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## Effects of a rapidly receding ice edge on the abundance, age structure and feeding of three dominant calanoid copepods in the Weddell Sea, Antarctica

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**Abstract** Open-water, marginal-ice and in-ice zones were sampled in the Weddell Sea during November and December, 1993 in an effort to examine the influence of the early spring bloom on the diet and population structure of the three biomass dominant copepods: *Metridia gerlachei*, *Calanus propinquus*, and *Calanoides acutus*. The abundance of all three species in the upper 200 m was highest at stations in the open water, but individually, each species displayed a unique trend. *M. gerlachei*, which showed the least variability, was significantly more abundant in open water than in the marginal-ice zone. The abundance of *Calanus propinquus* was higher in open water than in the marginal-ice zone or in the ice. *Calanoides acutus* displayed the highest variability, with significant differences between all three ice-cover zones. Diet analysis revealed no significant differences in the number of food items within each ice-cover zone and diatoms were the most numerous item identified in the guts of all three species. However, *M. gerlachei* and *Calanus propinquus* also contained metazoan material, while *Calanoides acutus* did not. There were dramatic differences in the age composition of the species between the zones. Early copepodite stages of all three species predominated at the ice edge and in open water. Numbers of *M. gerlachei* adult females were roughly equivalent in all three zones while *Calanoides acutus* and *Calanus propinquus* adult females composed a higher fraction of the total population within the ice. These results compare well with life-history data compiled by other authors and reinforce the importance of the ice edge to bloom-dependent Antarctic zooplankton.

### Introduction

During the austral spring and summer the ecology of the seasonal ice zone in the Southern Ocean is dominated by the retreat of the pack ice, as the oceanic system experiences a rolling wave of increased primary productivity associated with the ice edge (Smith and Nelson 1985, 1986, 1990; Sullivan et al. 1988). The result is a frontal feature that poses a significant problem to the pelagic community in that primary consumers have a limited time during which food is abundant. The dynamics of the marginal ice zone (MIZ) affect microplankton community structure (Robins et al. 1995), mesozooplankton vertical distributions (Hopkins and Torres 1988; Robins et al. 1995), and trophic structure (Hopkins and Torres 1989). The retreat of the ice edge, along with its associated bloom, are pivotal events in the life-cycles of some Antarctic copepods.

The three dominant copepods south of the Polar Front in terms of biomass are *Calanoides acutus*, *Calanus propinquus*, and *Metridia gerlachei*. Hopkins and Torres (1988) found that they represented 47–56% of the mesozooplankton biomass in the MIZ of the western Weddell Sea. Each of the three has different foraging and life-history strategies. *Calanoides acutus* exhibits the most extreme adaptation to a polar environment in that late copepodite stages overwinter at depths of 500 m or more, remaining trophically inactive during this period. Molt-ing to adults and mating occur at diapause depth. Females then ascend into the upper 100 m to spawn, allowing development of younger stages to take place at the place and time of highest productivity (Andrews 1966; Marin 1988; Atkinson 1991; Bathmann et al. 1993; Lopez et al. 1993; Schnack-Schiel and Hagen 1994, 1995). *Calanus propinquus* has an intermediate life-cycle in which a portion of the population remains in surface waters throughout the year. Feeding continues during winter but metazoans and microheterotrophs appear to compose a greater portion of the diet. Mating and spawning occur during the productive period, but for a

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more protracted period than in *Calanoides acutus* (Marin 1988; Bathmann et al. 1993; Hopkins et al. 1993a, 1993b; Schnack-Schiel and Hagen 1994; Hagen and Schnack-Schiel 1996). Of the three species, *M. gerlachei* depends least on the spring bloom. Ontogenetic vertical migration is relatively weak, feeding occurs throughout the year, and the diet tends to be diverse throughout the year. Mating and spawning appear to be less closely coupled with the bloom, and it is possible that more than one generation is produced per year (Huntley and Escritor 1992; Schnack-Schiel and Hagen 1994; Metz and Schnack-Schiel 1995). Life-cycle data on *Calanus propinquus* and *M. gerlachei* show less clear patterns than those for *Calanoides acutus*. In all three species, it is unclear exactly how tightly coupled the timing is between reproduction and arrival of the bloom.

The research presented here was based upon a cruise of the M/V *Polar Duke* to the western Weddell Sea in November/December of 1993. The overall purpose of the cruise was to elucidate the effect of the receding ice edge on the entire pelagic community. The present study targeted the reproductive and trophic ecology of the three biomass-dominant copepods discussed above. Specifically, we addressed the following questions: how clear was the change in population and trophic structure across the ice edge? Is the ice-edge bloom a significant influence on species that do not rely solely on herbivory as a means of nutrition?

## Materials and methods

The cruise plan consisted of an initial transect along the marginal ice zone (Fig. 1). Following this, we moved north until out in ice-

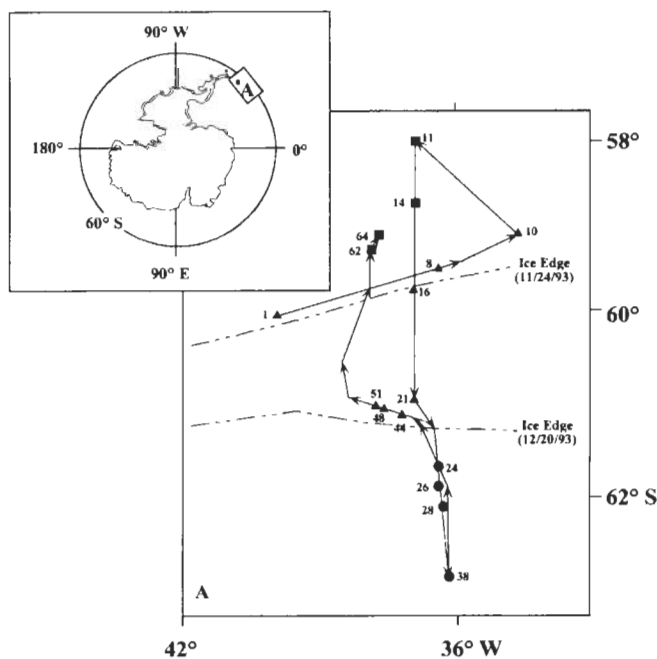


Fig. 1 Sampling locations. Open-water stations (■), ice-edge stations (▲), pack-ice stations (●)

free, low-chlorophyll water, and conducted a north to south transect from open water to within the pack ice. In addition, a series of stations were occupied in each of three distinct zones of ice cover (open water, ice edge, and within-ice) for a period of several days. At each station during the transects, the water column was profiled with a CTD rosette for salinity, temperature, and chlorophyll data. During the periods when residence was maintained in the distinct ice-cover zones, plankton was sampled with a plummet net and 30-l Niskin bottles. The plummet net is an opening/closing net deployed vertically, allowing for discrete depth sampling of the water column even within heavy ice cover. The mouth area was  $1 \text{ m}^2$  and the net mesh  $162 \mu\text{m}$ . Volumes filtered were calculated as the cross-sectional area of the net multiplied by the vertical distance sampled assuming 100% filtration efficiency.

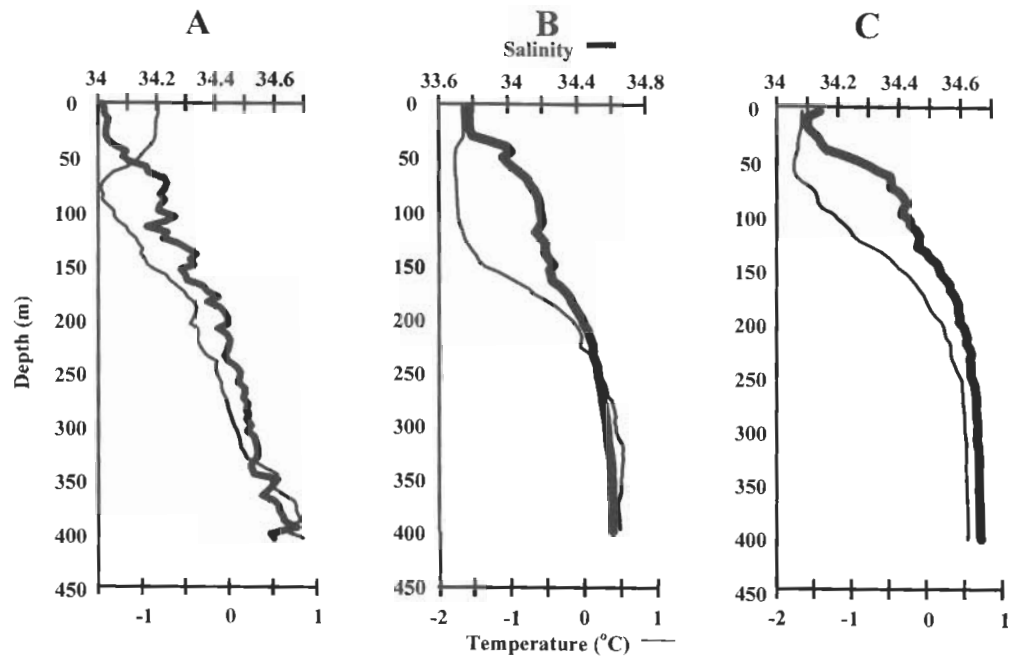
Within each ice-cover zone, the water column was sampled in six discrete depth zones (0–40, 40–100, 100–200, 200–400, 400–600, 600–1000 m). In addition, several deployments sampled the entire upper 200 m of the water column. The 0- to 200-m tows were primarily to collect material for physiological experiments on zooplankton, but data from those samples are included here. All plummet net samples were initially fixed in 5–7% buffered formalin and subsequently transferred to 50% isopropyl alcohol for storage and analysis. Plummet net data were used to obtain the abundance of the three biomass-dominant copepods: *Calanoides acutus*, *Calanus propinquus*, and *Metridia gerlachei*. Samples were subdivided in a Motoda box splitter to a fraction of 1/4 to 1/8 and the total numbers of each of the three species were enumerated by copepodite stage. Stage was determined by recording size distribution data for each species while performing total counts, with life stages being determined from distinct size peaks in these data. The mean life-stage of samples was calculated after Marin (1987). Size was converted to biomass using the length : biomass equations for each species presented by Franz (1988). All abundance and biomass data were tested using the general linear models procedure. The 30-l bottles were used for one vertical series in each ice-cover zone: samples were collected at depths of 0, 10, 20, 40, 80, 100, 150, 200, 400, 600, 800 and 1000 m. Niskin samples were filtered through  $28\text{-}\mu\text{m}$  gauze and used for counts of copepod nauplii.

Diet of each species was analyzed by light microscopy. Individuals were measured, their life-stage determined, and then guts were dissected out. Gut contents were spread on glass slides in a mixture of glycerol, water, and fuchsin acid stain. Food items were identified to lowest possible taxonomic level and counted at  $\times 400$  magnification using Nomarski DIC optics on a research-grade compound microscope. Each slide was transected 20 times, with the number of food items standardized to total coverslip area to give a measure of relative gut fullness between slides. No attempt was made to convert food items to biomass.

## Results

The CTD data suggested we were not impacted by the Weddell-Scotia confluence (Patterson and Sievers 1980) even at  $58^\circ\text{S}$  (three representative plots from each ice-cover zone are shown in Fig. 2). Therefore, we felt any differences we saw in abundance and population structure were not due to sampling of different water masses. The CTD casts also detected a meltwater lens ( $\sigma_t \leq 27.3$ ) between  $59^\circ$  and  $61^\circ\text{S}$  associated with the MIZ (Fig. 3). Peak chlorophyll biomass ( $2.5 \text{ mg m}^{-3}$ ,  $113 \text{ mg m}^{-2}$  integrated 0–40 m) was associated with this lens (Fig. 4). The pack ice had the lowest chlorophyll of the three zones ( $15 \text{ mg m}^{-2}$ ), while open-water stations were intermediate (mean =  $69 \text{ mg m}^{-2}$ ), indicating that our study area conformed to the classical model of primary productivity following a receding ice edge (Sullivan et al.

**Fig. 2** CTD data from three different stations along the N-S transect. **A** Station 11 at 58°S; **B** station 16 at 60°S; **C** station 38 at 62°S

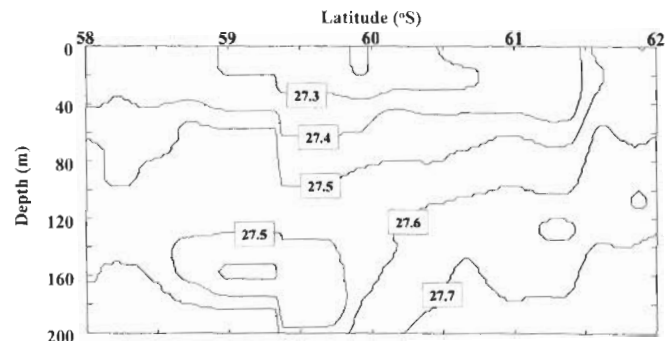


1988). Thus, data presented here as trends in copepod abundance and population structure from within the ice into the open water can be considered, not only as traversing a geographical area, but compressing a period of time as well.

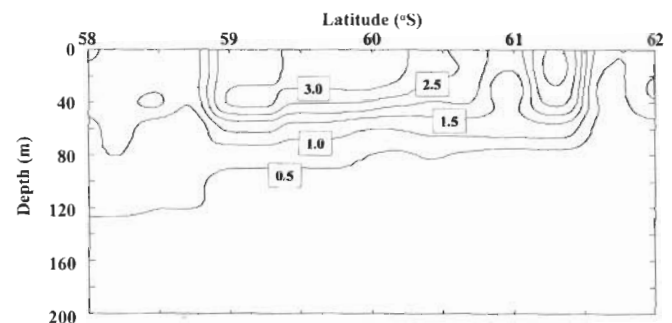
#### Species biomass and abundance comparisons

Combined, the abundance of the three species in the upper 200 m of the water column increased from within the ice to open water (Table 1, Fig. 5). *Calanoides acutus* was most abundant, with an average of 4.0 ind.  $m^{-3}$  over all three ice-cover zones. *Calanus propinquus* was least abundant (2.1 ind.  $m^{-3}$ ) and *M. gerlachei* was intermediate (3.7 ind.  $m^{-3}$ ). *Calanoides acutus* also had the highest biomass, averaging 1.2 mg  $m^{-3}$  (DW) per station in the upper 200 m. The average biomass per station of *Calanus propinquus* and *M. gerlachei* were 0.5 and 0.3 mg  $m^{-3}$  (Table 1, Fig. 6). Total naupliar counts were highest in the MIZ (2200 ind.  $m^{-3}$ ) while values were intermediate within the ice (1800 ind.  $m^{-3}$ ) and lowest in the open water (900 ind.  $m^{-3}$ ). These numbers were subjected to a Kruskal-Wallis test followed by a multiple comparison (Zar 1984) which suggested that their abundance in the MIZ was higher than that in the open water, but not statistically separable from in-ice abundances.

Analysis of abundance and biomass was limited primarily to the upper 200 m because this is where the majority of all three copepod populations reside during the productive season. It should be noted that the biomass and numbers of *M. gerlachei* in the upper 200 m may be somewhat misleading due to the vertical distribution of this species. The fraction of the population



**Fig. 3** North-south  $\sigma$ - $t$  transect



**Fig. 4** North-south chlorophyll transect (chlorophyll in  $mg\ m^{-3}$ )

sampled below 200 m was always at least 30% (30% in ice, 34% MIZ, 42% open water; Fig. 7). In contrast, only 4–16% of *Calanus propinquus* and 3–15% of *Calanoides acutus* individuals were sampled below 200 m

**Table 1** Abundance and biomass of copepods at each station in the upper 200 m (+ indicates present in number  $<0.1$  individuals  $m^{-3}$ )

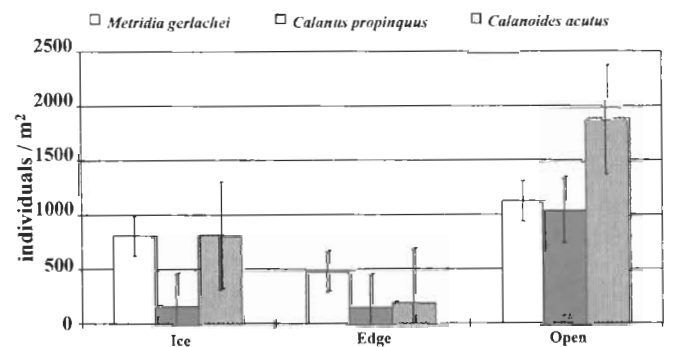
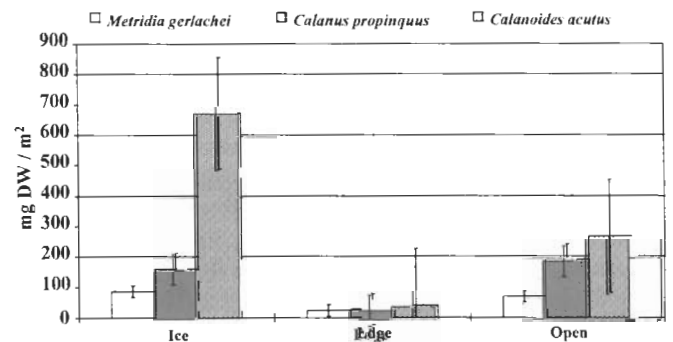
Ice-cover zone	Station number	<i>Metridia gerlachei</i>		<i>Calanus propinquus</i>		<i>Calanoides acutus</i>	
		Individuals $m^{-3}$	mg DW $m^{-3}$	Individuals $m^{-3}$	mg DW $m^{-3}$	Individuals $m^{-3}$	mg DW $m^{-3}$
Ice	24	4.9	0.5	0.8	0.8	2.9	2.9
	26	4.5	0.5	1.1	1.0	5.1	4.3
	28	2.7	0.3	0.6	0.6	4.2	2.9
	Zone mean	4.0	0.4	0.8	0.8	4.1	3.4
MIZ	8	0.4	+	0.1	+	0.1	+
	10	1.4	0.2	0.4	+	0.3	0.3
	16	7.2	0.1	1.4	0.2	1.1	0.1
	21	1.0	+	0.3	+	0.3	0.1
	44	2.3	0.1	0.6	+	0.8	0.2
	48	2.2	0.1	0.5	0.1	1.6	0.3
	51	2.4	0.3	2.3	0.5	2.8	0.4
Zone mean	2.4	0.1	0.8	0.1	1.0	0.2	
Open water	11	0.6	0.1	7.0	1.7	10	0.3
	14	11	0.8	4.1	0.7	7.0	1.2
	62	4.4	0.2	4.6	0.8	10	2.0
	64	6.6	0.4	5.4	0.7	10	1.9
	Zone mean	5.7	0.3	5.3	0.9	9.3	1.3
Overall mean		3.7	0.3	2.1	0.5	4.0	1.2

(Figs. 8, 9 respectively). In fact, when only the 0- to 1000-m plummet net series is considered, *M. gerlachei* becomes the numerical dominant (Table 2), although *Calanoides acutus* remains the biomass dominant.

### *Metridia gerlachei*

When subjected to multiple comparison analysis, *M. gerlachei* showed a significant difference in abundance (0–200 m) only between the MIZ and the open water (Fig. 5). There were no significant differences in biomass between the three zones in the upper 200 m (Fig. 6). However, the age composition did change with respect to ice cover. The mean life-stage (MLS) averaged 4.3 at pack-ice stations but dropped to 3.4 in the MIZ, and 3.1 in open water. This was due to an increase in early copepodite stages (CI–III). While the percentage of adults remained between 11% and 18%, the percentage of CI–III rose from 21% within the ice to 69% in the MIZ and 74% in open water (Fig. 10A). Fortunately, *Metridia lucens* adults were present in only two net samples (in extremely low numbers) so analysis of life-stage data for *M. gerlachei* was not complicated by the occurrence of a similar species. The vertical distribution of *M. gerlachei* changed as well. This species was located deeper in open water than within the ice (Fig. 7). It does appear that the early copepodite stages (CI–III) remain a depth zone above the middle copepodites and adults.

Diet analysis revealed diatoms as the most commonly identified food item (Table 3). Other items, such as tintinnids and silicoflagellates, occurred only rarely. Metazoan material was found in the guts of this species, but there was no trend in its occurrence in diets between ice-cover zones. Empty guts were infrequent,

**Fig. 5** Abundance of the three copepods in the upper 200 m by ice-cover zone**Fig. 6** Biomass of the three copepods in the upper 200 m by ice-cover zone

and only occurred within the ice or MIZ. A Kruskal-Wallis test failed to find any differences in the number of food items per gut between the different ice-cover zones.

*Calanus propinquus*

This species was more abundant in open water than within the ice and the MIZ (Fig. 5), while biomass

was significantly lower at the MIZ than either within the ice or in open water (Fig. 6). *Calanus propinquus* showed a stronger trend of decreasing age of the population between ice-cover zones than *M. gerlachei*.

Fig. 7 Vertical distribution of *Metridia gerlachei* life-stages by ice-cover zone

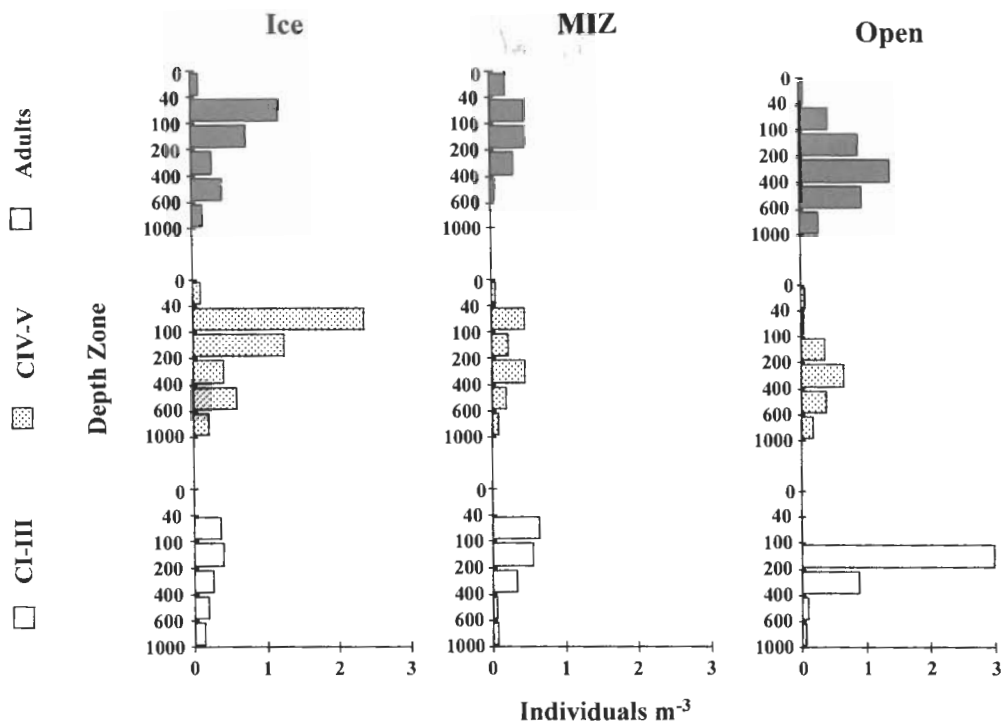
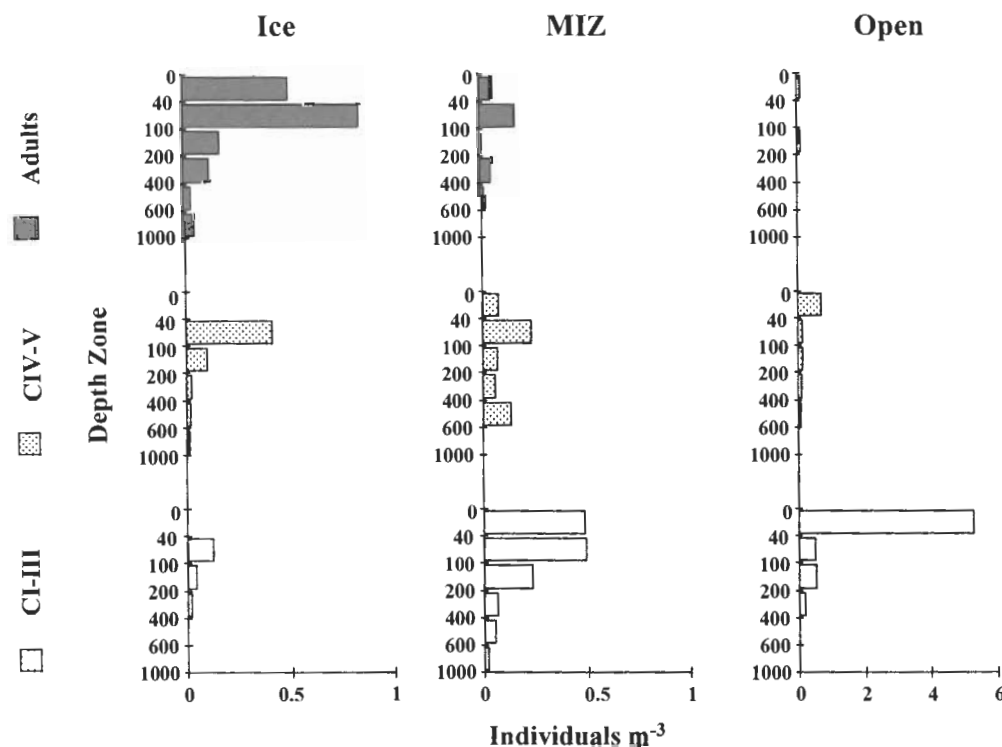


Fig. 8 Vertical distribution of *Calanus propinquus* life-stages by ice-cover zone

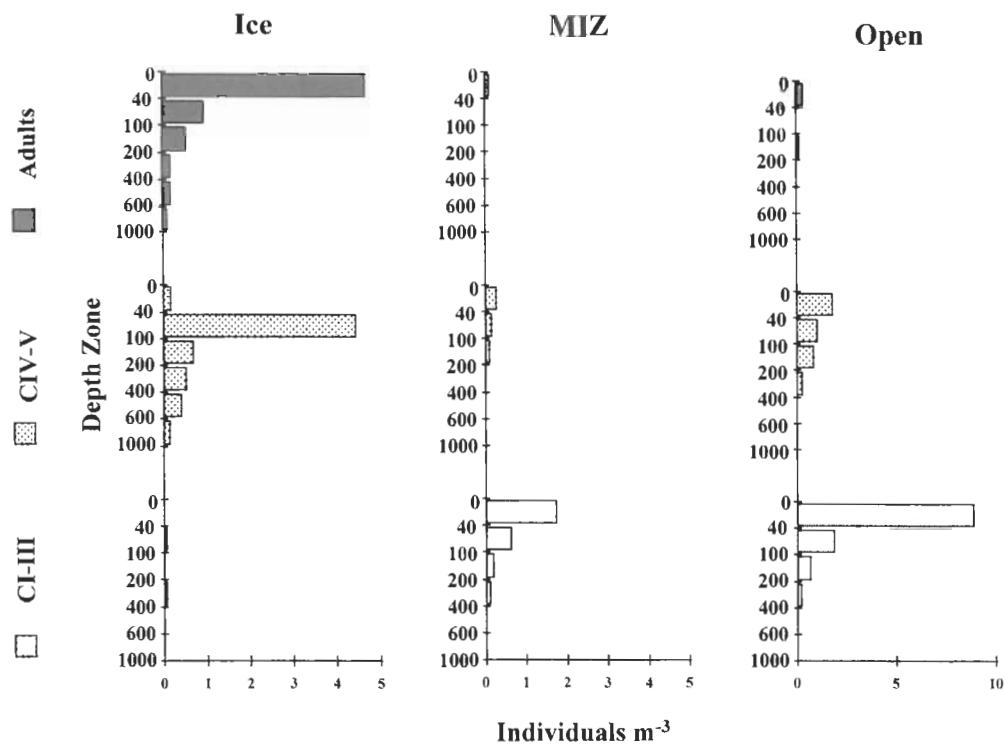


The MLS was 4.7 within the ice and only 2.6 and 2.4 in the MIZ and open water respectively. Unlike *M. gerlachei*, adults of *Calanus propinquus* composed less of the MIZ and open-water samples. While adults were 46% of the individuals within the ice, they were less than 5% in the MIZ and open-water stations (Fig. 10B). Meanwhile, the percentage of CI-III individuals increased from 19% to 84%. The drastic change in the age structure of this species made it difficult to compare vertical distributions between the different life-stages. However, both early and late copepodite stages were absent from the upper 40 m

within the ice (Fig. 8). In the MIZ the abundance modes for both groups were still found from 40 to 100 m, but individuals were present in the upper 40 m. At open-water stations, the abundance modes had moved into the upper 40 m.

Diatoms were the most commonly identified diet item (Table 3). This species also contained metazoan material, and there was no trend in its occurrence based on ice cover. Within the ice, 20% of the stomachs were empty, compared to none in the MIZ and 4% in open water. Despite this, there was no significant difference in the number of diet items between ice-cover zones.

**Fig. 9** Vertical distribution of *Calanoides acutus* life-stages by ice-cover zone

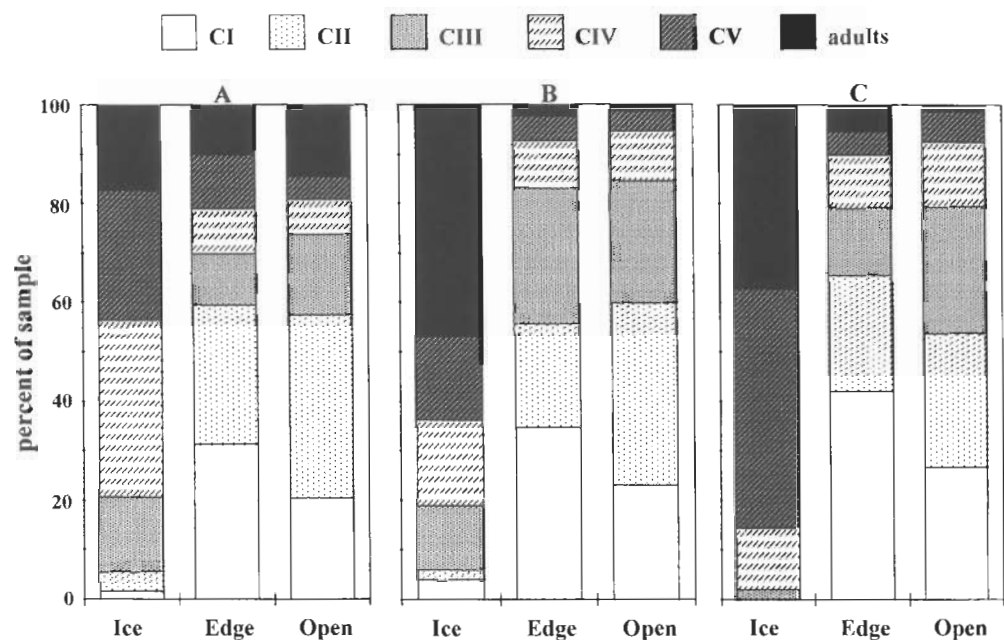


**Table 2** Abundance and biomass of copepods at each station from 0 to 1000 m

Ice-cover zone	Station number	<i>Metridia gerlachei</i>		<i>Calanus propinquus</i>		<i>Calanoides acutus</i>	
		Individuals m <sup>-3</sup>	mg DW m <sup>-3</sup>	Individuals m <sup>-3</sup>	mg DW m <sup>-3</sup>	Individuals m <sup>-3</sup>	mg DW m <sup>-3</sup>
Ice	24	1.4	0.1	0.2	0.2	0.7	0.7
	26	2.3	0.3	0.4	0.3	2.3	1.7
	28	1.6	0.1	0.2	0.2	1.4	0.9
	Zone mean	1.8	0.2	0.3	0.2	1.5	1.1
MIZ	48	1.2	0.1	0.3	0.1	0.4	0.1
	51	1.2	0.1	0.7	0.1	0.8	0.1
	Zone mean	1.2	0.1	0.5	0.1	0.6	0.1
Open	62	2.3	0.2	1.00	0.2	2.1	0.5
	64	3.5	0.3	1.4	0.2	2.4	0.5
	Zone mean	2.9	0.3	1.2	0.2	2.3	0.5
Overall mean		1.9	0.2	0.8	0.2	1.4	0.6

**Table 3** Categories of diet items and their frequency of occurrence within each ice-cover zone (OW open water)

	N	Empty	Diatoms	Dinoflagellates	Silicoflagellates	Tintinnids	Unidentified eukaryotes	Metazoan material
<i>Metridia gerlachei</i>	Ice	25	3	21	1		9	5
	MIZ	25	4	21			6	5
	OW	25		25	2	1	5	4
<i>Calanus propinquus</i>	Ice	25	5	20	2		13	4
	MIZ	25		25	3	1	9	3
	OW	25	1	24		1	14	5
<i>Calanoides acutus</i>	Ice	25	6	19	2		9	
	MIZ	25		25	1	1	4	
	OW	25		25			3	

**Fig. 10** Life-stages distributions of **A** *Metridia gerlachei*, **B** *Calanus propinquus* and **C** *Calanoides acutus* in the upper 200 m

### *Calanoides acutus*

This copepod exhibited the most distinct pattern in abundance with all three zones significantly different (Fig. 5). MIZ stations had the lowest abundance and open-water stations the highest. Biomass was also significantly different between each of the three zones and, like the abundance data, lowest values were in the MIZ. However, contrary to the abundance pattern, the highest biomass values were seen within the ice (Fig. 6). This discrepancy between the abundance and biomass data reflects the age structure of the population. The MLS consistently decreased moving from ice to MIZ to open water (5.2, 3.2 and 2.6 respectively). Adults females composed from 37% of the 0- to 200-m population within the ice but 1% in the open water while CI-III rose from only 2% within the ice to 79% in the MIZ and open water (Fig. 10C). No adult males were found. The vertical distribution data for *Calanoides acutus* showed middle copepodite

stages tended to be somewhat deeper than adults under the ice (Fig. 9). It should be noted that the mode for CIV-V is in the 40- to 100-m depth interval while that for adults is in the 0- to 40-m range. Additionally, 53% of the CIV-Vs were found below 100 m, as opposed to only 37% of the adults.

Diatoms were the most commonly identified diet item for this species as well; however, unlike *M. gerlachei* and *Calanus propinquus*, there was no occurrence of metazoan material (Table 3). Empty guts were found only within the ice samples; however, the Kruskal-Wallis test did not indicate any significant differences in number of diet items between the zones.

### Discussion

The primary hypothesis of the present study was that the rapidly receding ice edge was a vital event in the life-cycles of the three species considered. It was expected

that copepod populations would display the most winter-like characteristics within the ice and the most summer-like characteristics in the open water. Therefore we looked for the following changes moving along the space/time transect of Ice  $\Rightarrow$  MIZ  $\Rightarrow$  Open water:

1. Dietary shifts in *Calanus propinquus* and *M. gerlachei* (less omnivorous at the MIZ and open-water stations), as well as *Calanoides acutus* (trophically inactive within the ice).
2. Change in the vertical distribution of *Calanoides acutus* (ascent of the population).
3. Increased abundance of all three species (due to increase in juveniles in the population).
4. Proportionally more young life-stages present.

Of the three copepods, *M. gerlachei* has a life-cycle least specialized for the high latitudes (Schnack-Schiel and Hagen 1994, 1995; Atkinson 1998). It is, therefore, not surprising that the data for *M. gerlachei* show the least variability with respect to ice cover. The abundance of *M. gerlachei* in open water was higher than that at the MIZ, but the difference was not significant between the pack-ice and open-water stations. The greatest difference was in the number of early copepodite stages (CI-III) found in the pack ice and in open water (29% and 74% respectively). Atkinson and Shreeve (1995) saw a similar shift in population structure across an ice edge in the Bellingshausen Sea, except that adults dominated their ice-bound stations while late copepodite stages dominated ours. In the Bransfield Strait, Huntley and Escritor (1992) found a similar shift in age structure over a very similar time period. Schnack-Schiel and Hagen (1994, 1995) reported age structure of this species in the summer as being dominated by CIs and later stages (CIV, adults) in the southeastern Weddell Sea. Furthermore, by autumn, early copepodite stages composed the vast majority (~80%) of their samples. The November/December life-stage data from our samples within the ice most closely resemble their October/November samples, while within the MIZ and open water we obtained very similar percentages of early copepodite stages (about 70%) to what they reported in summer and autumn (Schnack-Schiel and Hagen 1994, 1995). Therefore, the change in the age structure of the population we observed appeared to be compressed relative to their data. This is not surprising as theirs was a seasonal study, while we attempted the equivalent of compressing time by sampling across a rapidly receding ice edge.

The predominance of diatoms in the guts of *M. gerlachei* has been reported previously. An investigation in the western Weddell Sea in autumn (Hopkins and Torres 1989) placed *M. gerlachei* in a feeding guild characterized by 97% of the identifiable food items being composed of phytoplankton. The results presented here certainly do not contradict that assignment. It should be noted, however, that the type of diet analysis used in the present study did not detect small, non-thecate diet items. This may be especially important in

the case of *M. gerlachei*, as Atkinson (1995) and Atkinson et al. (1996) suggested such motile organisms are important in the diet of this species.

*Calanus propinquus* resembles *M. gerlachei* in that a portion of the population remains in surface waters and stays trophically active in winter (Bathmann et al. 1993; Hopkins et al. 1993a; Spiridonov and Kosobokova 1997). However, there were some differences in the present data to suggest that the seasonal surge in primary productivity was more important to *Calanus propinquus* than to *M. gerlachei*. First, stations in the open water had a higher abundance of *Calanus propinquus* than those within the ice or MIZ. The copepodite stage data indicated this was due to the addition of younger individuals to the population. Second, the life-stage percentages showed some differences. For example, while the percentage of adults of *M. gerlachei* varied little, that of *Calanus propinquus* dropped dramatically. Within the ice, adult *Calanus propinquus* made up 46% of the samples, but the percentage dropped to 3% at the MIZ and remained low at open-water stations. Data from Atkinson and Shreeve (1995) showed adults were never abundant and early copepodite stages were always prevalent, regardless of ice cover in the Bellingshausen Sea in the spring. Compared to Schnack-Schiel and Hagen (1994, 1995), the age structure within the ice most closely resembles their October/November data, while the MIZ and open-water samples most closely resemble their January/February data.

There was no difference in gut fullness based on food item counts for *Calanus propinquus* among the different zones. It is worth noting that the majority of empty stomachs were found in the pack ice (five vs only one between the other two zones). Perhaps more significant than the gut fullness data was the lack of a trend in the amount of metazoan material in the guts like that found by Hopkins and Torres (1989).

Of the three species, *Calanoides acutus* displayed the strongest trends. The low abundance of copepodites and adults at the ice edge was counterintuitive. However, the fact that naupliar counts were higher at the MIZ than within the other two ice regimes may provide an explanation for this, as *Calanoides acutus* may have been present at the ice edge in high numbers, but as naupliar stages. The dramatic increase in abundance in the open water was due to the addition of younger individuals into the population. The presence of copepodite stages CIV, CV and adults of this species in the upper 200 m even within the ice is significant as it indicates that the summer ascent of this seasonal vertical migrant has already taken place.

Based on the lack of males occurring in surface waters, Marin (1988) proposed a scenario in which *Calanoides acutus* females mate at depth and then ascend into surface waters in the spring. In the southeastern Weddell Sea, Schnack-Schiel et al. (1991) primarily found mature females made the vertical ascent, which agrees with Marin's model. Therefore, the large numbers of CIV and CV individuals in the upper 200 m

in our study were not expected. Since no males were present in our samples, there was no evidence to suggest mating was taking place in the upper 200 m. One possible explanation is the suggestion that *Calanoides acutus* may, at times, have a 2-year life-cycle (Atkinson 1991; Atkinson et al. 1997). Annual variability in production may make it difficult for an entire cohort to complete their life-cycle within 1 year. Indeed, there is evidence for failure of the classical MIZ bloom to develop at times (Jacques and Panouse 1991; Jochem et al. 1995). In this scenario, the late copepodite stages found in surface waters would have overwintered at an earlier stage, and therefore would not have been ready to spawn at the onset of spring. Such individuals could presumably overwinter twice before reproducing. Other studies have found *Calanoides acutus* concentrating in the upper 200 m at least a full month later than our data indicate (Schnack-Schiel et al. 1991; Schnack-Schiel and Hagen 1994, 1995), a discrepancy possibly due to the difference in latitude between their sampling locations and ours (72–73°S vs 58–62°S).

Life-stage data for *Calanoides acutus* were similar to those of *Calanus propinquus*. The percentage of adults dropped from 37% within the ice to 1% in the open water. The dramatic difference in the age structure of the samples explains the higher biomass of *Calanoides acutus* within the ice despite a higher numerical abundance at open-water stations. There was a greater percentage of young (CI–III) *Calanus propinquus* than *Calanoides acutus* within the ice, indicating that the species may have started breeding earlier than *Calanoides acutus*, which has been found before (Schnack-Schiel et al. 1991; Atkinson and Shreeve 1995).

Lack of a trend in diet composition across ice-cover zones was expected for *Calanoides acutus*. Previous studies have shown that this species remains trophically inactive in winter rather than showing a shift in diet (Schnack-Schiel et al. 1991; Hopkins et al. 1993a; Atkinson 1995). The herbivorous nature of its diet was consistent with previous results (Hopkins and Torres 1989; Hopkins et al. 1993b) and highlights the specialized nature of its lifestyle. The most important result of the diet study was the fact that individuals were feeding within the ice at all. Despite the proportionally higher occurrence of empty stomachs within the pack ice, and the total lack of empty stomachs in the MIZ or in open water, there was no statistically significant trend in gut fullness for *Calanoides acutus* across the three ice zones. This indicated trophically that it had already partly switched to spring/summer mode, and that “grazable” phytoplankton was available in the water column under the ice. This is not surprising considering that chlorophyll values within the ice were higher than those typically reported in winter (Garrison et al. 1993; Scharek et al. 1994), and around the range suggested to be at the threshold for egg production (Lopez et al. 1993).

Regarding our basic hypotheses, the diet data were of little help in highlighting the importance of the receding ice edge. Although there was a trend in the number of

empty stomachs in the ice for *Calanoides acutus* and *Calanus propinquus*, there was no significant trend in the number of identifiable diet items for any species. Additionally, *M. gerlachei* and *Calanus propinquus* did not display any compositional trends (e.g. more metazoan material within the ice compared to the edge and open water). The type of diet analysis performed for this study requires caution to be used in making any statements regarding diet changes related to ice cover, especially if there are no apparent trends in the readily observable (e.g. diatoms) food items. There is growing data on the importance of small soft-bodied forms of eukaryote plankton in the diets of copepods. Such items cannot usually be effectively detected by microscopic examination of gut contents. Additionally, sample size was small, and collection was limited to the late afternoon (and therefore may miss any trends induced by a diel feeding pattern). However, the higher occurrence of empty stomachs within the ice for *Calanus propinquus* and *Calanoides acutus* is worth noting. Vertical distribution data were also of little help in the case of *Calanoides acutus*, the strongest seasonal migrant, as this species was in the epipelagial in all three ice-cover zones.

Abundance data favored accepting the basic hypotheses. The two species which are affected most by season, *Calanus propinquus* and *Calanoides acutus*, showed trends of increasing abundance from within the ice to open water. *M. gerlachei*, which has shown the least variability in seasonal studies, did not show as pronounced a change in abundance with ice cover (within-ice and open-water values not significantly different). The strongest evidence for importance of the receding ice edge came from the life-stage data. Adult females of all three species were well represented within the ice. The change in age structure of the *Calanus propinquus* and *Calanoides acutus* samples across the MIZ was dramatic, with adults of both species all but disappearing. Even the *M. gerlachei* population became younger across the ice-cover cline. Other studies have shown a similar shift in age structure, but generally over a longer period of time.

In conclusion, the data support the idea that the receding ice edge is an important feature in the life-cycles of these organisms. Despite the fact our ice stations obviously did not represent winter conditions, we were still able to detect changes in the abundance and age structure of the populations. These changes also seemed to show a gradation of being strongest in *Calanoides acutus* and weakest in *M. gerlachei*. Our data fit in very well with previous work on the life-cycles of these copepods, and further demonstrate that the response to the seasonal production pulse may occur over fairly small time and space scales.

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## References

- Andrews KJH (1966) The distribution and life-history of *Calanoides acutus* (Giesbrecht). *Discovery Rep* 34:117–162
- Atkinson A (1991) Life cycles of *Calanoides acutus*, *Calanus similimus*, and *Rhincalanus gigas* (Copepoda: Calanoida) within the Scotia Sea. *Mar Biol* 109:79–91
- Atkinson A (1995) Omnivory and feeding selectivity in five copepod species during spring in the Bellingshausen Sea, Antarctica. *ICES J Mar Sci* 52:385–396
- Atkinson A (1998) Life cycle strategies of epipelagic copepods in the Southern Ocean. *J Mar Systems* 15:289–311
- Atkinson A, Shreeve RS (1995) Response of the copepod community to a spring bloom in the Bellingshausen Sea. *Deep Sea Res* 42:1291–1311
- Atkinson A, Shreeve RS, Pakhomov E, Priddle J, Blight SP, Ward P (1996) Zooplankton response to a phytoplankton bloom near South Georgia, Antarctica. *Mar Ecol Prog Ser* 144:195–210
- Atkinson A, Schnack-Schiel SB, Ward P, Marin V (1997) Regional differences in the life cycle of *Calanoides acutus* (Copepoda: Calanoida) within the Atlantic Sector of the Southern Ocean. *Mar Ecol Prog Ser* 150:99–111
- Bathmann UV, Makarov RR, Spiridonov VA, Rohardt G (1993) Winter distribution and overwintering strategies of common Antarctic copepod species (Crustacea, Calanoida) in the Weddell Sea. *Polar Biol* 13:333–346
- Franz HG (1988) Vernal abundance, structure and development of epipelagic copepod populations of the eastern Weddell Sea (Antarctica). *Polar Biol* 9:107–114
- Garrison DL, Buck KR, Gowing MM (1993) Winter plankton assemblage in the ice-edge zone of the Weddell and Scotia Seas: composition, biomass and spatial distributions. *Deep Sea Res* 40:311–338
- Hagen W, Schnack-Schiel SB (1996) Seasonal lipid dynamics in dominant Antarctic copepods: energy for overwintering or reproduction? *Deep Sea Res* 43:139–158
- Hopkins TL, Torres JJ (1988) The zooplankton community in the vicinity of the ice edge, western Weddell Sea, March 1986. *Polar Biol* 9:79–87
- Hopkins TL, Torres JJ (1989) Midwater food web in the vicinity of a marginal ice zone in the western Weddell Sea. *Deep Sea Res* 36:543–560
- Hopkins TL, Laneract TM, Torres JJ, Donnelly J (1993a) Community structure and trophic ecology of zooplankton in the Scotia Sea marginal ice zone in winter (1988). *Deep Sea Res* 40:81–105
- Hopkins TL, Ainley DG, Torres JJ, Laneract TM (1993b) Trophic structure in open waters of the marginal ice zone in the Scotia-Weddell confluence region during spring (1983). *Polar Biol* 13:389–397
- Huntley ME, Escritor F (1992) Ecology of *Metridia gerlachei* Giesbrecht in the western Bransfield Strait, Antarctica. *Deep Sea Res* 39:1027–1055
- Jacques G, Panouse M (1991) Biomass and composition of size fractionated phytoplankton in the Weddell-Scotia Confluence area. *Polar Biol* 11:315–328
- Jochem FJ, Mathot S, Queguiner B (1995) Size-fractionated primary production in the open Southern Ocean in austral spring. *Polar Biol* 15:381–392
- Lopez MDG, Huntley ME, Lovette JT (1993) *Calanoides acutus* in Gerlache Strait, Antarctica. I. Distribution of late copepodite stages and reproduction during late spring. *Mar Ecol Prog Ser* 100:153–165
- Marin V (1987) The oceanographic structure of the eastern Scotia Sea. IV. Distribution of copepod species in relation to hydrography in 1981. *Deep Sea Res* 34:105–121
- Marin V (1988) Qualitative models of the life cycles of *Calanoides acutus*, *Calanus propinquus*, and *Rhincalanus gigas*. *Polar Biol* 8:439–446
- Metz C, Schnack-Schiel SB (1995) Observations on carnivorous feeding in Antarctic calanoid copepods. *Mar Ecol Prog Ser* 129:71–75
- Patterson SL, Sievers HA (1980) The Weddell-Scotia Confluence. *J Phys Oceanogr* 10:1584–1610
- Robins DB, Harris RP, Bedo AW, Fernandez E, Fileman TW, Harbour DS, Head RN (1995) The relationship between suspended particulate material, phytoplankton and zooplankton during the retreat of the marginal ice zone in the Bellingshausen Sea. *Deep Sea Res* 42:1137–1158
- Scharek R, Smetacek V, Fahrbach E, Gordon LI, Rohardt G, Moore S (1994) The transition from winter to early spring in the eastern Weddell Sea, Antarctica: plankton biomass and composition in relation to hydrography and nutrients. *Deep Sea Res* 41:1231–1250
- Schnack-Schiel SB, Hagen W (1994) Life cycle strategies and seasonal variations in distribution and population structure of four dominant calanoid copepod species in the eastern Weddell Sea, Antarctica. *J Plankton Res* 16:1543–1566
- Schnack-Schiel SB, Hagen W (1995) Life-cycle strategies of *Calanoides acutus*, *Calanus propinquus*, and *Metridia gerlachei* (Copepoda: Calanoida) in the eastern Weddell Sea, Antarctica. *ICES J Mar Sci* 52:541–548
- Schnack-Schiel SB, Hagen W, Mizdalski F (1991) Seasonal comparison of *Calanoides acutus* and *Calanus propinquus* (Copepoda: Calanoida) in the southeastern Weddell Sea, Antarctica. *Mar Ecol Prog Ser* 70:17–27
- Smith WO Jr, Nelson DM (1985) Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. *Science* 227:163–166
- Smith WO Jr, Nelson DM (1986) Importance of ice edge phytoplankton production in the Southern Ocean. *Bioscience* 36:351–357
- Smith WO Jr, Nelson DM (1990) Phytoplankton growth and new production in the Weddell Sea marginal ice zone in the austral spring and autumn. *Limnol Oceanogr* 35:809–821
- Spiridonov VA, Kosobokova KN (1997) Winter ontogenetic migrations and the onset of gonad development in large dominant calanoid copepods in the Weddell Gyre (Antarctica). *Mar Ecol Prog Ser* 157:233–246
- Sullivan CW, McClain CR, Comiso JC, Smith WO Jr (1988) Phytoplankton standing crops within an Antarctic ice edge assessed by satellite remote sensing. *J Geophys Res* 93:12487–12498
- Zar JH (1984) *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, NJ