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Diet of the Antarctic krill (*Euphausia superba* Dana): II. Selective grazing in mixed phytoplankton assemblages

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Abstract

Diatoms, prymnesiophytes, and cryptophytes are the major taxonomic classes of phytoplankton available to Antarctic krill as primary food resources. However, the relative contribution of each class to the diet of krill is unknown. In this study, selectivity for different phytoplankton taxa by *Euphausia superba* was examined during laboratory experiments with *E. superba* grazing on mixed phytoplankton assemblages from the wild and from laboratory cultures. Clearance rates and changes in relative concentrations of diatoms, prymnesiophytes and cryptophytes were measured by analysis of taxon-specific accessory photopigments with high performance liquid chromatography (HPLC). *E. superba* grazed diatoms at higher rates than *Phaeocystis* and cryptophytes. Grazing was negligible in cryptophyte-dominated assemblages. Increases of up to 369% in 19′ -hexanoyloxyfucoxanthin (HF)/fucoxanthin (FUCO) (prymnesiophyte/diatom) ratios indicated a high level of selectivity for diatoms over *Phaeocystis*. This selectivity occurred even for *Phaeocystis* colonies of similar size to diatoms, and thus cannot be entirely attributed to differential sieving efficiency based on particle size. The results suggest that krill actively select diatoms in phytoplankton mixtures.

Keywords: Antarctic krill; Cryptophyte; *Euphausia superba*; Grazing; HPLC; *Phaeocystis*; Selectivity

1. Introduction

The key taxonomic groups available to the Antarctic krill, *Euphausia superba*, in the coastal regions of the Antarctic Peninsula are diatoms, prymnesiophytes and cryptophytes.

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Although one group may periodically dominate, there are often mixtures present (Moline and Prézelin, 1996). At the Weddell Sea ice edge, the highest concentrations of both diatoms and the prymnesiophyte *Phaeocystis* sp. were generally in mixtures of the two groups (Fryxell and Kendrick, 1988). The relative abundance of these phytoplankton taxa may be relevant to the feeding ecology of zooplankton grazers. This study examines whether Antarctic krill are selective for one or more of these key taxonomic groups.

Other species of filter-feeding zooplankters, copepods in particular, have demonstrated taxon-specific selectivity. In one study, several species of copepods ingested diatoms at higher rates than prymnesiophytes within natural phytoplankton assemblages (Head and Harris, 1994), while in another, dinoflagellates were avoided (Quiblier-Llobéras et al., 1996). *Acartia* spp. selected diatoms over *Phaeocystis pouchetii* in laboratory grazing experiments, although this result may have been a consequence of particle size (Verity and Smayda, 1989). Some copepods appear to discriminate on the basis of food quality, preferentially ingesting cells of higher nutritional value within mixtures (Cowles et al., 1988) and rejecting low quality particles such as polystyrene spheres, dead phytoplankton, and phytoplankton species resistant to digestion (Donaghay and Small, 1979; Paffenhöfer and Van Sant, 1985; DeMott, 1989), as well as toxic species (Huntley et al., 1986).

Feeding mechanisms and absolute size differ between krill and copepods. Krill capture many particles simultaneously with compression–filtration (Hamner, 1988), while copepods tend to actively capture individual particles (Price and Paffenhöfer, 1985). Thus, selectivity in euphausiids will not necessarily follow that in copepods. Krill are less effective at grazing small particles, especially those less than 10-μm equivalent spherical diameter (ES.D.; McClatchie and Boyd, 1983; Boyd et al., 1984; Ishii et al., 1985). In one study, clearance rates were correlated with particle size up to 50-μm ES.D. (Quetin and Ross, 1985). This selectivity has been linked to efficiency of the sieving apparatus (McClatchie and Boyd, 1983), and not to an active process. However, Stuart (1989) found that *Euphausia lucens* selected dinoflagellates in preference to diatoms in field-collected phytoplankton mixtures, despite the smaller size of the dinoflagellates and the high abundance of diatoms. There may be an upper size limit for effective compression–filtration. Haberman et al. (2002) showed that small colonies of the prymnesiophyte *Phaeocystis antarctica* were grazed at higher rates than larger colonies. Euphausiids may also graze diatoms in chains more effectively than solitary cells (Meyer and El-Sayed, 1983; Stuart, 1989; Haberman et al., 2002) but this criterion is difficult to evaluate separately from size.

If only size selection occurs, krill would graze cryptophytes less effectively than diatoms, since they are <10 μm in diameter. On the other hand, high cryptophyte concentrations could compensate for their smaller size. With regard to prymnesiophytes, Haberman et al. (2002) found that *E. superba* could graze small colonies of the prymnesiophyte *P. antarctica* at rates comparable to similarly sized particles (cells and chains) of the diatom *Thalassiosira antarctica* in uniagal treatments, but the study did not address selectivity between the two taxonomic groups in mixed assemblages.

This study was designed to test whether *E. superba* selectively grazes one or more of the key taxonomic groups in the Antarctic Peninsula region. Grazing by *E. superba* on the different phytoplankton groups during laboratory experiments was measured using taxon-

specific accessory photopigments to track the phytoplankton levels in the experimental containers. Krill were presented with mixtures of phytoplankton cultures as well as phytoplankton assemblages collected from the field.

2. Methods

2.1. Collection and maintenance of phytoplankton and krill

Krill were collected from either a rubber skiff or the M/V Polar Duke, and maintained in flow-through seawater tanks at Palmer Station (details in Haberman et al., 2002). Phytoplankton for experiments utilizing laboratory cultures were isolated from the Palmer Station region and maintained in culture at Palmer Station. Culture techniques and assessment are described in Haberman et al. (2002). Water samples for experiments with natural phytoplankton assemblages were collected within 2 miles of Palmer Station by deploying Go-Flo bottles to the chlorophyll maximum layer, as determined by a vertical profile of in situ fluorescence. Immediately following collection, these samples were transferred to the experimental containers. Alternately, water was collected from the unfiltered seawater intake at Palmer Station.

Within 24 h prior to the experiment, cultures or collected phytoplankton were sampled for chlorophyll *a* (chl *a*) and elemental (CHN) analysis (Haberman et al., 2002), and 100-ml subsamples were preserved in 0.35% glutaraldehyde/Lugol's solution (Rousseau et al., 1990) for later microscopic evaluation. Chl *a*, C and N concentrations from these analyses were used to calculate ratios of C/N and C/chl *a*. Selected cultures were also analyzed for pigment content using high performance liquid chromatography (HPLC), as described in Section 2.3.

2.2. Experimental set-up and sampling

Two identical containers were prepared for each experiment, one for acclimation of krill to feeding conditions, and the other for the measurement of control and experimental grazing rates. Details of the experimental set-up are in Haberman et al. (2002). Eight experiments (N1–N8) were conducted with field-collected phytoplankton at ambient concentrations. Six additional experiments (M1–M6) were conducted with mixtures of *T. antarctica* and *P. antarctica* cultures in approximately equal proportions (based on chl *a*) and diluted with 0.45 μm filtered seawater to final chl *a* concentrations ranging from 3–18 $\mu g\ l^{-1}$. Ten to thirty krill, ranging in size from 34–42 mm, were included in each experiment.

Most experiments lasted 12 h. During the first 6 h, krill were acclimated to experimental food conditions in one of the replicate containers. Krill were then transferred to the experimental container, where they grazed for an additional 6 h. Three 100-ml water samples were collected from the acclimation container at the beginning and end of the acclimation period. Five 200-ml (or three 350-ml) water samples were collected from the experimental container at 2-h intervals throughout the 12-h experiment. These samples were used to calculate the rate of change of phytoplankton pigments without grazing for

the first 6-h period (“control period”), and with grazing for the second 6-h period (“experimental period”).

For two of the six experiments with culture mixtures (M5 and M6), the krill were not acclimated to experimental feeding conditions and there was no control period (Table 2). The control rate for pigment loss and ratio change for these experiments was assumed to be 0, since no significant changes occurred during the control period for any of the other experiments with the same phytoplankton cultures.

Immediately after collection, 100 to 250 ml of each sample was filtered onto 0.45-μm nylon filters for HPLC, while the remaining 100 ml was filtered onto GF/C filters for fluorometry. Filters were frozen at −70 °C and analyzed within 4 weeks of collection.

2.3. Pigment analysis

The HPLC method used for pigment analysis was modified from Wright et al. (1991). The system consisted of a Hitachi Instruments L-6200 A pump and gradient controller, L-4250 UV/VIS detector set at 436 nm, and D-6000 software connected via a Hitachi interface. A Waters Resolve C-18 5μm, 3.9 × 300-mm column was used for pigment separation. All solvents were HPLC grade, and included:

Solvent A: 80:20 (v/v) Methanol/0.5 M ammonium acetate,
Solvent B: 90:10 (v/v) Acetonitrile/water,
Solvent C: Ethyl acetate.

The solvent gradient protocol is shown in Table 1.

Samples were extracted in 3–5 ml (depending upon sample concentration) of 90% HPLC grade acetone for 24 h at 0 °C. Samples were then centrifuged to remove debris, and the supernatant used for pigment analysis. Extracted samples were kept at 0 °C prior to analysis.

To identify and quantify sample pigments, columns were calibrated with commercially obtained pigment standards of known concentrations (VKI Water Quality Institute,

Table 1
Solvent gradients for HPLC

Time	%A	%B	%C
0.0	100	0	0
0.1	100	0	0
2.0	0	100	0
2.6	0	75	25
13.6	0	30	70
18.0	0	30	70
20.0	0	100	0
22.5	100	0	0
30.0	100	0	0

Flow rates were 1.0 ml/min.
See text for identification of Solvents A, B and C.

Hørsholm, Denmark) and with chl *a* derived from *Anacystis* sp. (Sigma). The key accessory photopigments present in field-collected water samples, and used to evaluate grazing selectivity, were fucoxanthin (FUCO) as a diagnostic pigment for diatoms, 19′-hexanoyloxyfucoxanthin (HF) as a diagnostic pigment for prymnesiophytes, and alloxanthin (ALLO) as a diagnostic pigment for cryptophytes (Wright et al., 1991).

2.4. Clearance rate calculations

Pigment-specific clearance rates, i.e. the wet-weight specific rate at which a given volume of seawater is swept clear of that pigment by krill (Frost, 1972), were calculated for each key pigment type (chl *a*, FUCO, HF and ALLO). These calculations were based on the changes in pigment concentrations in the water, as measured with HPLC for both the experimental and control periods. Best fit exponential regressions of time (t) and concentration (subsample mean) for each specific pigment were used to determine phytoplankton growth and grazing coefficients, which were then used to calculate clearance rates (Haberman et al., 2002). Tests for homogeneity of slope between the experimental and control containers were conducted to determine if grazing had actually occurred. Significant grazing was considered as $p < 0.05$.

2.5. Pigment ratio calculations

Pigment ratios were calculated from individual chromatograms to minimize variability due to injection volume, and averaged for each time period. In addition, percent change in these ratios from the beginning (Time 6) and end (Time 12) of the experimental period was used to determine the magnitude of selectivity for experiments with significant changes in pigment ratios. Ratio changes during control periods were not significant (see Results), so they were not included in this calculation. Percent ratio change was calculated as:

$$\%\ \text{ratio change} = 100\%(\text{ratio, T12} - \text{ratio, T6})/\text{ratio, T6}$$

3. Results

3.1. Characterization of P. antarctica and T. antarctica cultures used for 1:1 mixtures

Particle sizes for *P. antarctica* and *T. antarctica* were similar. The *P. antarctica* cultures used in these experiments were comprised of small spherical or elliptical colonies between 50 and 100 μm, with <20% single cells. Cells of *T. antarctica* were 25 μm in diameter, occurring singly and in chains predominantly two to four cells and 30–90 μm in length. C/N values for the two cultures were similar, 5.3 ± 1.1 (S.D.) for *P. antarctica* and 5.5 ± 1.7 for *T. antarctica*. C/chl *a* for *P. antarctica* was roughly double that of *T. antarctica*, 60 ± 18 compared to 30 ± 6.

The 1:1 mixtures (by chl *a*) of *P. antarctica* and *T. antarctica* cultures had HF/FUCO ratios between 0.3 and 0.7 for the six experiments (Table 2). The *P. antarctica* cultures used in the mixture experiments had FUCO/chl *a* ratios of 0–0.07, compared to 0.64–0.69

Table 2
Initial conditions, clearance rates, and ratio changes for experiments

Experiment	Initial conditions			Clearance rates				% Change in ratio	
	ALLO/HF/FUCO	Phytoplankton	chl *a*	chl *a*	FUCO	HF	ALLO	HF/FUCO (%)	ALLO/FUCO (%)
Culture mixtures									
M1	(0.0):0.5:1.0	1:1 *P.a./T.a.*	3.4	0.54	0.45	0	–	17	–
M2	(0.0):0.5:1.0	1:1 *P.a./T.a.*	3.4	1.36	1.45	0.59	–	74	–
M3	(0.0):0.3:1.0	1:1 *P.a./T.a.*	5.0	2.32	1.73	0	–	108	–
M4	(0.0):0.7:1.0	1:1 *P.a./T.a.*	6.6	0.82	0.70	0.36	–	10	–
M5*	(0.0):0.4:1.0	1:1 *P.a./T.a.*	8.4	1.64	1.37	0.33	–	369	–
M6*	(0.0):0.3:1.0	1:1 *P.a./T.a.*	18.4	1.32	0.97	0.42	–	22	–
Natural assemblages									
All groups approximately equal									
N1	1.1:1.4:1.0	Cryp, *Pha.*, diat	2.6	0.48	0.73	0.44	0.29	64	120
N2	1.2:1.3:1.0	Cryp, *Pha.*, diat	3.1	0.15	0.22	0.08	0.12	30	0
Cryptophytes dominant									
N3	2.6:0.6:1.0	Cryp, *Pha.*, diat	3.0	0.07	0.07	0	0	11	0
N4	2.3:0.5:1.0	Cryp, *Pha.*, diat	3.0	0	0	0	0	9	14
N5	4.2:1.8:1.0	Cryp, *Pha.*, diat	6.7	0	0	0	0	0	0
N6	7.9:1.5:1.0	Cryp, *Pha.*, diat	6.7	0	0	0	0	0	0
Cryptophytes absent									
N7	(0.0):1.0:1.0	*Pha.*, diat	0.73	0	0	0	0	0	–
N8	(0.0):1.0:1.0	*Pha.*, diat	0.74	0	0	0	0	0	–

See Figs. 1, 2, 3 and 4 for further details of % change in ratios. Asterisk (*) indicates experiments with no acclimation period. ALLO = Alloxanthin, HF = 19′-hexanoyloxyfucoxanthin, FUCO = fucoxanthin, *T.a.* = *T. antarctica*, *P.a.* = *P. antarctica*, Cryp = cryptophytes, *Pha* = *Phaeocystis*, diat = mixed diatoms.

for the *T. antarctica* cultures used in experiments (Table 3). This means that most (>90%) of the FUCO in the mixtures were derived from *T. antarctica*, and support the use of FUCO concentrations as a proxy for diatoms in these experiments.

3.2. Clearance rates on 1:1 mixtures

E. superba measurably grazed phytoplankton in all experiments with 1:1 mixtures of *P. antarctica* and *T. antarctica* cultures. Chl *a* clearance rates were 0.54–2.32 l g wet wt^{-1} h^{-1} (Table 2). FUCO clearance rates were similar to, or slightly lower than, those for chl *a*

Table 3
Pigment ratios for cultures used in experiments

Species	Description	FUCO/chl *a*	HF/chl *a*	HF/FUC
P. antarctica	mostly sm col (20–100 μm)	0	0.19	N/A
P. antarctica	mostly sm col (20–100 μm)	0	0.40	N/A
P. antarctica	mix, sm col and single	0.07	0.80	11.4
T. antarctica	25 μm diam cells, 1/3 in chains	0.69	N/A	N/A
T. antarctica	25 μm diam cells, 2/3 in chains	0.64	N/A	N/A

(Wilcoxon signed rank test, $p = 0.06$; Table 2). In contrast, HF clearance rates were significantly lower than for chl *a* or fucoxanthin ($p < 0.05$), and ranged between 0% and 51% of FUCO clearance rates, indicating selectivity for diatoms in all experiments.

Overall, chl *a*-based clearance rates varied considerably among experiments. This variability was not significantly correlated with initial chl *a* concentration (regression, $r^2 = 0.13$, $p = 0.48$). An inverse correlation of chl *a*-based clearance rate and initial HF/FUCO ratio is suggested by the data but this relationship was also not significant ($r^2 = 0.57$, $p = 0.08$). Furthermore, there was a large difference in clearance rates between experiments M1 and M2, which were conducted simultaneously and used nearly identical phytoplankton mixtures and krill.

3.3. Pigment ratio changes for 1:1 mixtures

Coincident with the differences in pigment-specific clearance rates, the HF/FUCO ratios increased significantly during all experiments compared to controls (test for homogeneity of slopes, $p \leq 0.02$), with increases of 10–369% (Fig. 1, Table 2). There were no significant ratio changes in any of the control containers, although the M1 control container showed a near-significant decrease in HF/FUCO ratio ($p > 0.25$, except M1, $p = 0.08$). In general, experiments with the highest clearance rates showed the largest changes in pigment ratios, although this relationship was not significant (regression analysis, $r^2 = 0.49$, $p = 0.12$).

3.4. Characterization of natural phytoplankton assemblages

The eight grazing experiments with field-collected phytoplankton assemblages were grouped based upon initial ratios of ALLO/HF/FUCO (Table 2). The phytoplankton concentrations were assumed to be roughly equivalent to the corresponding accessory pigment concentrations. In two experiments, the three pigments were present in approximately equal concentrations. In four other experiments, ALLO concentrations were more than double those of HF and FUCO, indicating a relatively high proportion of cryptophytes. In the two remaining experiments, no ALLO was detected, and HF and FUCO were present in approximately equal concentrations.

For the six cryptophyte-containing experiments, initial chl *a* concentrations were between 3 and 7 μg l^{-1}, and C/chl *a* ratios were between 66 and 109. C/N ratios were similar, with a mean value of 5.3 ± 0.6. The two experiments without cryptophytes had C/N ratios of 10.43, nearly double the values of other experiments, and high C/chl *a* ratios of 367, three to six times the values of the other natural assemblage experiments.

3.5. Clearance rates and pigment ratio changes for natural phytoplankton assemblages

In the two experiments with approximately equal concentrations of the three phytoplankton groups (N1 and N2), clearance rates based on chl *a* were 0.48 and 0.15 l·g wet wt^{-1} h^{-1}. In both experiments, clearance rates for all three accessory photopigments were measurable and HF/FUCO ratios increased significantly, by 64% and 30%, respectively (Fig. 2, Table 2; test for homogeneity of slopes, $p \leq 0.001$). The ALLO/FUCO ratio also

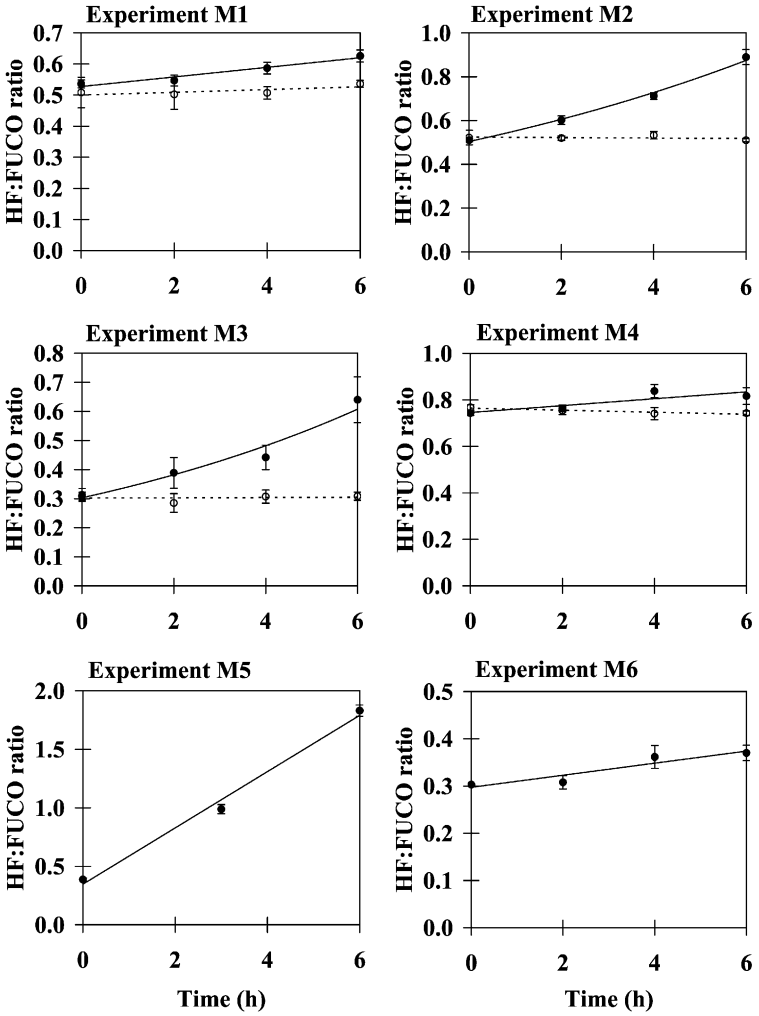

Fig. 1. HF/FUCO ratios for 1:1 mixtures of *P. antarctica* and *T. antarctica*. Open circles and dashed lines show control periods (no krill), solid circles and lines show grazing periods (with krill). The slopes for all grazing periods were significantly different from control periods (test for homogeneity of slopes, $p \leq 0.02$). Slopes were not significant for any of the control periods (regression analysis, $p>0.25$). Lines shown are best fit curves, either linear or exponential.

increased significantly, by 120%, in one of the experiments (N1; Fig. 3, Table 2; $p<0.001$), but changes for the other experiment (N2) did not differ from the control (Fig. 3, $p=0.47$). Overall, the pigment-specific clearance rates and pigment ratio changes indicated that *E. superba* selectively grazed on diatoms in these experiments.

For the phytoplankton assemblages with relatively high concentrations of cryptophytes, no measurable grazing occurred in three out of four experiments. In the fourth experiment (N3), both chl *a*-based and FUCO-based clearance rates were 0.07 l g wet wt^{-1} h^{-1}

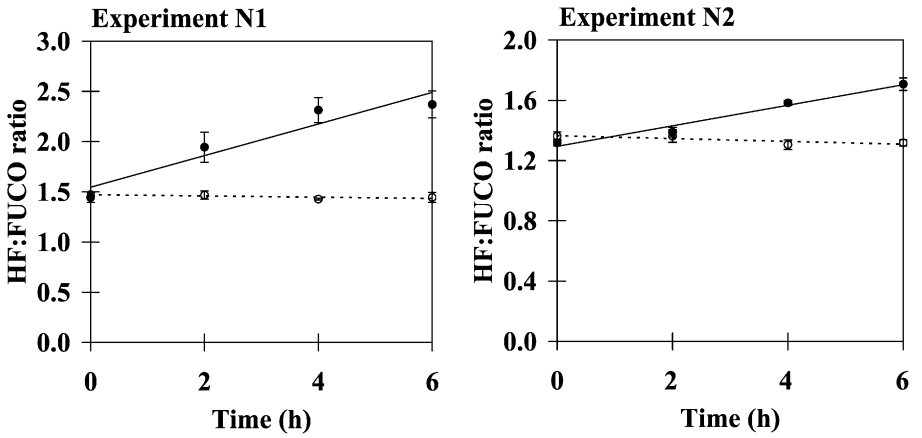

Fig. 2. HF/FUCO ratios for natural phytoplankton assemblages with approximately equal ALLO/HF/FUCO ratios. Symbols as in Fig. 1. For both experiments, the slope for the grazing period was significantly different from the slope for control period (test for homogeneity of slopes, $p = 0.000$). Slopes were not significant for either control period (regression analysis, $p \geq 0.15$).

(Table 2), while clearance rates for HF and ALLO were not significant. In two of these experiments (N3 and N4), there was a significant increase in the HF/FUCO ratios of approximately 10% (test for homogeneity of slopes, $p = 0.01$; Fig. 4). These results indicated that even with no measurable grazing, as for experiment N4, the selective grazing of *E. superba* on diatoms affected pigment ratios. The paradox of a significant ratio change despite a nonsignificant grazing loss probably reflects the fact that diatoms were such a minor component of the assemblage.

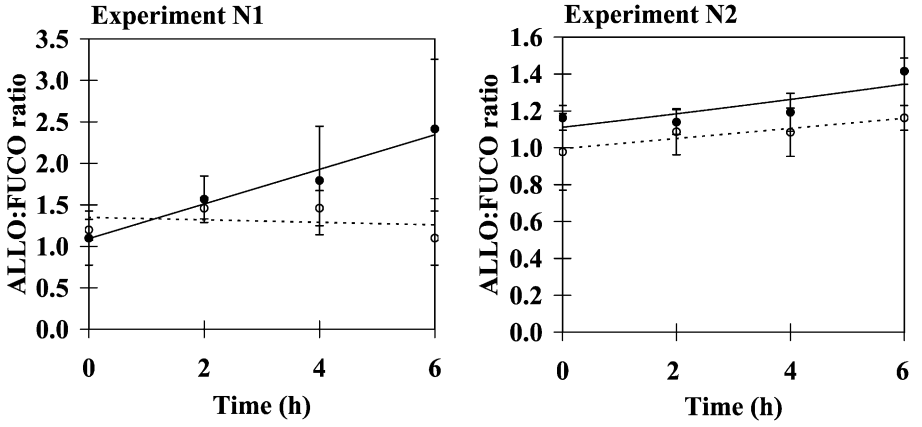

Fig. 3. ALLO/FUCO ratios for natural phytoplankton assemblages with approximately equal to ALLO/HF/FUCO ratios. Symbols as in Fig. 1. For N1, the slope for the grazing period was significantly different from the slope for control period (test for homogeneity of slopes, $p < 0.001$). The control period did not have a significant slope ($p = 0.23$). For Experiment N2, there was no significant difference between the two slopes (test for homogeneity of slopes, $p = 0.47$), which were both significant (regression analysis, $p < 0.001$).

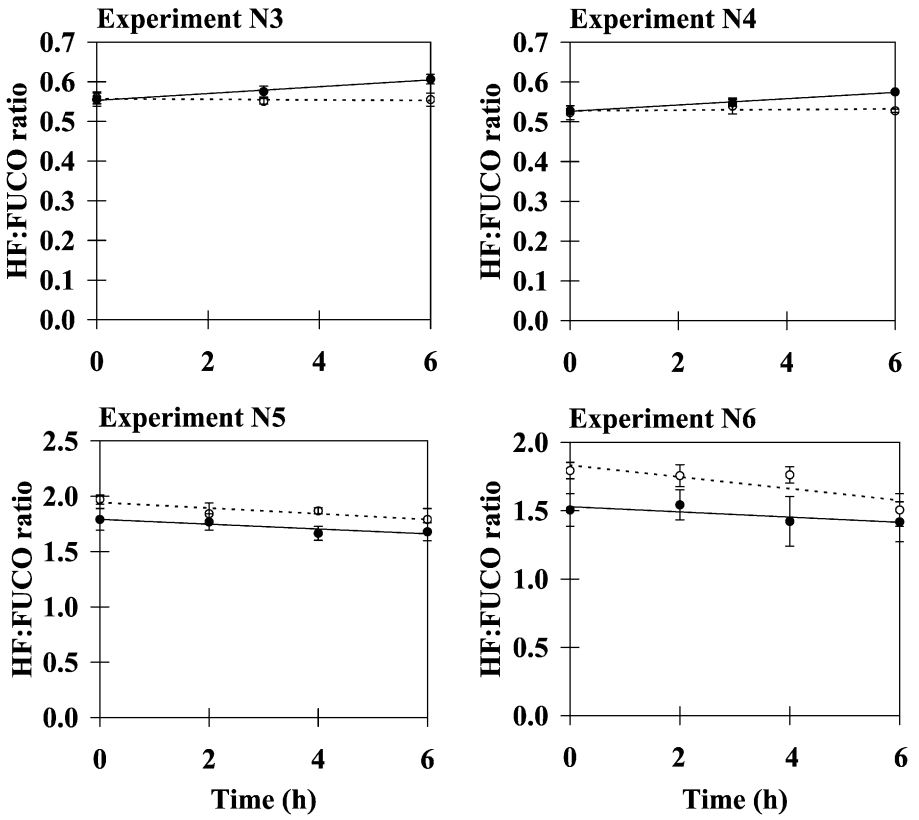

Fig. 4. HF/FUCO ratios for natural phytoplankton assemblages with relatively high cryptophyte concentrations. Symbols as in Fig. 1. For N3 and N4, the slopes for the grazing periods were significantly different from the slopes for control periods (test for homogeneity of slopes, $p < 0.01$). The control periods did not have significant slopes ($p > 0.8$). For Experiments N5 and N6, slopes are not significant for either the control or grazing periods.

Clearance rates for the two field-collected phytoplankton experiments with diatoms and prymnesiophytes only were not significantly different from controls (Table 2). No significant pigment ratio changes were found.

4. Discussion

4.1. Methodological considerations

The use of accessory photopigments to study taxon-specific grazing on phytoplankton has been applied to both microzooplankton and macrozooplankton grazers (Burkill et al., 1987; Head and Harris, 1994; Quiblier-Llobéras et al., 1996; Buffan-Dubau et al., 1996). This approach is based on two major assumptions: (1) accessory photopigments are taxon-specific; (2) changes in accessory photopigment concentrations in experimental containers

are not confounded by pigments in fecal material. The first assumption is not strictly accurate. FUCO, representing diatoms, is also found in varying concentrations in prymnesiophytes (Wright et al., 1991). However, colonial *P. antarctica* cultures used in these mixture experiments contained very low concentrations of FUCO (Table 3). In contrast, single-cell *P. antarctica* cultures appear to have significant concentrations of FUCO (Buma et al., 1991; Haberman, 1998). Mixed assemblages collected from the field contained single-cell *P. antarctica*. Thus, selectivity for diatoms was probably underestimated by HF/FUCO ratio changes because there would be less of a percent change in the FUCO as diatoms were grazed selectively than if FUCO was found only in the diatoms. As for the second assumption, changes in pigment concentrations do not appear to have been confounded by pigments in fecal material in these experiments, since few fecal pellets per water sample were found for later sampling periods, resulting in little contamination. Also, most of the FUCO ingested by krill are degraded during gut passage (Daly, 1998).

In this study, we assumed that accessory photopigment ratios roughly mirrored relative concentrations of phytoplankton taxa, so accessory photopigment values for natural phytoplankton assemblages were not converted to absolute concentrations of phytoplankton taxa. One reason for leaving them as raw values is that available conversion factors are not in agreement. Specifically, HF/FUCO ratios for 1:1 mixtures of *P. antarctica* and *T. antarctica* cultures ranged between 0.3 and 0.7 (Table 2) whereas HF/FUCO ratios for an equal mixture of *Phaeocystis* sp. and diatoms, determined by multiple regression of accessory photopigments versus chl *a* in field-collected phytoplankton, ranged between 1.25 and 1.30 (Bidigare et al., 1996; Vernet, personal communication). Also, the question of what is meant by equal is unclear; C/chl *a* ratios as well as pigments must be considered when determining equal amounts of phytoplankton, and these values varied among experiments.

Another methods-related issue is whether transfer of krill from the acclimation to experimental containers affects the krill's behavior. This transfer is necessary due to the high rate of grazing during acclimation. Krill were transferred individually with a taut net in order to minimize trauma. The krill resumed what appeared to be normal swimming and feeding basket movement shortly after being transferred. Also, while the transfer may affect feeding rates, it is unlikely to affect selectivity.

4.2. Grazing selectivity by E. superba

E. superba exhibited three distinct grazing patterns during this study. First, *E. superba* selected diatoms over *P. antarctica* in both culture mixtures and in most natural phytoplankton assemblages with measurable grazing rates. Second, based on clearance rates, *E. superba* usually selected diatoms over cryptophytes. However, ALLO variability between subsamples, along with relatively high concentrations of ALLO, made small changes in ALLO/FUCO ratios difficult to detect. Third, negligible grazing occurred in phytoplankton assemblages dominated by cryptophytes, even when chl *a* concentrations were above 6 $\mu g\ l^{-1}$.

In two of the three experiments with the highest percent change in ratio (M2 and M3), selectivity apparently remained constant as diatoms became proportionally more scarce

through time. This inference is based on the exponential relationship between HF/FUC ratios and time found for these experiments (Fig. 1). Mathematically, a positive exponential curve is predicted for HF/FUC over time if the phytoplankton loss coefficients for each phytoplankton type (b_{FUC} and b_{HF}) are constant through time, and $b_{FUC} < b_{HF}$ (both coefficients are negative). This result is intriguing because optimal foraging theory predicts that selectivity will decline when the high-quality food becomes scarce (MacArthur and Pianka, 1966; Lehman, 1976), as found for the copepods *Eudiaptomus* spp. (DeMott, 1989). Possibly, diatom density may never have been low enough in these experiments to cause a shift in selectivity.

Particle size differences may account for selection of diatoms over cryptophytes. During experiments N1 and N2, krill cleared cryptophytes at approximately half their rate on diatoms, similar to size-based selectivity previously described (Boyd et al., 1984; Quetin and Ross, 1985; McClatchie and Boyd, 1983). However, the complete lack of grazing on cryptophytes when cryptophytes dominated cannot be explained by retention efficiency alone, since krill consumed cryptophytes in the more equal mixtures.

Size differences were probably also a factor in the selectivity of diatoms over *Phaeocystis* in the natural phytoplankton experiments, since the *Phaeocystis* was a mixture of colonies and single cells approximately 8 μm in diameter. However, size alone cannot explain consistent selection of *T. antarctica* over *P. antarctica* by krill in the culture mixtures because *T. antarctica* and *P. antarctica* were approximately the same size, based on both ranges and median values of maximum particle dimension (Haberman et al., 2002). Furthermore, monoculture experiments showed that krill were capable of clearing small colonies of *P. antarctica*, identical to those used in these experiments, at rates similar to *T. antarctica* (Haberman et al., 2002). Thus, in mixtures, krill must have either actively avoided filtering *P. antarctica* or rejected *P. antarctica* after filtration. Particle rejection is more likely because the phytoplankton was well-mixed.

Possibly, krill actively selected *T. antarctica* on the basis of food quality. In general, *Phaeocystis* has been considered a sub-optimal food resource for macrozooplankton grazers. Much of the evidence is indirect, i.e. low grazing rates or complete lack of grazing on *Phaeocystis* in experiments (reviewed by Davidson and Marchant, 1992; Hansen and van Boekel, 1991; Hansen et al., 1994). A recent study yielded more direct evidence; growth rates of juvenile *E. superba* (15–25 mm) were negatively correlated with percent *Phaeocystis* sp. in the phytoplankton community (Ross et al., 2000).

To date, discussion of food quality in Antarctic *Phaeocystis* has focused on lipids. Antarctic *Phaeocystis* strains, especially colonies, are generally low in the essential fatty acids 22:6($n-3$) and 20:5($n-3$) (Nichols et al., 1991; Virtue et al., 1993). The importance of lipids in *E. superba*'s diet is unclear. Pond et al. (1995) reported considerable alteration of the ingested lipid pool for *E. superba* grazing on diatoms. Similarly, experiments conducted by Virtue et al. (1993) suggested that krill can convert shorter chain fatty acids into 20:5 ($n-3$), reducing the importance of this "essential" fatty acid in their diet.

Possibly, protein content of food is a key factor. For example, larval *E. superba* exhibited high turnover of carbon and conservation of nitrogen (Frazer et al., 1997)

suggesting that proteins are more limiting than lipids for *E. superba*. If so, C/N ratios may be a predictor of food quality. In these experiments, C/N ratios were similar for cultures of the two species; however, C/chl *a* ratios for *P. antarctica* were nearly double those of *T. antarctica*. Given these ratios, it is likely that nearly half of the carbon and nitrogen was associated with the extracellular matrix. Most of the extracellular carbon in colonial *Phaeocystis* are likely to be in the form of mucopolysaccharides low in nutritional value (Sargent et al., 1985) while the form of nitrogen and its ability to be assimilated by krill is unknown (Verity et al., 1988). Selectivity based on C/N and C/chl *a* ratios has been demonstrated in another crustacean, the copepod *Acartia tonsi* (Cowles et al., 1988).

Additional studies which monitor assimilation, growth, condition and egg production of *E. superba* fed different Antarctic phytoplankton species are needed to test the link between selectivity and nutrition. Particular attention must be paid to both the krill's life stage and the season, since nutritional requirements may vary considerably depending upon whether a krill is growing, reproducing or overwintering. This is especially critical given recent evidence that diatoms may inhibit reproduction in copepods (Ban et al., 1997; Ianora, 2001). No similar evidence exists for krill. Similarly, growth conditions of phytoplankton, such as light level, day length, temperature and nutrients, may significantly affect its chemical composition (Hawes, 1990; Davies et al., 1992; Verity et al., 1988) and thus its nutritional value.

Selectivity may be due to factors other than size and nutrition. In particular, chemical defenses of phytoplankton may play a role. For example, *Phaeocystis* contains acrylic acid (Sieburth, 1960) and dimethylsulfide, either of which could deter grazers (Estep et al., 1990). However, krill are able to graze small colonies of *P. antarctica* at rates similar to diatoms (Haberman et al., 2002) suggesting that they are not chemically deterred.

The complete lack of grazing on cryptophytes when they are virtually the only food available is puzzling. However, this behavior may reflect an adaptive strategy. According to optimal foraging theory, animals have evolved mechanisms to maximize their energy intake (MacArthur and Pianka, 1966) or some more relevant measure of food value (Rapport, 1981). Accordingly, mobile foragers may respond to cues indicative of "good food" by remaining in a patch and feeding, and to cues indicative of "poor food" by searching for an alternate food resource. In the nearshore region of the Antarctic Peninsula, cryptophytes were associated with near-surface, low saline water, especially glacier run-off (Moline and Prézelin, 1996), while diatoms were associated with more saline water (Moline et al., 1997) found deeper or further offshore. Perhaps krill minimize feeding on cryptophyte-dominated surface waters and swim downward or offshore, where they are likely to encounter higher proportions of diatoms. In contrast, when cryptophytes are in mixtures with diatoms, the krill stay and feed because desirable food (i.e. diatoms) is available, and cryptophytes are ingested along with the preferred diatoms. Certainly, euphausiids are highly mobile and capable of locating patchy food resources (Price, 1989), although mechanisms for detection are not known.

Just as phytoplankton community composition influences krill grazing, selectivity by krill can impact phytoplankton community composition. Kopczynska (1992) suggested

that krill grazing, along with physical mixing, shifted the phytoplankton assemblage towards flagellates. In this study, krill selected diatoms even when diatoms were rare, suggesting that krill may suppress diatom blooms, and that the influence of krill on diatom populations may be out of proportion to average grazing rates measured for a mixed phytoplankton community.

5. Conclusions

Antarctic krill selectively grazed diatoms in preference to both prymnesiophytes and cryptophytes in this study. Conversely, *P. antarctica* was consumed at disproportionately low levels compared to its availability in the experimental containers. Mixtures dominated by cryptophytes were not appreciably grazed. The level of selectivity demonstrated cannot be attributed to particle size differences alone and appears to involve more active mechanisms. The specific advantages of diatoms as a food resource, as well as the effects of this selectivity on phytoplankton community composition, are unknown and merit further study.

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