



Composition and structure of macrozooplankton and micronekton communities in the vicinity of free-drifting Antarctic icebergs

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ABSTRACT

Recent warming in the Antarctic has led to increased production of icebergs; however, the ecological effects of icebergs on pelagic communities within the Southern Ocean have not been well-studied. We used a 10 m² MOCNESS to collect macrozooplankton and micronekton in the upper 300 m of the water column near free-drifting icebergs in the Atlantic sector of the Southern Ocean during three seasons: December 2005 (late spring), June 2008 (late fall) and March–April 2009 (late summer). Communities were dominated in all three seasons by Antarctic krill (*Euphausia superba*) and salps (*Salpa thompsoni*), which collectively comprised 60–95% of the community wet biomass in most cases. During our spring and summer cruises, mean biomass was elevated by 3.1–4.3x at a distance of 0.37 km from large icebergs vs. 9.26 km away. These differences were not statistically significant, and no trend in biomass with distance was apparent in samples from fall 2008, when total biomass was an order of magnitude lower. Biomass levels near icebergs during Dec 2005 and Mar–Apr 2009 were comparable to values reported from marginal ice zones, suggesting that waters around icebergs support macrozooplankton and micronekton communities comparable in magnitude to those in some of the most productive areas of the Southern Ocean. Sample variance also was significantly higher within 1.85 km of icebergs during Dec 2005 and Mar–Apr 2009, reflecting increased patchiness on scales sampled by the MOCNESS (20–40 × 10³ m³ filtered per sample). This pattern was not significant during Jun 2008. Large predatory medusae were observed within 1.85 km of icebergs and in Iceberg Alley, an area through which icebergs pass frequently, but were virtually absent in areas remote from icebergs. Small euphausiids showed an inverse distribution, with low densities in areas populated by large medusae. A shift in community composition from a near-iceberg assemblage dominated by herbivores to a carnivore-dominated community in Iceberg Alley may reflect a transition from bottom-up to top-down control with increasing distance and time. Body sizes of dominant species varied seasonally but did not show consistent trends with distance from icebergs. Concentrations of photosynthetic pigments in the guts of *E. superba* and *S. thompsoni* corresponded broadly to patterns in surface chlorophyll *a* concentrations and were comparable to maximum gut pigment concentrations measured in animals collected from highly productive marginal ice zones. Our results suggest that the macrozooplankton and micronekton assemblages near free-drifting icebergs can be quantitatively and qualitatively different from those in surrounding, iceberg-free waters, perhaps due to both bottom-up and top-down processes as well as physical forcing by the passage of a large object through the upper ocean.

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1. Introduction

Icebergs are conspicuous features of the Southern Ocean, arising from glaciers and ice shelves attached to the Antarctic continent and ranging in largest dimension from meters to over 300 km. Increased production of large Antarctic icebergs has been associated with regional warming and the breakup of large ice shelves around the continent (e.g., Scambos et al., 2000; Long et al., 2002; Cook and Vaughan, 2010).

The impact of this increasing iceberg population on Southern Ocean ecosystems has not been characterized, although the available evidence suggests a range of effects across multiple trophic levels (Arrigo et al., 2002; Smith et al., 2007; Schwarz and Schodlok, 2009).

Early evidence suggested that icebergs may release mineral-rich terrestrial material as they break up and melt (e.g., Azetsu-Scott and Syvitski, 1999; Smetacek et al., 2002; Raiswell et al., 2006, 2008). In addition, icebergs with deep keels have the potential to mix nutrients from below the pycnocline into surface waters and thus enhance local primary production (Neshyba, 1977; Sancetta, 1992; Schwarz and Schodlok, 2009). Elevated concentrations of chlorophyll *a* (Smith et al., 2007), nanoplankton (de Baar et al., 1995) and

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acoustic targets likely to be macrozooplankton or micronekton (Kaufmann et al., 1995) have been found in the vicinity of free-drifting icebergs, and top predators such as penguins and flying seabirds have been observed in high abundance on and near icebergs (e.g., Joiris, 1991; Ribic et al., 1991; Veit and Hunt, 1991).

In contrast, the influence of icebergs on macrozooplankton and micronekton communities has not been well studied. If icebergs enhance primary production, elevated densities of herbivorous zooplankton might be expected in areas with richer food resources. Zooplankton could graze down phytoplankton stocks and enhance the sinking flux of organic carbon through the production of fecal material. In addition, zooplankton could provide a food source for higher-level predators such as fishes, predatory gelatinous animals, seabirds and marine mammals.

The goal of this study was to examine the abundance and species composition of macrozooplankton and micronekton in the vicinity of free-drifting Antarctic icebergs compared to assemblages in surrounding, iceberg-free areas. The physical characteristics of dominant species were investigated to determine whether animals in proximity to icebergs were different from conspecifics at greater distances away.

2. Methods

2.1. Study sites

Macrozooplankton and micronekton were collected at various distances from free-drifting icebergs in the Atlantic sector of the

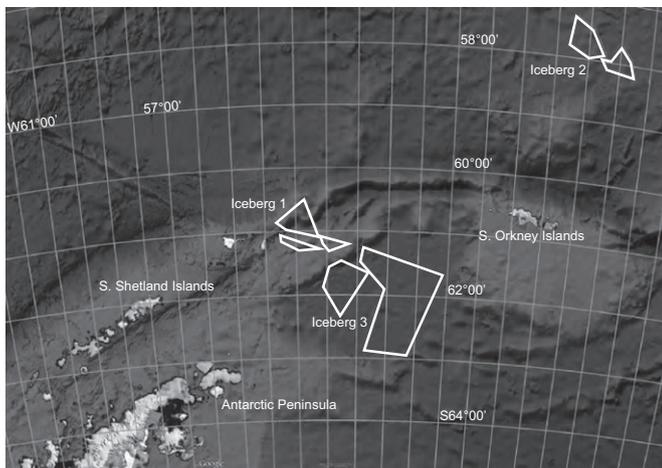


Fig. 1. Boundaries of study areas in the Atlantic sector of the Southern Ocean during three cruises in December 2005 (Iceberg 1), June 2008 (Iceberg 2) and March–April 2009 (Iceberg 3).

Southern Ocean during three seasons: December 2005 (late spring), June 2008 (late fall) and March–April 2009 (late summer) (Fig. 1). In all, five icebergs were studied, ranging from 2.0 to 39 km in maximum dimension (Table 1). In Dec 2005 and Mar–Apr 2009, sampling was conducted in the NW Weddell Sea, whereas the Jun 2008 cruise took place in the Scotia Sea (Fig. 1). In Dec 2005, MOCNESS deployments were carried out as close as 0.185 km to the face of each iceberg. The closest sampling distance on the other two cruises was 0.37 km. In Dec 2005 and Jun 2008, the MOCNESS was deployed as distant as 9.26 km from each iceberg. In Mar–Apr 2009, we also collected samples 18.5 km from iceberg C-18a and at two other, more distant locations: a “control” site 74 km east of C-18a (e.g., Smith et al., 2011) and Iceberg Alley, more than 100 km to the south.

2.2. Sample collection and processing

Macrozooplankton and micronekton were sampled with a six-net MOCNESS trawl towed at an average speed of 1 m s^{-1} (2 knots). Each net had a 10 m^2 mouth opening with 4-mm circular mesh in the body and $505 \mu\text{m}$ mesh cod ends (Wiebe et al., 1985). Individual nets were towed obliquely between the surface and ca. 300 m and typically were open for one hour, filtering 20,000–40,000 m^3 of water (Table 2). Maximum depth for each net sample was intended to be 300 m but sometimes exceeded that target depth for short periods of time. Tow profiles for each net generally were balanced across depths, with approximately equal amounts of time spent within 100 m strata between the surface and 300 m.

The MOCNESS was deployed parallel to the “coastline” of the three large icebergs (A-52, A-43k and C-18a) at fixed distances from one of the long faces of the iceberg (Table 1). A single deployment within 1.85 km of a large iceberg usually involved sampling at two different distances. For example, in several cases, two to three nets were deployed at a constant distance of 0.37 km from the long face, then one net along a smooth diagonal from 0.37 to 1.85 km as the ship moved away from the iceberg, and the remaining two to three nets at 1.85 km. The diagonal net in those instances was reported as 1.11 km from the iceberg. Deployments at distances > 1.85 km from a large iceberg did not involve any diagonal change in distance.

For two smaller icebergs (W-86 and SS-1), different trawling plans were used. For W-86, which was shaped roughly like an equilateral triangle when viewed from above, circuits around the iceberg were made while maintaining a fixed distance from the closest face. For SS-1, which was much more elongate, nets were towed upward at fixed distances from one of the long faces of the iceberg and downward while turning around one end of the iceberg prior to a pass along the other long face. While turning, bridge personnel tried to maintain the ship at a nearly constant distance from the closest point on the iceberg.

Table 1

Characteristics of the five icebergs studied. See Smith (2011) for images and additional information about each iceberg.

Iceberg	Max. Dimension (km) Aerial Height (m)	Dates/Season	Region	Initial Position	Final Position	Sampling Strategy (Icebergs)
A-52	21	Dec 2005	NW Weddell Sea	60° 52.0'S, 54° 06.3'W		Oblique trawls parallel to “coastline”
	24–32	Late Spring	Powell Basin	60° 30.2'S, 52° 48.6'W		
W-86	2.0	Dec 2005	NW Weddell Sea	61° 10.2'S, 52° 03.8'W		Circuits around iceberg at fixed distances
	41	Late Spring	Powell Basin	61° 08.0'S, 51° 22.1'W		
A-43k	39	Jun 2008	Scotia Sea	58° 02.1'S, 43° 36.6'W		Oblique trawls parallel to “coastline”
	40	Late Fall		57° 55.8'S, 42° 21.0'W		
SS-1	4.6	Jun 2008	Scotia Sea	57° 40.8'S, 44° 10.4'W		Oblique trawls parallel to “coastline” for upward-fishing nets
(TK230)	40	Late Fall		57° 24.9'S, 43° 59.3'W		Oblique trawls while turning for downward-fishing nets
C-18a	32	Mar–Apr 2009	NW Weddell Sea	62° 01.2'S, 51° 25.1'W		Oblique trawls parallel to “coastline”
	28	Late Summer	Powell Basin	61° 39.4'S, 50° 26.8'W		
Iceberg Alley		Mar–Apr 2009	NW Weddell Sea	62° 48.9'S, 50° 08.0'W		
		Late Summer	Powell Basin	62° 46.0'S, 50° 35.1'W		

Table 2

Characteristics of 10 m² MOCNESS deployments on all three cruises. “No. nets” refers to numbers of individual samples (one sample per net) collected at each distance.

	No. nets	Mean vol. filtered (m ³)	Max. depth (m)	No. nets	Mean vol. filtered (m ³)	Max. depth (m)
Iceberg 1						
Iceberg 1						
0.185 km	5	33,500	374	4	29,500	344
0.37 km	5	32,800	413	5	30,000	418
0.93 km	6	33,500	322	5	31,000	413
1.85 km	4	40,200	425	4	31,300	430
3.7 km	4	37,700	310	4	36,400	447
9.26 km	6	31,100	420	5	34,500	381
Iceberg 2						
Iceberg SS-1						
0.37 km	7	27,500	309	11	26,700	319
1.11 km	11	21,100	350	3	26,300	305
1.85 km	5	30,600	330	8	29,500	317
9.26 km	6	29,000	305	12	28,800	304
Iceberg 3						
Iceberg C-18a						
0.37 km	9	27,800	312			
1.11 km	3	26,600	323			
1.85 km	8	21,900	303			
9.26 km	6	28,200	302			
18.5 km	6	31,600	303			
74 km	4	28,400	303			
Iceberg Alley	12	28,000	307			

During the Jun 2008 and Mar-Apr 2009 cruises, all MOCNESS tows were conducted at night, typically beginning just before local midnight and concluding before dawn. Complete darkness was not available during the Dec 2005 cruise, and all tows were carried out with at least some sunlight on the sea surface.

After retrieval of the trawl, samples were placed in a 2 °C cold room before being sorted on ice to lowest identifiable taxon and counted. Displacement volumes were measured to the nearest 0.1 ml, and the samples were weighed (Jun 2008 and Mar-Apr 2009 cruises). For weighing, sorted samples were blotted dry and weighed wet to the nearest 0.1 g using a motion-compensated balance on a table that isolated the balance from the ship's vibration. After mass and displacement volume measurements were completed, all samples were preserved in 3.7% buffered formalin. Displacement volumes were converted to wet weights, assuming a conversion of 1.0 g ml⁻¹ (e.g., Ross et al., 1998).

A subsample of the euphausiids and all of the fishes were measured (total length for euphausiids, standard length for fishes). For invertebrate taxa that were extremely abundant, not all individuals were counted. Instead, 25–50 randomly-selected individuals were counted and weighed or evaluated for displacement volume. Weight or displacement volume measurements also were made on the remaining, uncounted individuals of each taxon, and the total number of individuals in the sample then was estimated based on that weight or displacement volume.

During the Dec 2005 and Mar-Apr 2009 cruises, some of the samples were very large, and there was insufficient time to sort each sample completely. In such situations, all of the fishes were removed and processed as described previously. For the remainder of the collection, a subsample (typically 3–4 l) was removed randomly, sorted completely and processed as described previously. The unsorted portion of the samples was measured volumetrically but not sorted. Relative proportions of taxa in the sorted subsample were considered to be representative of the entire sample, and total abundances were estimated accordingly.

Copepods were collected in a number of the samples. However, these small mesozooplankton may not be captured quantitatively with 4.0 mm mesh (e.g., Hubold et al., 1988; Hosie et al., 1997). Because of the likely sampling bias, copepods are not included in the results reported here.

Gut pigments were extracted and measured from *Euphausia superba* (all three cruises) and *Salpa thompsoni* (Jun 2008 and Mar-Apr 2009). For *E. superba*, abdomens were removed and the cephalothorax extracted in the dark with 10 ml of 90% acetone for 24 hours at –20 °C. For *S. thompsoni*, the gut was dissected out of individual zooids and extracted as described for *E. superba*. Fluorescence was measured with a digital Turner Designs Model AU10 fluorometer following the methods of Holm-Hansen et al. (1965). Measurement and calibration procedures for this instrument are described by Vernet et al. (2011).

2.3. Statistical analysis

For each iceberg, estimates of abundance and biomass per unit volume were compared among sampling distances (n values for each distance are reported in Table 2) using a Kruskal-Wallis non-parametric ANOVA (Zar, 1999). If significance was established by the Kruskal-Wallis test, an *a posteriori* Mann-Whitney U-test was used to determine where statistical significance occurred among samples (Zar, 1999). Homogeneity of variance for abundance and biomass among sampling distances was evaluated with a Levene test.

Multidimensional scaling (MDS) analysis of community composition was performed using both biomass and abundance data. Stress (a measure of the difficulty of fitting 3d points into 2d space) for all analyses was 0.15 (moderate). Krill body lengths were compared among samples and distances using a Permutational MANOVA (Permanova) based on Bray-Curtis similarity (PRIMER-E 6.0).

3. Results

3.1. Environmental characteristics

In general, water column structure varied between icebergs within a single sampling season and among MOCNESS deployments. Distinct differences sometimes were observed with distance from an iceberg, although this was not true in all cases.

In Dec 2005, water column structure varied between icebergs W-86 and A-52 and among MOCNESS deployments. Surface temperatures near (≤ 1.85 km from) W-86 ranged from –0.5 to

−0.8 °C (Fig. 2). During some descents, the water column was nearly isothermal to 300 m depth, whereas other profiles showed a sharp thermocline in the upper 100 m to temperatures near −1.0 °C. Salinity was more consistent among deployments, with surface values from 34.3–34.4 psu, increasing smoothly with depth

to 34.45–34.55 psu at 300 m. The greatest variability among profiles was evident from deployments within 1.85 km of A-52 (Fig. 2).

In Jun 2008, water-column structure was much more consistent among deployments. Near iceberg SS-1, surface temperatures

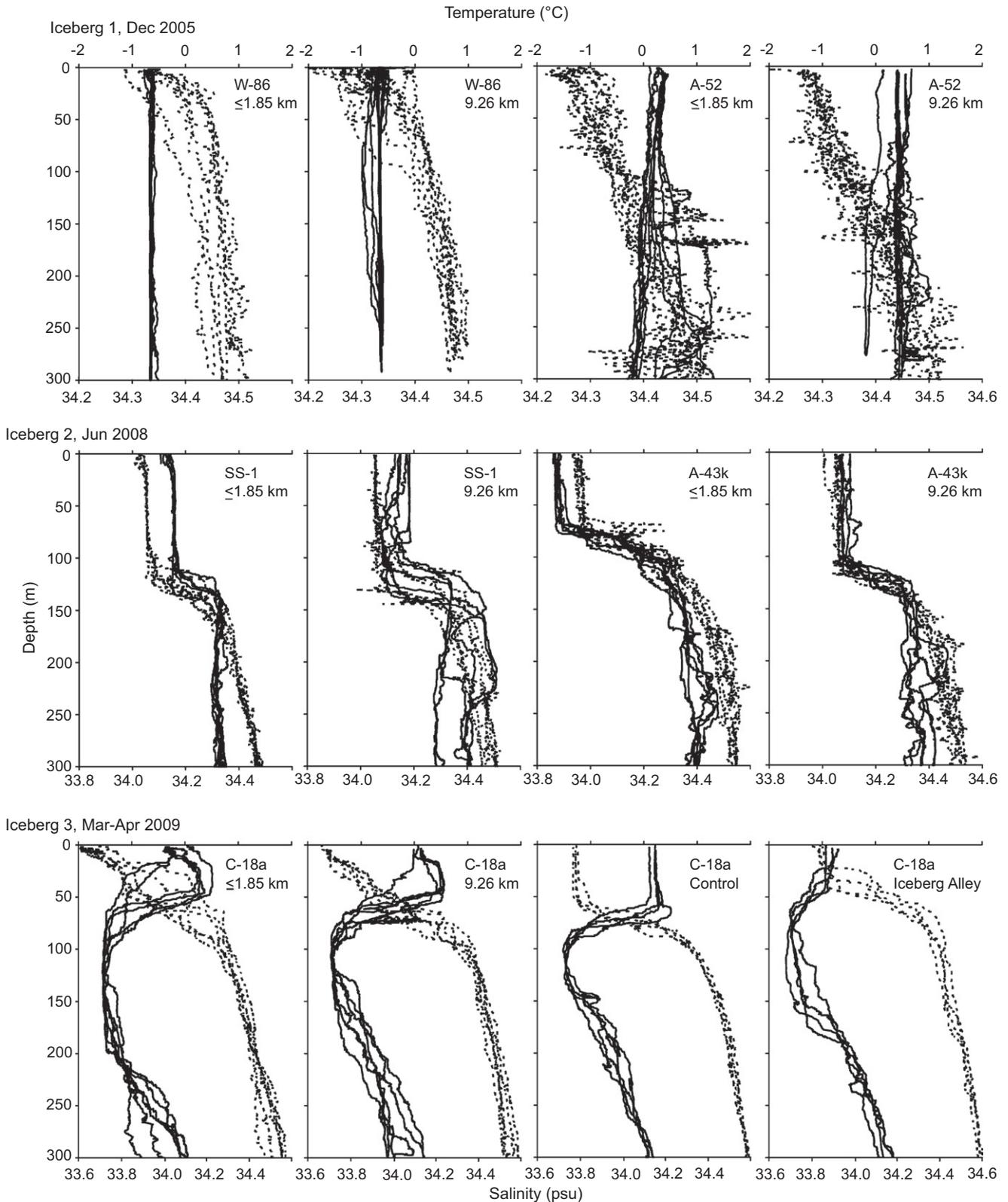


Fig. 2. Representative depth profiles of temperature (solid traces) and salinity (dashed traces) at various distances from icebergs in Dec 2005 (Iceberg 1), Jun 2008 (Iceberg 2) and Mar-Apr 2009 (Iceberg 3) and at the control site and in Iceberg Alley in Mar-Apr 2009. Note that X-axis scales for salinity are consistent within but not among cruises.

ranged from -0.1 to -0.4 °C, with a nearly isothermal water column to ca. 100 m, a sharp thermocline between 100 and 150 m, and a nearly isothermal water column between 150 and 300 m (Fig. 2). Salinity profiles near SS-1 were very consistent, with nearly constant values in the upper 100 m, a sharp halocline in the same depth range as the thermocline, and a consistent increase from the bottom of the halocline to 300 m depth (Fig. 2). Profiles near A-43k were variable by comparison. Surface temperatures ranged from -0.5 to -0.8 °C across four deployments and from -0.6 to -1.7 °C over the last two deployments. In all cases, the upper portion of the water column was nearly isothermal, with a sharp thermocline between 75 and 150 m and a nearly isothermal water column in most cases between the bottom of the thermocline and 300 m. In most cases, the thermocline was shallower within 1.85 km of A-43k than at greater distances, with the base at ca. 110 m vs. 135–155 m at 9.26 km. Temperatures at 300 m ranged from 0.5–1.2 °C and sometimes spanned 0.5 °C among multiple lowerings during a single deployment (Fig. 2). Salinity was much more consistent, with a halocline coincident with the thermocline in most cases and a progressive increase from the base of the halocline to 300 m.

Water column structure during Mar–Apr 2009 was studied in greater detail than on either of the previous two cruises (e.g. Helly et al., 2011; Stephenson et al., 2011). Within 1.85 km of iceberg C-18a, surface temperatures ranged from -0.35 to 0.2 °C, with a mixed layer to ca. 50 m depth and a thermocline between 50 and 100 m (Fig. 2). A layer of cold (-1.3 to -1.5 °C) winter water was present between the bottom of the thermocline and 150–200 m, with progressive warming between the bottom of this layer and 300 m. Similar temperature profiles were observed 9.26–18.5 km from C-18a and at the control site, although with increasing distance from C-18a the surface mixed layer became progressively more homogeneous, the thickness of the winter water layer was reduced and the temperature at 300 m increased. In Iceberg Alley, the winter water layer was intermediate in thickness between profiles collected within 1.85 km of C-18a and those from farther away. Profiles from Iceberg Alley also showed a shallower surface mixed layer, colder surface temperatures and a more nearly isothermal water column than any of the other profiles (Fig. 2). Salinity profiles near and at 9.26 km from C-18a were similar, with a gradual increase from surface values to the base of the thermocline. Salinity continued to increase below ca. 100 m but with a shallower slope. By contrast, salinity profiles at greater distances from C-18a and in Iceberg Alley displayed more homogeneous surface mixed layers that resembled the temperature profiles, with sharper haloclines at 60–100 (18.5 km and control) and 20–70 m (Iceberg Alley).

3.2. Biomass and density

Total macrozooplankton and micronekton biomass was elevated in the vicinity of icebergs (“close”) compared to distances 9.26 km away during Dec 2005 (mean biomass 0.37 km from iceberg A-52 was 4.3x higher vs. 9.26 km away) and Mar–Apr 2009 (mean biomass 0.37 km from iceberg C-18a was 3.1x higher vs. 9.26 km away; Fig. 3). This trend was not statistically significant (Kruskal–Wallis ANOVA; $\alpha=0.05$) in Dec 2005 or Mar–Apr 2009, though the p-value for trawls near iceberg C-18a in Mar–Apr 2009 was not far above the α value ($p=0.086$; Table 3). In Dec 2005, lower biomass was observed at 0.185 km from both icebergs compared to 0.37–1.85 (A-52) and 0.93 km away (W-86). No significant trend of biomass with distance was apparent in Jun 2008. Biomass at comparable distances from icebergs was highest in Mar–Apr 2009 and lowest in Jun 2008. In Mar–Apr 2009, biomass values from Iceberg Alley were comparable to those from 9.26 km away and higher than those from greater distances outside Iceberg

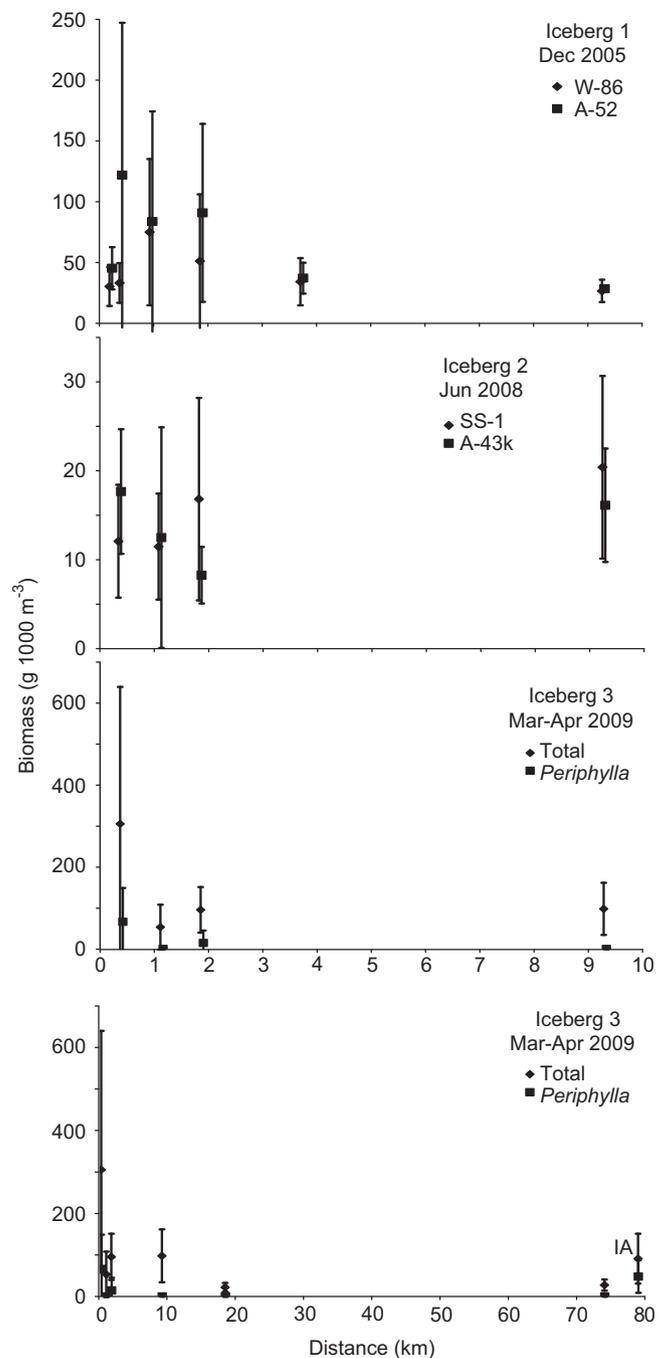


Fig. 3. Mean \pm 95% confidence interval for biomass of macrozooplankton and micronekton in relation to distance from icebergs. Bottom two panels show biomass of large (> 1000 g wet weight) *Periphylla periphylla* collected on Iceberg 3. X-axis values are the same for the top three panels. The bottom panel includes all the locations sampled on Iceberg 3, with the third panel showing just locations < 10 km from an iceberg for comparison with samples from the first two cruises. An offset of 0.05 km was added to some distance values to reduce overlap of symbols and error bars. IA=Iceberg Alley. X-axis scale does not represent actual distance between C-18a and Iceberg Alley site, which was > 100 km south of the iceberg during our study.

Alley. Also in Mar–Apr 2009, a substantial portion of the total biomass at 0.37 km from iceberg C-18a and in Iceberg Alley was made up of the predatory medusa, *Periphylla periphylla* (Fig. 3). Most individuals of this species ranged in size from 1–6 kg, and we seldom collected more than a single individual in any one net.

Density patterns were somewhat different than those for biomass. In Dec 2005, significantly higher densities of macrozooplankton and

Table 3
Results of Kruskal–Wallis nonparametric ANOVA and Levene test for homogeneity of variance for macrozooplankton and micronekton biomass and density at various distances from icebergs. Numbers in table are *p*-values. **p* < 0.05, ***p* < 0.01.

	Biomass (g 1000 m ⁻³)	Density (no. 1000 m ⁻³)	Biomass (g 1000 m ⁻³)	Density (no. 1000 m ⁻³)
Iceberg 1	Iceberg W-86		Iceberg A-52	
ANOVA (K-W)	0.56	0.54	0.25	0.036*
Levene	0.023*	0.00042**	0.00016**	0.0055**
Iceberg 2	Iceberg SS-1	Iceberg A-43k		
ANOVA (K-W)	0.39	0.26	0.15	0.21
Levene	0.54	0.54	0.095	0.28
Iceberg 3	Iceberg C-18a			
ANOVA (K-W)	0.086	0.0029**		
Levene	0.025*	0.091		

micronekton were captured up to 3.7 km from iceberg A-52 compared to 9.26 km away (*p*=0.036; Table 3). This trend was not observed near the much smaller W-86 (Fig. 4; Table 3). Generally, densities were higher near the much larger A-52 compared to W-86. In Mar–Apr 2009, significant differences in density with distance from iceberg C-18a were detected (*p*=0.0029) (*p*=0.0029); however, peak densities were measured at the control site ca. 74 km away, primarily due to high densities of small krill at this location (see below). No significant differences in density with distance were apparent during Jun 2008. Temporal patterns in density were similar to those for biomass, with highest densities in Mar–Apr 2009 (late summer) and lowest in Jun 2008 (late fall).

One particularly interesting result is the observation of elevated variation in both biomass and density in proximity to icebergs in Dec 2005 and Mar–Apr 2009. For all three icebergs studied during those time periods, variance in biomass was noticeably higher within 1.85 km of icebergs than at greater distances away. In all three cases, the number of relatively large catches in individual MOCNESS nets decreased with distance from the iceberg, although several large catches were obtained in Iceberg Alley in Mar–Apr 2009. Relatively small catches occurred at all distances. This observation is supported by an analysis for homogeneity of variance among samples from various distances from each iceberg that revealed significant differences for both biomass and density in Dec 2005 and for biomass in Mar–Apr 2009 (Levene test; Table 3). No significant differences in variance of biomass or density were detected among distances for either iceberg studied in Jun 2008.

3.3. Species composition

For ease of comparison, the macrozooplankton and micronekton assemblages were separated into functional groups (Table 4). The assemblage was dominated by large (total length ≥ 20 mm) Antarctic krill (*Euphausia superba*) during Dec 2005 and by krill and salps (predominantly *Salpa thompsoni*) in Jun 2008 and Mar–Apr 2009 (Fig. 5). Collectively, these two taxa comprised 76–94% of total biomass at all but one distance in Dec 2005, 41–71% at all distances in Jun 2008 and 55–88% at all but one distance in Mar–Apr 2009 (Fig. 5). Individual nets with less than 50% krill+salps invariably contained at least one large (1–6 kg) *Periphylla periphylla* that dominated the biomass for that net. Large *P. periphylla* were collected almost exclusively within 1.85 km of icebergs in Dec 2005 and Mar–Apr 2009 and in Iceberg Alley during Mar–Apr 2009. Of 15 *P. periphylla* > 1 kg in weight captured across all three cruises, nine were collected ≤ 1.85 km from icebergs and five in Iceberg Alley during Mar–Apr 2009.

Among cruises, large *E. superba* were dominant in Dec 2005, while salps were dominant during Jun 2008 and Mar–Apr 2009. In Jun 2008, a number of *Euphausia triacantha* also were collected

(Table 4), but these typically constituted a much smaller portion of the community than *E. superba*. Removing large euphausiids and gelatinous herbivores from the analysis allowed us to examine other constituents of the community in greater detail. In Dec 2005, small euphausiids (primarily *Thysanoessa macrura*) and gelatinous carnivores (mainly siphonophores and chaetognaths) made up the bulk of the “non-dominant” catch. Small euphausiids tended to be more abundant in the vicinity of Iceberg A-52, while gelatinous carnivores were more abundant near W-86. The “other” category was dominated by polychaetes, primarily *Tomopteris carpenteri*, and some amphipods, notably *Themisto gaudichaudii*. Fishes did not make up a substantial fraction of the catch in Dec 2005, when some sunlight was visible at all hours.

In Jun 2008, small euphausiids were proportionately less abundant than in Dec 2005, and fishes comprised a substantial fraction of the catch (Fig. 5). The most abundant species were *Electrona antarctica* and *Gymnoscopelus braueri* as well as two species of *Protomyctophum* (*P. bolini* and *P. choriodon*), all of which are known to exhibit diel vertical migration (Torres et al., 1988; Collins et al., 2008). As in Dec 2005, the “other” category consisted principally of polychaetes and amphipods.

Gelatinous carnivores made up the largest proportion of the non-dominant assemblage at most distances from iceberg C-18a in Mar–Apr 2009. This dominance was particularly apparent within 1.85 km of the iceberg and in Iceberg Alley, in part as a result of large *P. periphylla* (see above). The proportion of small euphausiids exhibited a complementary distribution, with small proportions near C-18a and in Iceberg Alley and large proportions at the control site, where large *P. periphylla* were not collected (Fig. 5). This inverse relationship between the proportions of large *P. periphylla* and small euphausiids can be illustrated with a multidimensional scaling analysis (Fig. 6). Samples collected near C-18a and in Iceberg Alley showed > 50% similarity in composition, based in part on the relative proportions of large *P. periphylla* and small euphausiids. Fishes made up a substantial proportion of the non-dominant community in Mar–Apr 2009 and showed patterns with distance similar to those for small euphausiids (Fig. 5).

3.4. Body size of dominant species

Body lengths of *Euphausia superba* collected on all three cruises showed seasonal differences, with the longest individuals in Dec 2005 and the shortest in Jun 2008 (Fig. 7). In Dec 2005, mean lengths of krill collected near iceberg A-52 were much greater than those collected near W-86, even 9.26 km away from each iceberg. This difference may have been unrelated to iceberg size, assuming that 9.26 km from each iceberg represented “background” conditions in areas not impacted by the icebergs. Size-frequency distributions from Dec 2005 seem to indicate two to three

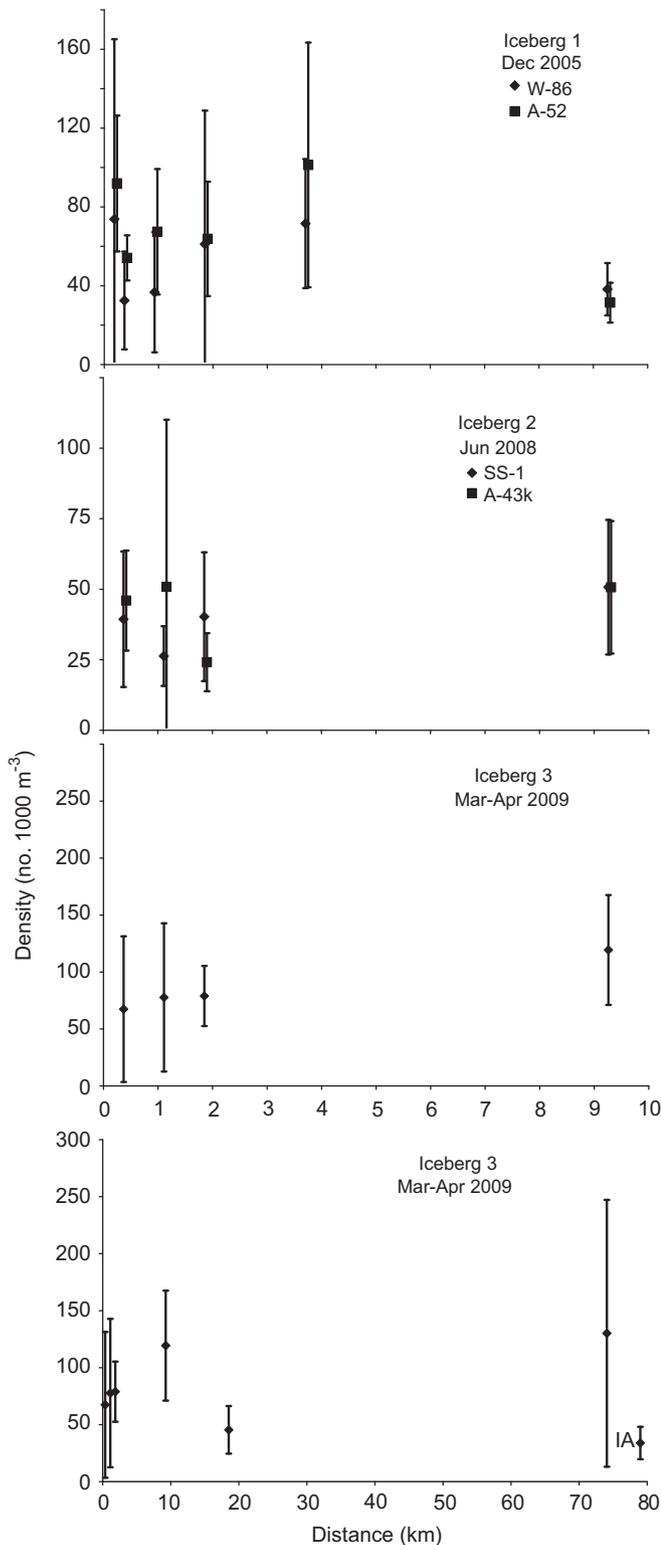


Fig. 4. Mean \pm 95% confidence interval for density of macrozooplankton and micronekton in relation to distance from icebergs. X-axis values are the same for the top three panels. The bottom panel includes all the locations sampled on Iceberg 3, with the third panel showing just locations < 10 km from an iceberg for comparison with samples from the first two cruises. An offset of 0.05 km was added to some distance values to reduce overlap of symbols and error bars. IA = Iceberg Alley. X-axis scale does not represent actual distance between C-18a and Iceberg Alley site, which was > 100 km south of the iceberg during our study.

overlapping modes for A-52 and W-86, respectively, perhaps indicative of multiple cohorts of krill. Distributions from the other two cruises appeared to be unimodal.

Table 4

Taxonomic makeup of groups reported in community composition analysis of macrozooplankton and micronekton.

Composition Group	Taxon/Taxa
Large Euphausiids	<i>Euphausia superba</i> \geq 20 mm, <i>E. triacantha</i> (Jun 2008 only)
Small Euphausiids	<i>E. superba</i> < 20 mm
Gelatinous Carnivores	Medusae (primarily <i>Atolla cf. wyvillei</i> , <i>Calyropsis borchgrevinki</i> , <i>Haliscera</i> spp., <i>Periphylla periphylla</i>) Ctenophores (<i>Callianira</i> spp., <i>Leuckartiara</i> spp., <i>Leucothea</i> spp.) Chaetognaths (<i>Pseudosagitta gazellae</i> , <i>Pseudosagitta lyra</i> , <i>Solidosagitta cf. zetesios</i>) Siphonophores (primarily <i>Diphyes antarctica</i>)
Gelatinous Herbivores	<i>Salpa thompsoni</i> , Unidentified salps
Fishes	<i>Bathylagus</i> spp., <i>Electrona</i> spp., <i>Gymnoscopelus</i> spp., <i>Protomyctophum</i> spp.
Other	Amphipods (<i>Cylopus lucasii</i> , <i>Eusirus</i> spp., <i>Hyperiella dilatata</i> , <i>Primno macropa</i> , <i>Themisto gaudichaudii</i> , <i>Vibilia antarctica</i>) Copepods Decapods Mysids Polychaetes (<i>Tomopteris carpenteri</i> , <i>Vanadis antarctica</i>) Pteropods (<i>Clio pyramidata</i> , <i>Spongiobranchaea australis</i>) Squids (<i>Alluroteuthis</i> , <i>Brachioteuthis cf. picta</i> , <i>Teuthowenia</i>)

Consistent trends in krill body length with distance from icebergs were not visually apparent in Dec 2005, though larger krill were observed 1.85 km from iceberg W-86 compared to other distances, and there was a slight increase in length with distance away from A-52. Trends also were difficult to evaluate statistically because of variability among samples collected at each distance. At most distances, *E. superba* from multiple samples were significantly different from each other in terms of body length (Kruskal-Wallis ANOVA, $p < 0.05$). This was not the case for iceberg SS-1 (Jun 2008), but krill body length did not differ significantly among distances from SS-1 (Kruskal-Wallis ANOVA, $p = 0.073$).

Among fishes, *Electrona antarctica* showed differences in length distribution between icebergs and cruises. In Jun 2008, longer individuals were collected near iceberg SS-1 vs. A-43k at all distances except 0.37 km, where the trend was reversed (Fig. 8). Individuals captured in Mar-Apr 2009 were still larger, and the population included a much greater proportion of individuals > 75 mm SL compared to Jun 2008. Significant differences in length from icebergs were detected only for C-18a (Kruskal-Wallis ANOVA, $p = 0.0007$), with significantly smaller individuals collected 0.37 and 1.85 km from C-18a compared to other distances (Fig. 8).

Gymnoscopelus braueri only was caught in substantial numbers in Jun 2008. Longer individuals were collected near A-43k compared to SS-1 at all distances except 1.85 km (Fig. 8). A significant difference in length among distances was observed for SS-1 (Kruskal-Wallis ANOVA, $p = 0.026$) but not for A-43k ($p = 0.63$).

3.5. Vertical distribution

Two MOCNESS deployments in Mar-Apr 2009 sampled 100 m depth strata from the surface to 300 m and back to the surface. One of these deployments was conducted 1.85 km from C-18a, and the other was carried out in Iceberg Alley. Vertical distributions of organisms differed substantially between these deployments. At 1.85 km from C-18a, biomass and density were highest in the 0–100 m stratum and decreased with depth (Fig. 9). Biomass was dominated by salps, while small krill and salps constituted the majority of the community numerically. Large *E. superba* were most

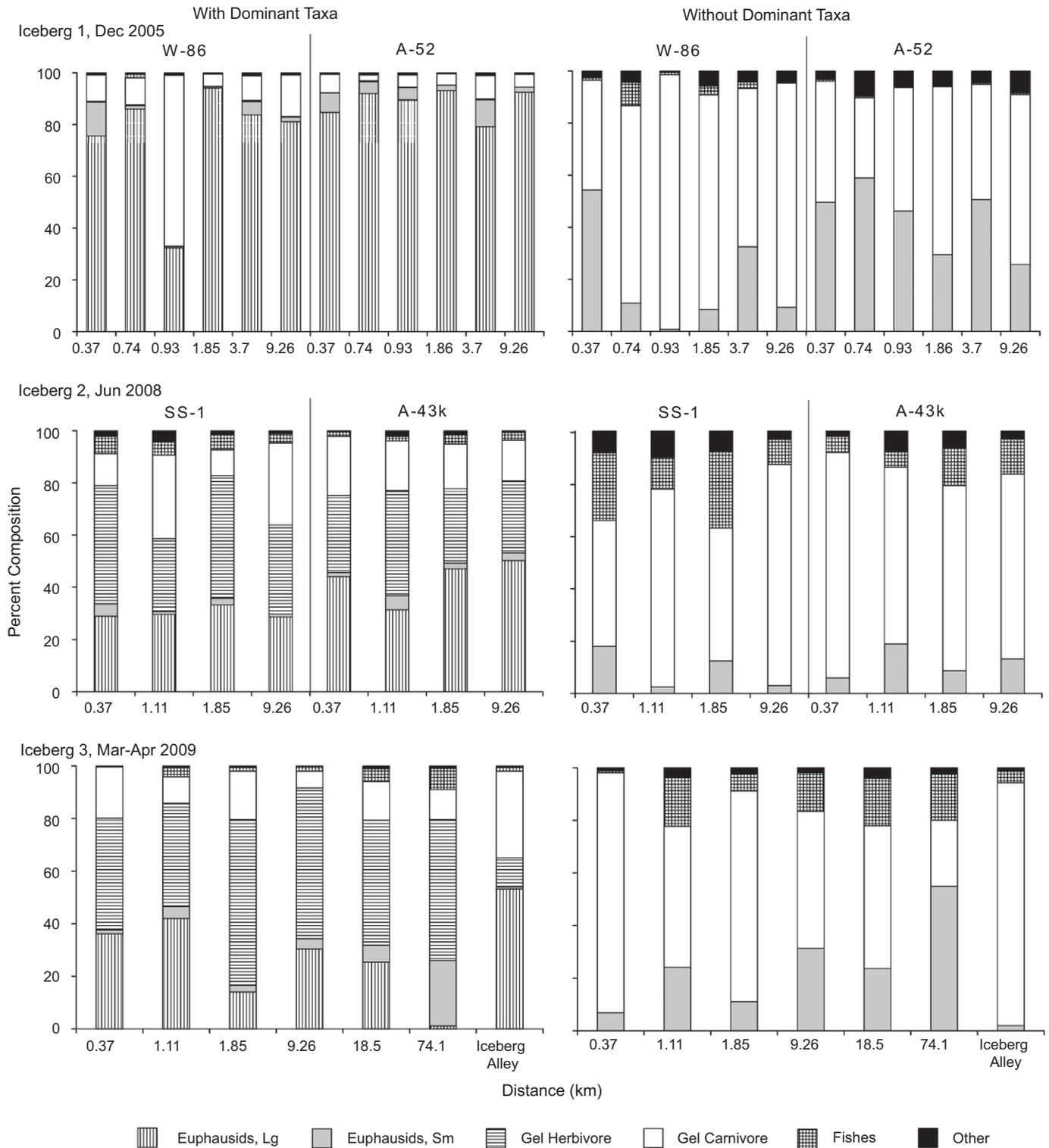


Fig. 5. Percent community composition based on shipboard measurements of biomass. Panels on left include all taxa. Panels on right show composition after removing dominant taxa (large krill and all salps). Sample sizes for each cruise and distance are given in Table 2. Taxa in each category are listed in Table 4.

abundant from 0-100 m and relatively rare at greater depths. Small euphausiids were caught in greatest numbers at 0-100 and 100-200 m and were much less abundant in the 200-300 m layer. Gelatinous carnivores were most abundant between 100 and 300 m, primarily due to the presence of cydippid ctenophores (*Callianira antarctica*) at these depths and not in the 0-100 m layer.

The vertical distribution of organisms was quite different in Iceberg Alley. Maximum biomass was collected at 100-200 m, with

highest densities at 200-300 m. Biomass in all depth strata was dominated by gelatinous carnivores, principally siphonophores (*Diphyes antarctica*) and medusae (*Calycopsis borchgrevinki*) at 0-300 m and ctenophores at 100-200 m. Large *E. superba* were most abundant at 0-100 and 100-200 m, and salps were relatively abundant only in the surface layer. Unlike the 1.85 km samples, small euphausiids were least abundant in the surface layer and increased in density with depth (Fig. 9). Fish biomass was highest in

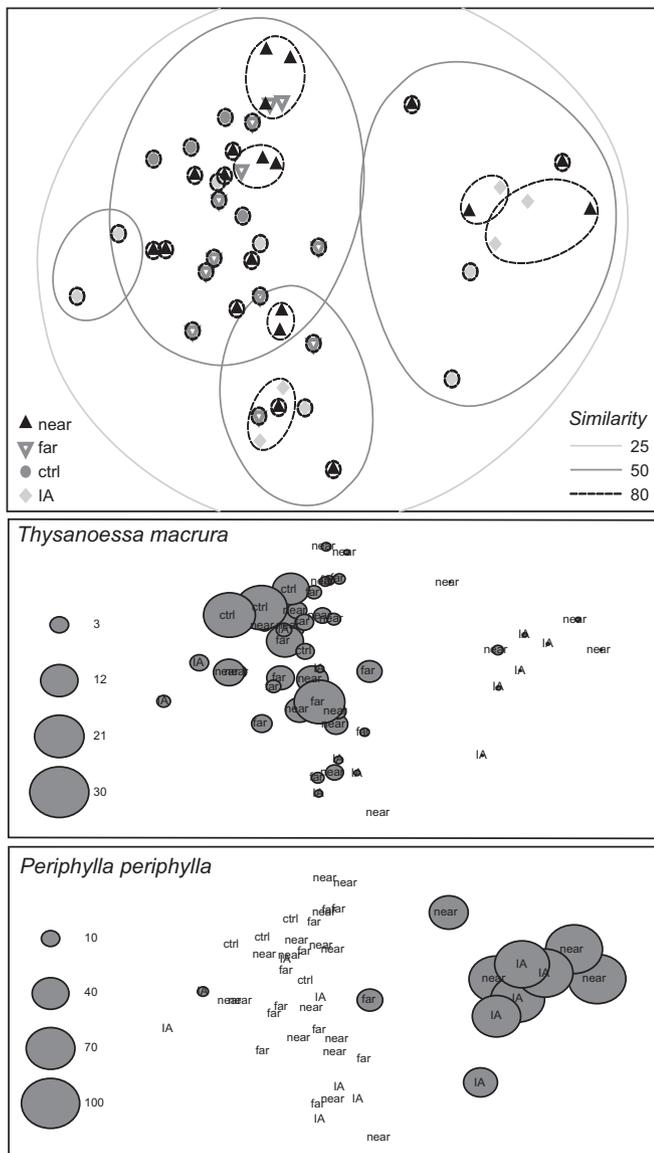


Fig. 6. Multidimensional scaling plots based on normalized biomass ($\text{g } 1000 \text{ m}^{-3}$) for samples collected in Mar–Apr 2009. Upper plot shows samples collected ≤ 1.85 km from C-18a (“near”) compared to those from 9.26–18.5 km (“far”), the control site (“ctrl”) and Iceberg Alley (“IA”). Lower plots show abundance of *Periphylla periphylla* (left) and *Thysanoessa macrura* (right). Units for bubble size are $\text{g } 1000 \text{ m}^{-3}$. Stress for all analyses was 0.15 (moderate).

the 100–200 m stratum because of two *Notolepis coatsi* (60 and 70 g wet weight) that were captured in one net.

3.6. Gut pigments

Gut pigment concentrations in *Euphausia superba* and *Salpa thompsoni* varied with distance from icebergs as well as temporally. In Dec 2005, mean gut pigment levels were significantly higher (Kruskal–Wallis ANOVA, $p < 0.0001$) in *E. superba* captured 0.185 and 1.85 km from iceberg W-86 compared to those from 1.57, 3.7 and 9.26 km away (Fig. 10). No obvious trend in gut pigment concentration with distance was observed in *E. superba* sampled near iceberg A-52. Krill collected 0.185 km from W-86 had much higher gut pigment concentrations than those from the same distance near A-52 (mean \pm 95% CI = $3.28 \pm 1.74 \mu\text{g individual}^{-1}$ near W-86 vs. $120 \pm 147 \text{ ng individual}^{-1}$ near A-52), while individuals collected ≥ 3.7 km away from both icebergs showed gut pigment concentrations of similar magnitude.

In Jun 2008, gut pigment concentrations in *E. superba* increased significantly with increasing distance from both icebergs ($p = 0.0028$ and $p = 0.014$ for SS-1 and A-43k, respectively), while concentrations in *S. thompsoni* increased significantly with distance from SS-1 ($p < 0.0001$) but not A-43k ($p = 0.14$). Highest concentrations for both species were measured at 9.26 km from each iceberg.

In Mar–Apr 2009, the highest mean gut pigment concentrations for both *E. superba* and *S. thompsoni* were measured in animals collected 1.85 km from iceberg C-18a. For *E. superba*, this peak concentration was significantly higher than those measured at any other distance ($p < 0.0001$). The lowest *E. superba* gut pigment concentrations occurred in Iceberg Alley, with the second lowest concentrations in animals collected 0.37 km from C-18a. For *S. thompsoni*, animals collected at the control site also had relatively high gut pigment concentrations. Gut pigment concentrations for *S. thompsoni* collected 1.85 km from C-18a and the control site were significantly higher ($p < 0.0001$) compared to animals from other distances and Iceberg Alley.

4. Discussion

Macrozooplankton and micronekton exhibited variability in biomass, density and species composition over space and time in relation to icebergs. A portion of the variability may have been due to differences in geographic location and season among sampling locations. Studying free-drifting icebergs requires locating such icebergs during scheduled cruises (i.e. opportunistically) rather than in a specific geographic area. In addition, icebergs must be sufficiently remote from land and the edge of the seasonal pack ice to minimize the influence of these confounding factors on the phenomena we wished to examine. In Dec 2005 and Mar–Apr 2009, we studied free-drifting icebergs in the Powell Basin area of the NW Weddell Sea (Fig. 1). In Jun 2008, pack ice covered most of the Weddell Sea, and we worked around two icebergs in the Scotia Sea. The fact that icebergs were studied in two different areas during three different seasons imposes some limitations on comparison across cruises. The majority of this discussion will be confined to within-cruise comparisons in relation to distances from individual icebergs, along with some broader comparisons across cruises where the data suggest more general patterns.

4.1. Environmental characteristics

Water column conditions varied noticeably among cruises and, in some cases, with distance from icebergs. In Dec 2005 the water column was nearly isothermal to 300 m, with a distinct salinity gradient from the surface to 300 m depth. This trend was more pronounced near the larger A-52, presumably reflecting the large difference in rates of meltwater discharge. In Jun 2008 and Mar–Apr 2009, distinct trends with distance from large icebergs were observed, with a shallower mixed layer in both seasons and pronounced surface freshening in Mar–Apr 2009 close to icebergs (Fig. 2). Multiple mechanisms may be responsible for these effects, including turbulent mixing by a large moving object (Schwarz and Schodlok, 2009; Helly et al., 2011) as well as subsurface melting with meltwater intrusion and mixing (Stephenson et al., 2011). The chemical composition of meltwater may affect biological processes. In Mar–Apr 2009, elevated concentrations of nitrate (Vernet et al., 2011) and iron (Lin et al., 2011) were detected close to iceberg C-18a. Vernet et al. (2011) concluded that elevated nitrate near C-18a probably originated from meltwater and likely was maintained by decreased phytoplankton biomass resulting from dilution and zooplankton grazing. Also, phytoplankton near C-18a showed higher photosynthetic efficiency than at greater

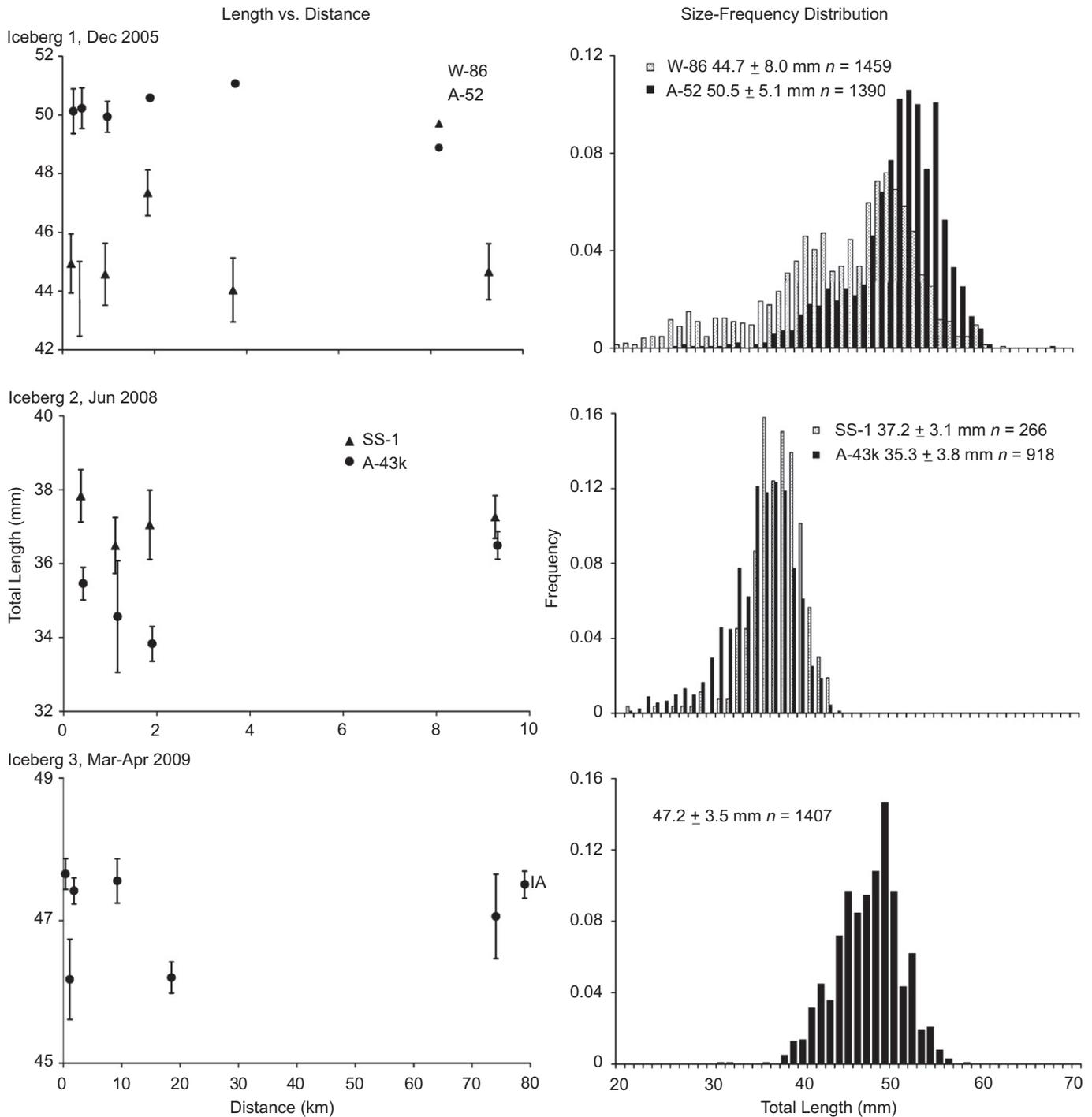


Fig. 7. Mean \pm 95% confidence interval for total length of *Euphausia superba* collected at various distances from icebergs. Right panels show size-frequency distributions for *E. superba* collected at all distances on each cruise. An offset of 0.05 km was added to some distance values to reduce overlap of symbols and error bars. IA=Iceberg Alley. X-axis scale does not represent actual distance between C-18a and Iceberg Alley site, which was > 100 km south of the iceberg during our study.

distances, suggesting enhancement from a locally enriched nutrient supply.

4.2. Biomass and density

Higher biomass and density of macrozooplankton and micro-nekton were observed near free-drifting icebergs during Dec 2005 and Mar-Apr 2009, compared to sites > 1.85 and 1.1 km away, respectively. This trend was most pronounced in Mar-Apr 2009, when mean biomass 0.37 km from iceberg C-18a exceeded 300 g

1000 m^{-3} , more than 3 times the highest mean from any other distance (Fig. 3). It should be noted that these differences were not statistically significant at $\alpha = 0.05$, however the lack of significance may be related to relatively small sample size and high spatial variability. Comparable biomass levels have been observed at night in the surface waters of the NW Weddell Sea during similar times of year (e.g., Fisher et al., 2004; Pakhomov and Froneman, 2004). However, mean biomass levels near icebergs in Dec 2005 and Mar-Apr 2009 were higher by 3–8 times compared to samples collected with a 9 m^2 Tucker trawl in the upper 200 m of the water column near the pack ice edge in summer and fall, respectively (Lancraft

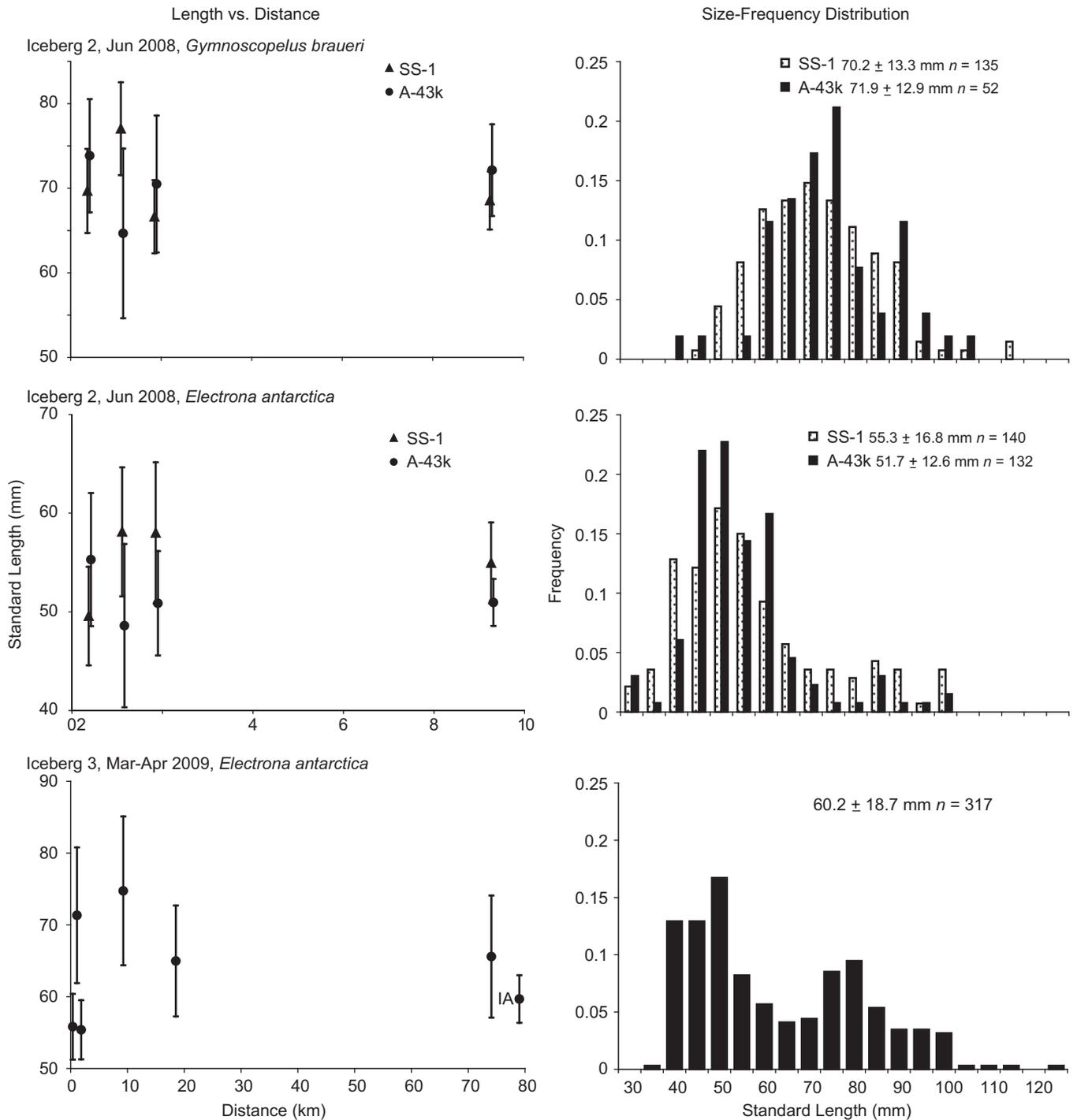


Fig. 8. Mean ± 95% confidence interval for standard length of *Gymnoscopelus braueri* and *Electrona antarctica* collected at various distances from icebergs on Iceberg 2 and Iceberg 3. Right panels show size-frequency distributions for fishes collected at all distances on each cruise. An offset of 0.05 km was added to some distance values to reduce overlap of symbols and error bars. IA=Iceberg Alley. X-axis scale does not represent actual distance between C-18a and Iceberg Alley site, which was > 100 km south of the iceberg during our study.

et al., 1989; Donnelly et al., 2006). Mean biomass near icebergs during these same two time periods was lower than levels reported in the upper 100 m near the ice edge during similar seasons by Fisher et al. (2004). However, macrozooplankton/micronekton biomass tends to decline with depth (Fisher et al., 2004; this study), suggesting that per-volume biomass measured from 0–300 m (this study) should be lower than biomass measured to 100 (Fisher et al., 2004) or 200 m (Lancraft et al., 1989, 1991; Donnelly et al., 2006). Thus, elevated macrozooplankton and

micronekton biomass observed near icebergs in this study is perhaps more noteworthy than might be apparent from a simple comparison of our estimates and previous studies in which biomass was integrated to shallower depths. Biomass elevation near icebergs was not apparent in all seasons. Biomass levels of macrozooplankton and micronekton near icebergs in the Scotia Sea (Jun 2008) did not display a significant trend with distance (Fig. 3) and were lower by a factor of 2–4 than in the upper 200 m of the ice edge zone (Lancraft et al., 1991). However, Lancraft et al. (1991) used a

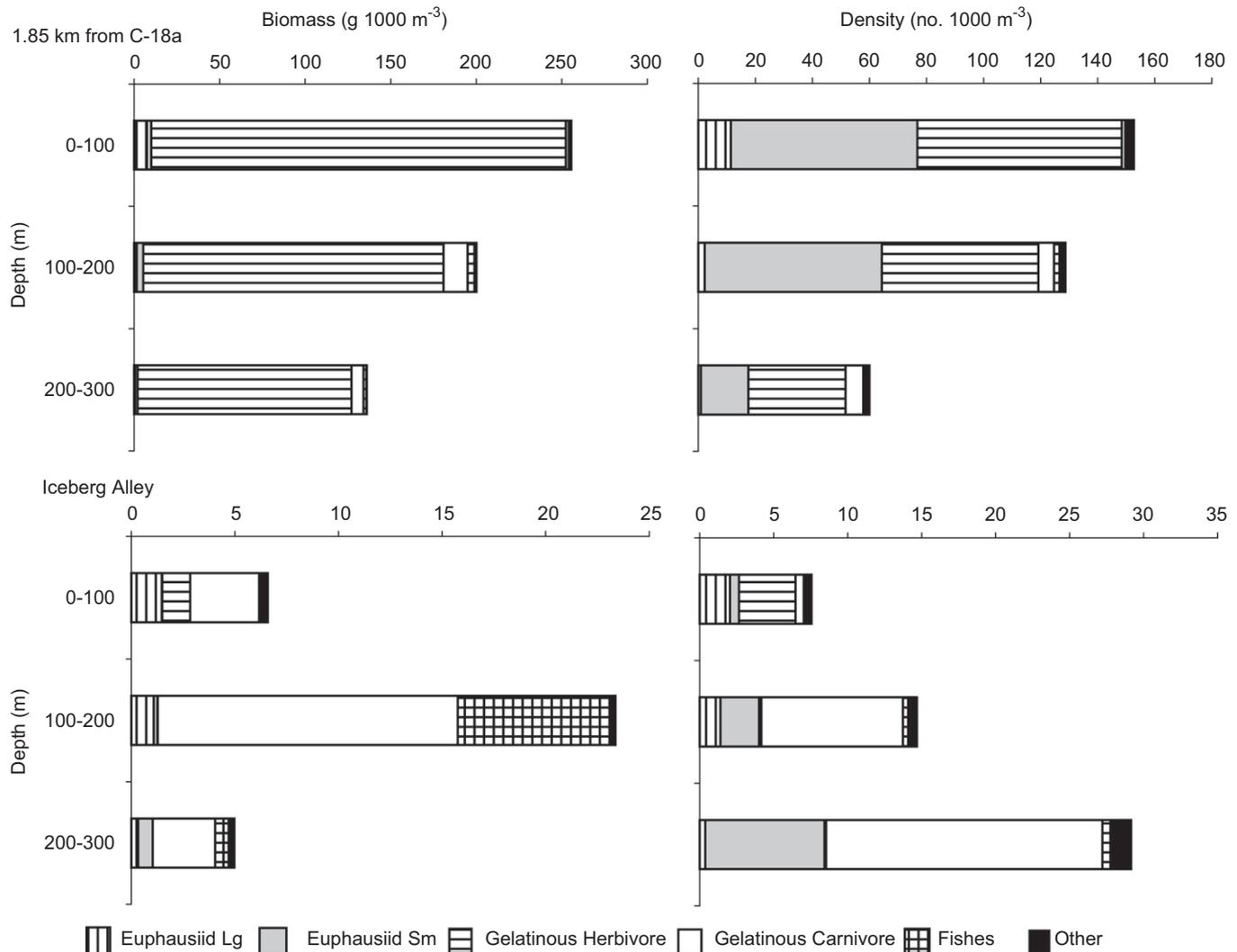


Fig. 9. Depth distribution in 100 m strata of biomass (left panels) and density (right panels) 1.85 km from iceberg C-18a (upper panels) and in Iceberg Alley (lower panels). Each bar represents a mean of two nets, one during the descent of the MOCNESS from the surface to 300 m depth and the other during the ascent back to the surface.

1.8 m² Tucker trawl, which doesn't facilitate a good comparison to the 10 m² MOCNESS used in this study.

The spatial distribution of biomass varied among icebergs and seasons. In Dec 2005, samples collected 0.185 km from iceberg A-52 and 0.185–0.37 km from W-86 had lower biomass than samples from 0.37–1.85 (A-52) and 0.93–1.85 km (W-86) away. Biomass at these close distances was comparable to that in samples collected 9.26 km away from each iceberg. One possible explanation for this observation is reduced food supply (phytoplankton) for grazers in close proximity to icebergs because of dilution by iceberg meltwater. Surface meltwater dilution was apparent near icebergs A-52 and W-86 (Smith et al., 2007), and close examination of iceberg C-18a during Mar–Apr 2009 showed subsurface meltwater 0.85 km from the iceberg at 80–230 m depth (Stephenson et al., 2011). The magnitude of this dilution should be greater near large icebergs, perhaps contributing to the greater difference in biomass compared to background near the larger A-52 vs. the smaller W-86. Vernet et al. (2011) concluded that lower densities of phytoplankton near iceberg C-18a in Mar–Apr 2009 were the result of meltwater entrainment in combination with grazing by elevated densities of macrozooplankton and micronekton.

Another possible explanation for lower macrozooplankton and micronekton biomass near A-52 and W-86 is predation by seabirds. Flying seabirds are known to aggregate on and near icebergs

(e.g. Joiris, 1991; Ribic et al., 1991; Veit and Hunt, 1991), and aquatic prey such as large euphausiids and small fishes constitute an important part of the diet for many species (e.g., Ainley et al., 1992). Seabird densities were elevated significantly within 0.46 km of icebergs in Dec 2005 (Ruhl et al., 2011), and foraging within that range may have reduced macrozooplankton and micronekton biomass. Elevated seabird densities in the same distance range were observed in Mar–Apr 2009 as well, with no apparent depletion of biomass. However, seabird densities near iceberg C-18a in Mar–Apr 2009 were several orders of magnitude lower than in Dec 2005 (Ruhl et al., 2011), and predation pressure on macrozooplankton and micronekton from seabirds foraging near the iceberg should have been correspondingly lower. In addition, *E. superba*, a prevalent prey item in flying seabird diets (e.g., Ainley et al., 1992), dominated the community near A-52 and W-86, whereas *Salpa thompsoni*, a less common prey species for seabirds, comprised a much larger proportion of the community near C-18a (Fig. 5). Thus, the macrozooplankton/micronekton assemblage near C-18a should have been much less affected by seabird predation compared to similar assemblages near A-52 and W-86.

Elevated zooplankton biomass near icebergs may result in part from enhanced food availability and quality. Icebergs may enhance surface phytoplankton biomass (e.g., Schwarz and Schodlok, 2009), and the size distribution and taxonomic composition of

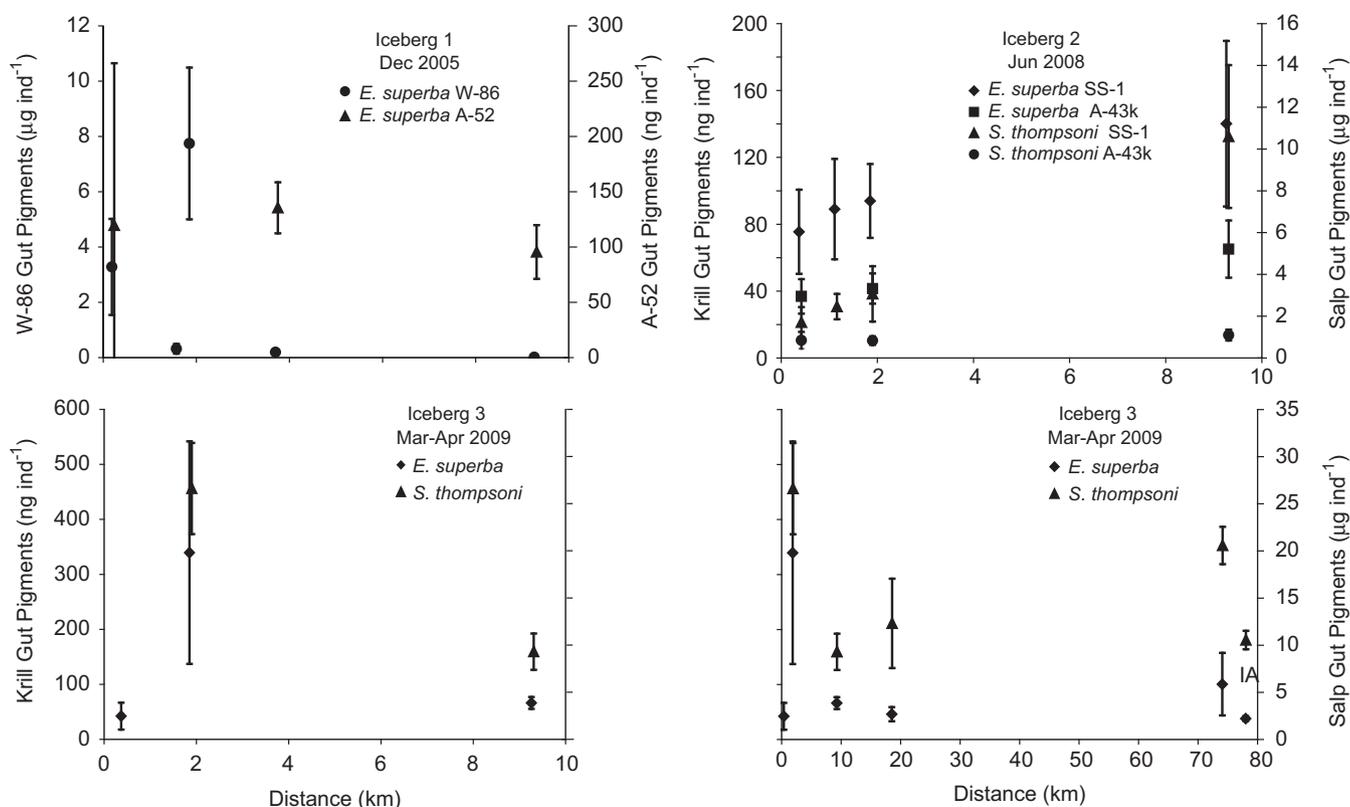


Fig. 10. Gut pigment concentrations in *Euphausia superba* and *Salpa thompsoni*. Symbols represent means \pm 95% confidence interval. X-axis values are the same for the top two panels and the bottom left panel, which shows just locations < 10 km from an iceberg during Iceberg 3 for comparison with samples from the first two cruises. The bottom right panel includes all the locations sampled on Iceberg 3. An offset of 0.05 km was added to some distance values to reduce overlap of symbols and error bars. IA=Iceberg Alley. X-axis scale does not represent actual distance between C-18a and Iceberg Alley site, which was > 100 km south of the iceberg during our study.

phytoplankton communities may be different in the vicinity of icebergs vs. distant areas. Densities of phytoplankton cells > 20 μm in diameter (primarily the diatom *Corethron pennatum*; Cefarelli et al., 2011) were elevated near iceberg C-18a compared to sites farther away (Vernet et al., 2011). Diatoms in this size range should be important food items for *Euphausia superba* (e.g. Meyer and El-Sayed, 1983; Schmidt et al., 2006). Guts from several *E. superba* collected near C-18a were examined and found to contain frustules of both *C. pennatum* and *Chaetoceros* spp. (A. Cefarelli, unpublished data). In addition, free-drifting icebergs have been found to support extensive diatom mats (Robison et al., 2011) that serve as aggregation sites for krill (Sherlock et al., 2011) and may provide an important food source. *Euphausia superba* distributions are affected strongly by food availability (e.g., Atkinson et al., 2008), and enhancement of primary production or production efficiency could affect krill distributions through bottom-up processes.

Prior to sampling near icebergs for the first time, it seemed to us that icebergs might provide krill with refuges from predation. ROV observations supported this expectation (Smith et al., 2007), and numerous krill were observed in close association with the sides of free-drifting icebergs (Sherlock et al., 2011). However, krill that remain within a few meters or tens of meters of an iceberg would not have been captured with the MOCNESS and thus not included in the data set being reported here.

The distribution of macrozooplankton/micronekton biomass around C-18a in Mar-Apr 2009 was somewhat different from those around A-52 and W-86, with no zone of reduced biomass in proximity to C-18a (Figs. 3 and 4). This difference may have multiple causes. The closest MOCNESS deployments to A-52 and W-86 were 0.185 km away, whereas the closest deployments near C-18a were conducted at 0.37 km. Lower biomass near A-52 was

observed in samples collected 0.185 but not 0.37 km away. In addition, fracturing, ablation and melting of A-52 in the late spring appeared to be much more rapid than for C-18a in the late summer. In support of these qualitative observations, A-52 exhibited a substantial reduction in size due to fracturing and ablation and had numerous large waterfalls cascading from its upper surface (Smith et al., 2007), suggesting rapid large-scale melting. No such waterfalls were observed on C-18a.

The dynamic physical environment created by the passage of an iceberg through the upper water column also may have influenced the patchiness of macrozooplankton and micronekton. Significantly higher variance in biomass and density was observed near icebergs in Dec 2005 and Mar-Apr 2009 compared to greater distances (Figs. 3 and 4, Table 3). Enhanced turbulence in proximity to icebergs (Schwarz and Schodlok, 2009; Helly et al., 2011) should have produced a very different physical setting compared to areas farther away. In addition, a melting iceberg can create a region characterized by patchy meltwater (Stephenson et al., 2011) and enhanced variation in the distribution of nutrients (Lin et al., 2011). In this chemically and physically complex setting, phytoplankton distributions also were affected.

Increased patchiness of chemical signals and potential food (phytoplankton) near icebergs also could have affected the behavior of macrozooplankton/micronekton, particularly schooling species like *E. superba* and *Thysanoessa macrura*. Krill are known to modify their swimming behavior and school structure in response to chemical cues (Hamner and Hamner, 2000) and food availability (O'Brien, 1989). The mechanism underlying elevated near-iceberg patchiness in the biomass of *Salpa thompsoni* is less clear, although significant heterogeneity of variance was observed near iceberg C-18a for this species as well (Levene test; $p=0.006$). Enhanced food availability in the form of phytoplankton near

icebergs certainly could attract herbivorous zooplankton like salps. However, the speed at which icebergs can move (0.145–1.45 km h⁻¹, Schodlok et al., 2006; Smith et al., 2007; Helly et al., 2011) potentially exceeds the swimming speeds of both solitary and colonial salps (e.g., Harbison and Campenot, 1979; Sutherland and Madin, 2010). Conceivably, salps and other pelagic organisms could be entrained to some extent in the boundary layer surrounding an iceberg or concentrated at the iceberg's leading edge (Sherlock et al., 2011) and could be carried by currents that also help to transport icebergs (speeds of 0.36–1.08 km h⁻¹ were typical near C-18a; Helly et al., 2011). Whether that zone extends to the closest distances sampled by the MOCNESS in this study (0.185–0.37 km) is unknown. Interestingly, in Mar–Apr 2009, patchiness was high near iceberg C-18a and in Iceberg Alley compared to sites that were farther from (and presumably affected to a lesser degree by) icebergs. Since the MOCNESS tows in Iceberg Alley were not carried out near individual icebergs, this result suggests that the spatial variability associated with icebergs may persist beyond the “life-span” of the icebergs themselves.

The effects of iceberg size on macrozooplankton/micronekton assemblages are less clear. Larger icebergs should release more meltwater than smaller icebergs, potentially generating a very large meltwater field and creating a larger “zone of influence” compared to a smaller iceberg (e.g. Helly et al., 2011). There is qualitative evidence from Dec 2005 that the near-iceberg zone of elevated density and biomass was more extensive around iceberg A-52 compared to the much smaller W-86 (Figs. 3 and 4). The magnitude of this difference can be estimated by integrating the biomass of macrozooplankton/micronekton between 0.185 and 3.7 km from these two icebergs. For A-52, integrated biomass over this range was 62.6% higher compared to W-86. Additional comparisons between icebergs of different sizes were not possible. No zone of influence was observed near either iceberg in Jun 2008, and only one (large) iceberg was studied in Mar–Apr 2009.

4.3. Species composition

Overall, the species composition of macrozooplankton and micronekton near icebergs was not distinctly different from communities farther away. Taxa that were common in our samples have been reported in previous studies from these same regions of the Southern Ocean (e.g., Lancraft et al., 1989, 1991; Fisher et al., 2004; Donnelly et al., 2006), and there were no species identified near icebergs yet absent from samples collected ≥ 9.26 km away. One notable exception to this rule was the large medusa *Periphylla periphylla*. These were much more common near icebergs and in Iceberg Alley than in surrounding waters, with all but one of 15 *P. periphylla* > 1 kg in weight collected ≤ 1.85 km from icebergs or in Iceberg Alley. This species is uncommon in trawl samples from the NW Weddell Sea and Scotia Sea, typically occurring below 150 m depth (Lancraft et al., 1989, 1991; Pagès and Kurbjewit, 1994; Donnelly et al., 2006) and rarely in the upper 100 m (Pagès et al., 1996; Fisher et al., 2004). The much higher incidence of *P. periphylla* near icebergs and in Iceberg Alley compared to non-iceberg locations could result from elevated abundance of zooplankton, including large *E. superba* near icebergs and in Iceberg Alley (Figs. 3–5). *Periphylla periphylla* is known to prey on large euphausiids in addition to other crustaceans (e.g., Sørnes et al., 2008). Gelatinous carnivores are known to be abundant in marginal ice zones (Pakhomov et al., 1999), and similar environmental and trophic conditions may exist near icebergs. These large medusae may exert top-down control on macrozooplankton populations, as indicated by the inverse relationship between the abundance of *P. periphylla* and *Thysanoessa macrura* during Mar–Apr 2009 (Fig. 6).

Spatial patterns in community composition during Mar–Apr 2009 suggest a general scenario for the effects of icebergs on pelagic

communities. Communities within 1.85 km of C-18a and in Iceberg Alley included higher proportions of gelatinous carnivores (medusae, ctenophores and siphonophores) than assemblages at 9.26–18.5 km away and the control site. Release of meltwater containing iron and nitrate (Lin et al., 2011; Vernet et al., 2011) should facilitate increased phytoplankton growth and elevate food availability for herbivores in proximity to a free-drifting iceberg. This effect should diminish with distance and time, and areas that are traversed by icebergs infrequently should return to “background” conditions within a period of weeks (after Helly et al., 2011) following an iceberg's passage. In areas through which icebergs pass frequently, e.g. Iceberg Alley (Stuart and Long, 2011), the effects of turbulent mixing, melting and ablation may persist for longer periods of time, allowing the pelagic community to pass through succession from nutrient input to phytoplankton, herbivore and carnivore. In this scenario, the upper water column within the zone of influence of a large iceberg (at least to 1.85 km for C-18a) would be expected to support higher proportions of herbivores, including both crustaceans and gelatinous forms. In contrast, the upper water column in Iceberg Alley should contain a more “mature” community with a higher proportion of carnivores. The composition of macrozooplankton and micronekton assemblages in these two different situations thus may reflect a contrast in both time and space between bottom-up control near icebergs and top-down control in Iceberg Alley.

4.4. Body size of dominant species

Mean body length of *Euphausia superba* varied among seasons and between icebergs within a cruise but did not change significantly as a function of distance from icebergs in most cases. *Euphausia superba* were largest near iceberg A-52 in Dec 2005 and smallest near A-43k in Jun 2008. The size distribution and largest individual near A-52 (mean body length = 50.5 mm, largest individual 68 mm, Fig. 7) were comparable to the largest reported in the literature (e.g., Siegel, 1987; Reid et al., 2002; Atkinson et al., 2006). Size distributions from Dec 2005 also were multimodal, presumably reflecting multiple age classes of *E. superba* (Siegel, 1987). Krill captured in Jun 2008 and Mar–Apr 2009 did not show the same multimodal size distribution.

The observation of consistently larger *E. superba* near iceberg A-52 vs. W-86 may be related to the regions in which those icebergs were studied. Atkinson et al. (2006) reported a trend in *E. superba* summer size distributions northeast of the Antarctic Peninsula, with smaller individuals to the southwest, larger individuals to the northeast and some bimodal distributions in between. We sampled W-86 in an area where Atkinson et al. reported smaller krill and a bimodal size distribution, whereas A-52 was sampled to the north and west, where Atkinson et al. found larger krill. Our sampling in this area took place three years after the collections analyzed by Atkinson et al. (2006), but our observations appear to agree with the trends they reported.

It might be expected that enhanced predation, e.g. in proximity to an iceberg that supports aggregations of seabirds and marine mammals (Ribic et al., 1991; Veit and Hunt, 1991; Ruhl et al., 2011), might lead to the removal of more desirable (i.e. larger) prey items, as has been reported for a number of Southern Ocean predators that feed on Antarctic krill (Reid et al., 1996). No evidence of this selective removal was apparent in the lengths of *E. superba* at various distances from icebergs (Fig. 7), but selective predation could have led to our finding of significantly smaller *Electrona antarctica* within 1.85 km of C-18a (Fig. 8). The dominant seabird species identified near C-18a included several (Antarctic petrels, cape petrels, Antarctic fulmars, Wilson's storm-petrels; Ruhl et al., 2011) that are known to prey on *E. antarctica* (Ainley et al., 1992;

Quillfeldt, 2002). Overall, length distributions for *E. antarctica* and *Gymnoscopelus braueri* near icebergs were similar to those reported for these species elsewhere in the Southern Ocean (e.g., Collins et al., 2008; Cherel et al., 2010).

4.5. Vertical distribution

Depth distributions of macrozooplankton and micronekton differed substantially between MOCNESS deployments 1.85 km from iceberg C-18a and in Iceberg Alley during Mar–Apr 2009. Near the iceberg, the community consisted primarily of herbivores and was dominated by salps gravimetrically and by salps and small krill numerically (Fig. 9). Biomass and density were highest in the surface 100 m and decreased with depth. In contrast, the community in Iceberg Alley consisted primarily of carnivores and was dominated gravimetrically by ctenophores, siphonophores and medusae, numerically by salps and large krill from 0–100 m and gelatinous carnivores from 100–300 m. The biomass mode was in the 100–200 m layer, whereas density increased with depth. Although these patterns are based on a single MOCNESS deployment at each location, the results reinforce the scenario proposed above for iceberg influence on pelagic macrozooplankton and micronekton.

Phytoplankton growth supported by the release of nutrient-containing meltwater should be highest in surface waters, decreasing with depth (Vernet et al., 2011). Herbivore biomass would be expected to track food availability, producing a vertical biomass distribution similar to that observed 1.85 km from C-18a. In Iceberg Alley, the carnivore-dominated community should be less tightly coupled to the vertical distribution of phytoplankton. Subsurface biomass modes for gelatinous carnivores have been reported elsewhere in the Antarctic (Lancraft et al., 1991; Kaufmann et al., 2003) and explained in relation to water column structure and prey distribution (Pagès and Kurbjeweit, 1994). Cydippid and lobate ctenophores, which dominated the gelatinous carnivore assemblage from this MOCNESS deployment, are known to consume small crustaceans (e.g., Scolardi et al., 2006), and the vertical distribution of gelatinous carnivore density tracked that of small krill (Fig. 9). Firm conclusions about the relationship between icebergs and the vertical distribution of macrozooplankton and micronekton are certainly premature, but these initial data suggest a mechanism by which icebergs may affect the depth distribution of pelagic fauna.

4.6. Gut pigments

Spatial patterns in *E. superba* and *S. thompsoni* gut pigments during Mar–Apr 2009 corresponded broadly to fluorescence measurements in surface waters reported by Vernet et al. (2011). Thus, icebergs appear to influence macrozooplankton and micronekton at least in part through effects on the phytoplankton food supply. Unfortunately, sampling locations for direct measurement of water column chlorophyll *a* concentrations did not correspond to MOCNESS sampling distances, precluding a robust statistical comparison between concentrations of photosynthetic pigments in the environment and in the guts of *E. superba* and *S. thompsoni*. A tight relationship between phytoplankton distributions and *E. superba* gut pigments was observed in Dec 2005 (see Smith et al., 2007), particularly with respect to iceberg W-86, but not in Jun 2008. This latter observation is not surprising, given the typically low density and productivity of phytoplankton during the winter.

In Mar–Apr 2009 phytoplankton cell size distributions near iceberg C-18a showed elevated proportions of diatoms > 20 µm in diameter (Vernet et al., 2011). This size fraction should be grazed effectively by large *E. superba* (e.g., Opalinski et al., 1997; Perissinotto et al., 1997), and the presence of these cells corresponded to lower gut pigment concentrations in krill collected

0.37 km from C-18a (Fig. 10). At the control site, in comparison, phytoplankton cells < 10 µm in diameter were depleted. Salps feed effectively on phytoplankton in this size range (e.g., Kremer and Madin, 1992), and salp gut pigment concentrations were high at this site. Small krill were also abundant at the control site (Fig. 5) and may have contributed to the removal of small phytoplankton. Grazing and subsequent export of organic material by salps and krill appears to constitute an important mechanism for removal of organic carbon from the euphotic zone (e.g., Shaw et al., 2011).

For *E. superba* and *S. thompsoni*, gut pigment concentration near icebergs were comparable to peak levels measured in highly productive coastal and ice-edge zones (Perissinotto et al., 1997; Perissinotto and Pakhomov, 1998; Pakhomov and Froneman, 2004). In combination with elevated biomass of macrozooplankton and micronekton near icebergs in late spring and late summer (see above), this result supports the conclusion that icebergs may enhance local food availability to a degree typically observed only in the most productive areas of the Antarctic.

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References

- Ainley, D.G., Ribic, C.A., Fraser, W.R., 1992. Does prey preference affect habitat choice in Antarctic seabirds? *Marine Ecology Progress Series* 90 (3), 207–221.
- Arrigo, K.R., van Dijken, G.L., Ainley, D.G., Fahnestock, M.A., 2002. Ecological impact of a large Antarctic iceberg. *Geophysical Research Letters* 29 (7), 1104. doi:10.1029/2001GL014160,2002.
- Atkinson, A., Shreeve, R.S., Hirst, A.G., Rothery, P., Tarling, G.A., Pond, D.W., Korb, R.E., Murphy, E.J., Watkins, J.L., 2006. Natural growth rates in Antarctic krill (*Euphausia superba*): II. Predictive models based on food, temperature, body length, sex, and maturity stage. *Limnology and Oceanography* 51 (2), 973–987.
- Atkinson, A., Siegel, V., Pakhomov, E., Rothery, P., Loeb, V., Ross, R.M., Quetin, L.B., Schmidt, K., Fretwell, P., Murphy, E.J., Tarling, G.A., Fleming, A.H., 2008. Oceanic circumpolar habitats of Antarctic krill. *Marine Ecology Progress Series* 362, 1–23.
- Azetsu-Scott, K., Syvitski, J.P.M., 1999. Influence of melting icebergs on distribution, characteristics and transport of marine particles in an East Greenland fjord. *Journal of Geophysical Research* 104 (C3), 5321–5328.
- Cefarelli, A.O., Vernet, M., Ferrario, M.E., 2011. Phytoplankton composition and abundance in relation to free-floating Antarctic icebergs. *Deep-Sea Research II* 58 (11–12), 1436–1450.
- Cherel, Y., Fontaine, C., Richard, P., Labat, J.-P., 2010. Isotopic niches and trophic levels of myctophid fishes and their predators in the Southern Ocean. *Limnology and Oceanography* 55 (1), 324–332.
- Collins, M.A., Xavier, J.C., Johnston, N.M., North, A.W., Enderlein, P., Tarling, G.A., Waluda, C.M., Hawker, E.J., Cunningham, N.J., 2008. Patterns in the distribution of myctophid fish in the northern Scotia Sea ecosystem. *Polar Biology* 31 (7), 837–851.
- Cook, A.J., Vaughan, D.G., 2010. Overview of areal changes of the ice shelves on the Antarctic Peninsula over the past 50 years. *The Cryosphere* 4 (1), 77–98.
- de Baar, H.J.W., de Jong, J.T.M., Bakker, D.C.E., Löscher, B.M., Veth, C., Bathmann, U., Smetacek, V., 1995. Importance of iron for plankton blooms and carbon dioxide drawdown in the Southern Ocean. *Nature* 373, 412–415.
- Donnelly, J., Sutton, T.T., Torres, J.J., 2006. Distribution and abundance of micronekton and macrozooplankton in the NW Weddell Sea: relation to a spring ice-edge bloom. *Polar Biology* 29, 280–293.

- Fisher, E.C., Kaufmann, R.S., Smith Jr., K.L., 2004. Variability of epipelagic macrozooplankton/micronekton community structure in the NW Weddell Sea, Antarctica (1995–1996). *Marine Biology* 144, 345–360.
- Hammer, W.M., Hammer, P.P., 2000. Behavior of Antarctic krill (*Euphausia superba*): schooling, foraging, and antipredatory behavior. *Canadian Journal of Fisheries and Aquatic Sciences* 57 (supplement 3), 192–202.
- Harbison, G.R., Campenot, R.B., 1979. Effects of temperature on the swimming of salps (Tunicata, Thaliacea): Implications for vertical migration. *Limnology and Oceanography* 24 (6), 1081–1091.
- Helly, J.J., Kaufmann, R.S., Stephenson Jr, G.R., Vernet, M., 2011. Cooling, dilution and mixing of ocean water by free-drifting icebergs in the Weddell Sea. *Deep-Sea Research II* 58 (11–12), 1346–1363.
- Holm-Hansen, O., Lorenzen, C., Homes, R., Strickland, J., 1965. Fluorometric determination of chlorophyll. *Journal du Conseil* 30, 3–15.
- Hosie, G.W., Cochran, T.G., Pauly, T., Beaumont, K.L., Wright, S.W., Kitchener, J.A., 1997. Zooplankton community structure of Prydz Bay, Antarctica, January - February 1993. Proceedings of the NIPR Symposium on Polar Biology 10, 90–133.
- Hubold, G., Hempel, I., Meyer, M., 1988. Zooplankton communities in the Southern Weddell Sea (Antarctica). *Polar Biology* 8 (3), 225–233.
- Joiris, C.R., 1991. Spring distribution and ecological role of seabirds and marine mammals in the Weddell Sea, Antarctica. *Polar Biology* 11, 415–424.
- Kaufmann, R.S., Fisher, E.C., Gill, W.H., King, A.L., Laubacher, M., Sullivan, B., 2003. Temporal patterns in the distribution, biomass and community structure of macrozooplankton and micronekton with Port Foster, Deception Island, Antarctica. *Deep-Sea Research II* 50 (10–11), 1765–1785.
- Kaufmann, R.S., Smith Jr., K.L., Baldwin, R.J., Glatts, R.C., Robison, B.H., Reisenbichler, K.R., 1995. Effects of seasonal pack ice on the distribution of macrozooplankton and micronekton in the northwestern Weddell Sea. *Marine Biology* 124 (3), 387–397.
- Kremer, P., Madin, L.P., 1992. Particle retention efficiency of salps. *Journal of Plankton Research* 14 (7), 1009–1015.
- Lancraft, T.M., Torres, J.J., Hopkins, T.L., 1989. Micronekton and macrozooplankton in the open waters near Antarctic ice edge zones (AMERIEZ1983 and 1986). *Polar Biology* 9 (4), 225–233.
- Lancraft, T.M., Hopkins, T.L., Torres, J.J., Donnelly, J., 1991. Oceanic micronektonic/macrozooplanktonic community structure and feeding in ice covered Antarctic waters during the winter (AMERIEZ 1988). *Polar Biology* 11 (3), 157–167.
- Lin, H., Rauschenberg, S., Hexel, C.R., Shaw, T.J., Twining, B.S., 2011. Free-drifting icebergs as sources of iron to the Weddell Sea. *Deep-Sea Research II* 58 (11–12), 1392–1406.
- Long, D.G., Ballantyne, J., Bertoia, C., 2002. Is the number of icebergs really increasing? *EOS. EOS Transactions of the American Geophysical Union* 83 (42) 469, 474.
- Meyer, M.A., El-Sayed, S.Z., 1983. Grazing of *Euphausia superba* Dana on natural phytoplankton populations. *Polar Biology* 1, 193–197.
- Neshyba, S., 1977. Upwelling by icebergs. *Nature* 267, 507–508.
- O'Brien, D.P., 1989. Analysis of the internal arrangement of individuals within crustacean aggregations (Euphausiacea, Mysidacea). *Journal of Experimental Marine Biology and Ecology* 128, 1–30.
- Opalinski, K.W., Maciejewska, K., Georgieva, L.V., 1997. Notes on food selection in the Antarctic krill, *Euphausia superba*. *Polar Biology* 17, 350–357.
- Pagès, F., Kurbjeweit, F., 1994. Vertical distribution and abundance of mesoplanktonic medusae and siphonophores from the Weddell Sea, Antarctica. *Polar Biology* 14, 243–251.
- Pagès, F., White, M.G., Rodhouse, P.G., 1996. Abundance of gelatinous carnivores in the nekton community of the Antarctic Polar Frontal Zone in summer 1994. *Marine Ecology Progress Series* 141 (1–3), 139–147.
- Pakhomov, E.A., Froneman, P.W., 2004. Zooplankton dynamics in the eastern Atlantic sector of the Southern Ocean during the austral summer 1997/1998-Part 2: Grazing impact. *Deep-Sea Research II*, 2617–2631.
- Pakhomov, E.A., Perissinotto, R., Froneman, P.W., 1999. Predation impact of carnivorous macrozooplankton and micronekton in the Atlantic sector of the Southern Ocean. *Journal of Marine Systems* 19, 47–64.
- Perissinotto, R., Pakhomov, E.A., 1998. The trophic role of the tunicate *Salpa thompsoni* in the Antarctic marine ecosystem. *Journal of Marine Systems* 17, 361–374.
- Perissinotto, R., Pakhomov, E.A., McQuaid, C.D., Froneman, P.W., 1997. In situ grazing rates and daily ration of Antarctic krill *Euphausia superba* feeding on phytoplankton at the Antarctic Polar Front and the Marginal Ice Zone. *Marine Ecology Progress Series* 160, 77–91.
- Quillfeldt, P., 2002. Seasonal and annual variation in the diet of breeding and non-breeding Wilson's storm-petrels on King George Island, South Shetland Islands. *Polar Biology* 25 (3), 216–221.
- Raiswell, R., Tranter, M., Benning, L.G., Siegert, M., De'ath, R., Huybrechts, P., Payne, T., 2006. Contributions from glacially derived sediment to the global iron (oxyhydr)oxide cycle: Implications for iron delivery to the oceans. *Geochimica et Cosmochimica Acta* 70, 2765–2780.
- Raiswell, R., Benning, L.G., Tranter, M., Tulaczyk, S., 2008. Bioavailable iron in the Southern Ocean: the significance of the iceberg conveyor belt. *Geochemical Transactions* 9, 7. doi:10.1186/1467-4866-9-7.
- Reid, K., Murphy, E.J., Loeb, V., Hewitt, R.P., 2002. Krill population dynamics in the Scotia Sea: variability in growth and mortality within a single population. *Journal of Marine Systems* 36, 1–10.
- Reid, K., Trathan, P.N., Croxall, J.P., Hill, H.J., 1996. Krill caught by predators and nets: differences between species and techniques. *Marine Ecology Progress Series* 140, 13–20.
- Ribic, C.A., Ainley, D.G., Fraser, W.R., 1991. Habitat selection by marine mammals in the marginal ice zone. *Antarctic Science* 3 (2), 181–186.
- Robison, B.H., Vernet, M., Smith, K.L., 2011. Algal communities attached to free-drifting icebergs. *Deep-Sea Research II* 58 (11–12), 1451–1456.
- Ross, R.M., Quetin, L.B., Haberman, K.L., 1998. Interannual and seasonal variability in short-term grazing impact of *Euphausia superba* in nearshore and offshore waters west of the Antarctic Peninsula. *Journal of Marine Systems* 17, 261–273.
- Ruhl, H.A., Ellena, J.A., Wilson, R.C., Helly, J.J., 2011. Seabird aggregation around free-drifting icebergs. *Deep-Sea Research II* 58 (11–12), 1497–1504.
- Sancetta, C., 1992. Primary production in the glacial North Atlantic and North Pacific oceans. *Nature* 360, 249–251.
- Scambos, T.A., Hulbe, C., Fahnestock, M., Bohlander, J., 2000. The link between climate warming and break-up of ice shelves in the Antarctic Peninsula. *Journal of Glaciology* 46 (154), 516–530.
- Schmidt, K., Atkinson, A., Petzke, K.-J., Voss, M., Pond, D.W., 2006. Protozoans as a food source for Antarctic krill, *Euphausia superba*: Complementary insights from stomach content, fatty acids, and stable isotopes. *Limnology and Oceanography* 51 (5), 2409–2427.
- Schodlok, M.P., Hellmer, H.H., Rohardt, G., Fahrbach, E., 2006. Weddell Sea iceberg drift: Five years of observations. *Journal of Geophysical Research* 111 (C06018). doi:10.1029/2004JC002661,2006.
- Scolardi, K.M., Daly, K.L., Pakhomov, E.A., Torres, J.J., 2006. Feeding ecology and metabolism of the Antarctic cydippid ctenophore *Callianira antarctica*. *Marine Ecology Progress Series* 317, 111–126.
- Schwarz, J.N., Schodlok, M.P., 2009. Impact of drifting icebergs on surface phytoplankton biomass in the Southern Ocean: Ocean colour remote sensing and in situ iceberg tracking. *Deep-Sea Research I* 56, 1727–1741.
- Shaw, T.J., Smith Jr, K.L., Hexel, C.R., Dudgeon, R., Sherman, A.D., Vernet, M., Kaufmann, R.S., 2011. 234Th-based carbon export around free-drifting icebergs in the Southern Ocean. *Deep-Sea Research II* 58 (11–12), 1384–1391.
- Sherlock, R.E., Reisenbichler, K.R., Bush, S.L., Osborn, K.J., Robison, B.H., 2011. Boundary layer zooplankton around free-drifting Antarctic icebergs. *Deep-Sea Research II* 58 (11–12), 1457–1468.
- Siegel, V., 1987. Age and growth of Antarctic Euphausiacea (Crustacea) under natural conditions. *Marine Biology* 96, 483–495.
- Smetacek, V., Klaas, C., Menden-Deuer, S., Rynearson, T.A., 2002. Mesoscale distribution of dominant diatom species relative to the hydrographical field along the Antarctic Polar Front. *Deep-Sea Research II* 49, 3835–3848.
- Smith Jr, K.L., Sherman, A.D., Shaw, T.J., Murray, A.E., Vernet, M., Cefarelli, A.O., 2011. Carbon export associated with free-drifting icebergs in the Southern Ocean. *Deep-Sea Research II* 58 (11–12), 1485–1496.
- Smith Jr, K.L., Robison, B.H., Helly, J.J., Kaufmann, R.S., Ruhl, H.A., Shay, T.J., Twining, B.S., Vernet, M., 2007. Free-drifting icebergs: Hot spots of chemical and biological enrichment in the Weddell Sea. *Science* 317, 478–482.
- Smith Jr, K.L., 2011. Free-drifting icebergs in the Southern Ocean: an overview. *Deep-Sea Research II* 58 (11–12), 1277–1284.
- Sørnes, T.A., Hosia, A., Båmstedt, U., Aksnes, D.L., 2008. Swimming and feeding in *Periphylla periphylla* (Scyphozoa, Coronatae). *Marine Biology* 153, 653–659.
- Stephenson Jr, G.R., Sprintall, J., Gille, S.T., Vernet, M., Helly, J.J., Kaufmann, R.S., 2011. Subsurface melting of a free-floating Antarctic iceberg. *Deep-Sea Research II* 58 (11–12), 1336–1345.
- Stuart, K.M., Long, D.G., 2011. Tracking large tabular icebergs using the SeaWinds scatterometer. *Deep-Sea Research II* 58 (11–12), 1285–1300.
- Sutherland, K.R., Madin, L.P., 2010. A comparison of filtration rates among pelagic tunicates using kinematic measurements. *Marine Biology* 157, 755–764.
- Veit, R.R., Hunt Jr, G.L., 1991. Broadscale density and aggregation of pelagic birds from a circumnavigational survey of the Antarctic Ocean. *The Auk* 108 (4), 790–800.
- Vernet, M., Sines, K., Chakos, D., Cefarelli, A.O., Ekern, L., 2011. Impacts on phytoplankton dynamics by free-drifting icebergs in the NW Weddell Sea. *Deep-Sea Research II* 58 (11–12), 1422–1435.
- Wiebe, P.H., Morton, A.W., Bradley, A.M., Backus, R.H., Craddock, J.E., Barber, V., Cowles, T.J., Flierl, G.R., 1985. New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. *Marine Biology* 87 (3), 313–323.
- Zar, J.H., 1999. *Biostatistical Analysis*, fourth edition Prentice-Hall, New Jersey 929 pp.