.*, 2007; Sampei *et al.*, 2008).

Fecal pellet retention in the water column can be estimated from *in situ* fecal pellet flux and FPP (Møller *et al.*, 2011). Using the average total copepod integrated egestion rate from our study ($\sim$1.4 mgC m^{-2}day^{-1}; adjusted to 170 m) and average copepod fecal pellet flux at 170 m from a sediment trap (0.61 mgC m^{-2}day^{-1}; Gleiber *et al.*, 2012), we estimate 58% retention of fecal pellets from large copepods in the upper 170 m of the water column. This compares to >80% retention of copepod fecal pellets in the southern Indian Ocean north of the APF (Møller *et al.*, 2011) and 37–96% in the Barents Sea (Wexels Riser *et al.*, 2002, 2007). This potentially high retention of copepod fecal pellets indicates they may not be efficient for C export in the WAP, at least compared with krill fecal pellets which dominate export flux in the region (Gleiber *et al.*, 2012).

Copepod grazing and egestion during a phytoplankton bloom

Sea ice extent was a record high during the 2013–2014 sea ice season in the WAP with the latest sea ice retreat (Julian day 366, near Anvers Island) since 1984–1985. The prior season (2012–2013) day of sea ice retreat was also later than average, but occurred about 44 days earlier compared with 2013–2014 (S. Stammerjohn, personal communication). Therefore, sampling in January 2014 coincided with the peak of the spring phytoplankton bloom (surface Chl *a* > 20 μgL^{-1}), while January 2013 sampling was during the decline of the spring bloom (surface Chl *a* < 10 μgL^{-1}). This interannual variability allows comparisons between copepod grazing and egestion during bloom versus post-bloom.

The three copepod species we examined represent a range of feeding and life history strategies. *Calanoides acutus* is a true polar species that undergoes diapause in the winter and feeds primarily on phytoplankton during the spring bloom, while *C. propinquus* feeds throughout

the winter (on protozoans and small copepods; Atkinson, 1998, 1991; Pasternak and Schnack-Schiel, 2001; Schnack-Schiel, 2001). *Rhincalanus gigas* falls between these two strategies, often (but not always) going through diapause and feeding preferentially on phytoplankton, detritus, protozoans, and metazoans (Ward *et al.*, 1997; Atkinson, 1998). All three species, however, shift their feeding strategies depending on food availability (Atkinson, 1998; Calbet *et al.*, 2006; Pasternak *et al.*, 2009). During the spring bloom, these copepods are expected to be almost entirely herbivorous. Comparing the 2 years, copepods had higher ($P < 0.001$) percent body C content during peak bloom in 2014, which is predicted for copepods feeding primarily on phytoplankton (Atkinson and Shreeve, 1995; Lee *et al.*, 2013). Higher daily C rations for all three species in 2014 (on average $1.2-3.3\%$) compared with 2013 ($0.3-1.6\%$) suggest a shift in diet, from phytoplankton during the bloom to other sources of C (i.e. protozoans or metazoans) post-bloom. This corresponds to ingestion rates more than double for all three species in 2014. *Rhincalanus gigas* daily ration increased nearly 10-fold from 2013 to 2014 ($0.4-3.3\%$). Despite this increase in ingestion rate, GER was similar for *R. gigas* during bloom and post-bloom conditions, while GERs were doubled for *C. acutus* and *C. propinquus* during the bloom. We suggest that *R. gigas* reached feeding saturation more quickly in higher Chl *a* conditions than the other species (Atkinson *et al.*, 1992, 1996a). *Calanus propinquus* grazing changed little between years, suggesting they gain much of their nutrition though omnivory, despite locally high phytoplankton biomass (Urban-Rich *et al.*, 2001).

While copepod grazing increased in 2014, egestion rates and fecal pellet C:N ratios remained similar to those in 2013. Increased egestion generally coincides with increased feeding rates (Dagg and Walser, 1987; Atkinson *et al.*, 2012a), but similar egestion at higher food concentrations could indicate that copepods are feeding while saturated (Dagg *et al.*, 2003).

CONCLUSIONS

Our study builds on prior Southern Ocean copepod grazing studies, with results that span a wide range of temperatures and Chl *a* conditions, and is the first to examine copepod grazing in the southern WAP. Total copepod community contribution to removal of phytoplankton biomass and PP was generally low ($\sim 1\%$), confirming that microzooplankton, as opposed to meso- and macrozooplankton (e.g. copepods, krill, salps, pteropods), are the dominant grazers in the WAP (Bernard *et al.*, 2012; Garzio *et al.*, 2013; Sailley *et al.*, 2013). However,

future studies on the grazing of smaller copepod species and copepodite stages of larger species are needed.

We saw a shift in feeding from mostly phytoplankton in high-bloom conditions on the coast, to increased reliance on other sources of C (i.e. metazoans and protozoans) in lower Chl *a* conditions and offshore. Climate change effects on WAP phytoplankton occurred with decreasing Chl *a* concentrations north of the study region, predicted to continue south-ward with increased warming due to lower sea ice and stronger winds (Stammerjohn *et al.*, 2008; Montes-Hugo *et al.*, 2009). Our results suggest copepods near the WAP could survive under lower phytoplankton concentrations by supplementing their diet with protozoans. However, currently unknown is the impact of increased top-down pressure by copepods on lower trophic levels, and survival of copepods during prolonged conditions of low phytoplankton biomass.

Egestion rates were high, even in low Chl *a* conditions, but with relatively high retention of fecal pellets in the upper water column. Thus, at least compared with krill, copepods may not be efficient exporters of C to depth in this region.

Long-term trends in WAP copepod abundance from 1993 to 2013 indicate they are increasing (Gleiber, 2015), and there are long-term changes in the dominant macrozooplankton too (Steinberg *et al.*, 2015). Therefore, understanding the role of copepods in energy transfer through the food web and export in the WAP further elucidates mechanisms leading to variability in biogeochemical cycling, and can be used to predict how the zooplankton community will respond to future environmental change.

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org.

ACKNOWLEDGEMENTS

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