Polar Biol (2001) 24: 724–728
DOI 10.1007/s003000100273

ORIGINAL PAPER

Sigrid B. Schnack-Schiel · Gerhard S. Dieckmann
Rolf Gradinger · I.A. Melnikov · Michael Spindler
David N. Thomas

Meiofauna in sea ice of the Weddell Sea (Antarctica)

Accepted: 23 March 2001 / Published online: 8 June 2001
© Springer-Verlag 2001

Abstract Sea-ice meiofauna was studied during various cruises to the Weddell Sea. Foraminifers dominate (75%) the sea-ice community in terms of numerical abundance while turbellarians dominate (45%) in terms of biomass. Distribution of organisms is patchy and varies considerably between cruises but also between sampling sites within one cruise. The bulk of the meiofauna is concentrated in the lowest parts of the sea ice, especially during winter and autumn. However, in porous summer sea ice, sympagic organisms also occur in high densities in upper and intermediate layers of sea ice. Proto- and metazoans associated with Antarctic sea ice include organisms actually living in sea ice, as well as those on the underside of floes and in the underlying water. The sea-ice habitat serves as a feeding ground, as well as an important nursery for juveniles, providing energy-rich food resources. The ice also constitutes a shelter from predators.

This paper presents results of the Midterm Symposium of the SCAR programme "Ecology of the Antarctic Sea Ice Zone" (EASIZ). The manuscript was edited by W. Arntz and A. Clarke.

S.B. Schnack-Schiel (✉) · G.S. Dieckmann
Alfred-Wegener-Institut für Polar-
und Meeresforschung,
Postfach 120161,
27515 Bremerhaven, Germany
E-mail: sschiel@awi-bremerhaven.de

R. Gradinger · M. Spindler
Institut für Polarökologie, Universität Kiel,
24148 Kiel, Germany

I.A. Melnikov
P.P. Shirshov Institute of Oceanology,
Russian Academy of Sciences,
Moscow 117857, Russia

D.N. Thomas
School of Ocean Sciences,
University of Wales-Bangor,
Menai Bridge, Anglesey,
LL59 5EY, UK

Introduction

The annual cycle of sea-ice growth and melt plays a pivotal role in polar ecosystems. Productivity, behaviour, ecophysiology and life-history patterns of a diverse group of organisms ranging from bacteria to whales are governed by this phase separation in the pelagic zone. The complexity of sea ice as a habitat, or rather range of habitats, is now well documented (e.g. Horner 1985) and microalgae are known to reach very high standing stocks (e.g. Ackley et al. 1979; Dieckmann et al. 1998). However, the heterotrophic component of sea-ice assemblages, other than bacteria, has received less attention. This is especially true for the metazoans. High algal biomass in sea ice clearly serves as the basis of a dynamic food web within and associated with the ice, particularly during winter when phytoplankton in the water column is scarce. Protozoans and metazoans associated with Antarctic sea ice include heterotrophic flagellates, ciliates, foraminifers, turbellarians and copepods (e.g. Spindler et al. 1990; Gradinger 1999). Nematodes have for the first time been found in an Antarctic pack-ice sample (Blome and Riemann 1999). Many organisms appear to spend their entire life-cycle, or at least a major part thereof, within the sea ice (e.g. Dahms et al. 1990; Schnack-Schiel et al. 1995; Tanimura et al. 1996). The sea-ice peripheries or ice/water interface, which include nooks and crannies, larger gaps and enclosures, as well as floe edges, represent a tremendous surface area for algal growth. These zones are frequented by larger grazers, particularly krill and amphipods, which feed directly on ice algae (e.g. Richardson and Whitaker 1979; Marschall 1988; Stretch et al. 1988; Daly 1990). The sea ice is an important nursery ground for juveniles of many species, providing an abundance of food as well as shelter from predators. It therefore plays a significant role in the survival of overwintering zooplankton. Recent studies have shown that even porous summer sea ice may act as an important refuge for life-history stages of several organisms (Thomas et al. 1998).

Table 1 Weddell Sea studies selected for analysis

	Date	Ship	References
ANT III/3	Jan/Feb 1985	Polarstern	Spindler et al. (1990); Schnack-Schiel et al. (1995)
ANT V/3	Oct/Dec 1986	Polarstern	Spindler et al. (1990); Schnack-Schiel et al. (1995)
ANT VIII/2	Sep/Oct 1989	Polarstern	Gradinger (1999)
ANT IX/3	Jan/Mar 1991	Polarstern	Gradinger (1999)
ANT X/3	Apr/May 1992	Polarstern	Schnack-Schiel et al. (1995); Gradinger (1999)
ISW-1	Feb/May 1992	Drift station	Menshenina and Melnikov (1995)
ANT XV/3	Jan/Mar 1997	Polarstern	Schnack-Schiel et al. (in press)

The objective of this study was to summarize results obtained during various studies in the Weddell Sea and to show that the meiofauna is a significant component of sea-ice biota.

Materials and methods

Sampling was carried out during several expeditions to the Weddell Sea (Table 1). Ice cores were drilled with a 7.5-cm or 10-cm-diameter ice auger and subsequently cut into subsections of between 1 and 20 cm length. The ice was melted after addition of 200 ml 0.2-μm filtered seawater per 1 cm core length (Garrison and Buck 1986). After complete melting, the volume was determined and ice meiofauna was concentrated over 20 μm gauze. The meiofauna (here defined as heterotrophs > 20 μm) was identified and organisms counted alive under a dissecting microscope immediately afterwards. Heterotrophic flagellates, although occurring frequently in sea ice, were not enumerated during all Weddell Sea cruises and hence are not included in this study. Under-ice sampling was carried out with an NIPR-I net (Fukuchi et al. 1979), a pump (Schnack-Schiel et al. 1995) or by scuba-diving (Menshenina and Melnikov 1995). All samples were preserved in 2–5% formaldehyde. Copepods were identified and counted in the entire samples or in subsamples (1/10–1/100) depending on the numbers. Biomass (expressed as carbon) was estimated according to Gradinger (1999). For further information of the sampling procedure and analyses of the samples, see Spindler et al. (1990), Menshenina and Melnikov (1995) and Gradinger (1999).

Results and discussion

Foraminifers dominated the sea-ice meiofauna by numbers (75%), ciliates, turbellarians, harpactoid and calanoid copepods making up between 4 and 19% (Fig. 1). However, in terms of carbon biomass, turbellarians were dominant (45%), followed by copepods (calanoids and harpacticoids each 20%). In contrast to Arctic sea ice, rotifers have not been recorded in the Antarctic (Gradinger 1999) while nematodes have only been seen once (Blome and Riemann 1999).

Data from different cruises have shown the occurrence of organisms in sea ice to be highly variable (Tables 2, 3, 4), but not necessarily attributable to seasonal changes. Even during the same cruise, abundances were patchy and differed between sampling sites, which is reflected in the high ranges observed. Similar spatial variations of sympagic Antarctic organisms have been described by other authors (e.g. Garrison and Close 1993; Scott et al. 1994; Swadling et al. 1997; Schnack-Schiel et al. 1998).

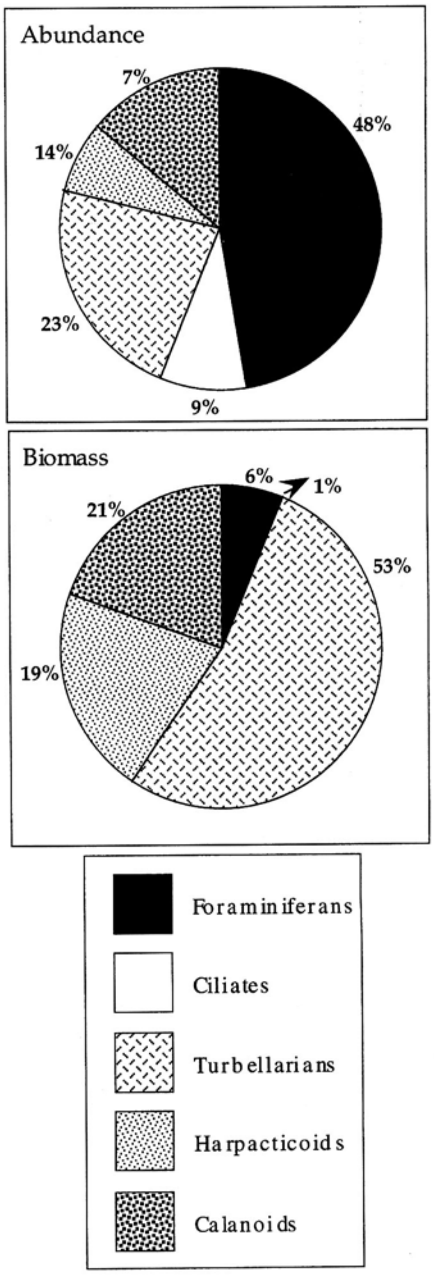

Fig. 1 Relative contribution of ice meiofauna taxa to mean abundance and biomass

The largest proportion of Antarctic sea ice is annual ice, resulting in the loss of organisms to the water when it melts in summer. The organisms therefore undergo a pelagic phase during their life-cycle. Ice formation and

Table 2 Summary of ice thickness and mean integrated chlorophyll *a* standing stock

	Year	Month	No. of cores	Average core length (cm)	Range of core length (cm)	Mean integrated Chl *a* (mg m^{-2})	Range of mean integrated Chl *a* (mg m^{-2})
ANT VIII	1989	Oct/Dec	32	75	21–170	4.17	0.14–18.40
ANT V	1986	Sep/Oct	29	216	190–270	5.48	0.01–35.43
ANT III	1985	Jan/Feb	13	209	80–285	131.66	5.90–435.3
ANT IX	1991	Jan/Mar	11	113	67–174	24.60	0.76–77.34
ANT XV	1997	Jan/Mar	17	107	16–224	3.87	0.31–26.79
ANT X	1992	Apr/May	17	58	20–180	7.95	0.08–32.24

Table 3 Mean integrated abundance of sea-ice meiofauna (– not counted)

Cruise	Foraminiferans		Ciliates		Turbellarians		Calanoid copepods		Harpacticoid copepods	
	Ind. × 10^3 m^{-2}	Range	Ind. × 10^3 m^{-2}	Range	Ind. × 10^3 m^{-2}	Range	Ind. × 10^3 m^{-2}	Range	Ind. × 10^3 m^{-2}	Range
ANT VIII	14.83	0–89	1.74	0–10	3.02	0–45	0.61	0–7	4.65	0–49
ANT V	47.85	0–440	10.36	0–67	–	–	2.02	0–21	0.32	0–2
ANT III	39.23	0–159	2.02	0–26	–	–	0.02	0–0.2	5.62	0–67
ANT IX	11.69	0–62	7.13	0.5–19	5.38	0–20	21.98	0.2–124	10.17	0–97
ANT XV	–	–	–	–	–	–	0.24	0–2	3.60	0–29
ANT X	33.5	0–383	–	–	34.17	0–436	2.13	0–20	26.68	0–226

Table 4 Mean integrated biomass of sea-ice meiofauna (– not counted)

Cruise	Foraminiferans		Ciliates		Turbellarians		Calanoid copepods		Harpacticoid copepods	
	mg C m^{-2}	Range	mg C m^{-2}	Range	mg C m^{-2}	Range	mg C m^{-2}	Range	mg C m^{-2}	Range
ANT VIII	0.46	0–3	0.02	0–0.1	1.18	0–17	0.55	0–8	1.79	0–15
ANT V	1.48	0–14	0.11	0–0.7	–	–	4.01	0–42	0.17	0–1
ANT III	1.22	0–5	0.02	0–0.3	–	–	0.02	0–0.2	3.37	0–40
ANT IX	0.36	0–2	0.08	0–0.2	2.09	0–8	8.38	0.01–44	2.51	0–24
ANT XV	–	–	–	–	–	–	3.2	0–33	0.93	0–9
ANT X	1.04	0–12	–	–	20.5	0–261	2.74	0–17	8.49	0–69

organism-incorporation or migration into an already existing ice cover transfer organisms between habitats with extremely different environmental constraints. Hence, the sympagic community must be able to tolerate a wide range of rapidly changing environmental conditions. The intricate sea-ice structure comprising ice crystals and brine channels forms a labyrinth of pockets and tubes ranging in diameters from a few micrometres to several centimetres (Weissenberger et al. 1992). The volume and degree of branching of the brine channels vary with temperature and ice texture. Temperature and salinity of the ice near the ice/water interface are similar to those of the underlying water (e.g. Bartsch 1989). This is one reason why the bulk of sympagic organisms frequents the peripheries of the sea ice, where living conditions are more benign (Hoshiai and Tanimura 1986; Schnack-Schiel et al. 1995). Figure 2 shows an example of the distribution within ice at two stations in the Weddell Sea in late winter where the meiofauna was concentrated in the lowest regions of ice floes. However, ice algae as well as heterotrophic organisms also occur in upper and intermediate layers of sea ice (Bartsch 1989; Schnack-Schiel et al. 1995). This is especially true in porous summer sea ice where brine channels and pockets are larger (Fig. 3). The higher temperatures result in a phase transition in permeability, permitting movement and exchange of seawater, as well as organisms, throughout the ice (Golden et al. 1998). This is in agreement with results from the Bellingshausen and Amundsen Seas, where peak abundances occurred in rotten slush layers flooded with seawater, and hence were closely associated with higher nutrient and dense algal concentrations (Schnack-Schiel et al. 1998; Thomas et al. 1998).

Strong interactions between the ice biota and pelagic animals exist during periods of complete ice coverage. The high algal biomass at the ice/water interface clearly serves as a food source for the diverse heterotrophic organisms. Many specialized metazoans begin to feed on ice algae during late winter and early spring when phytoplankton in the water column is scarce. These include amphipods and euphausiids, which have been recorded in high numbers during winter, spring and autumn at the underside of ice floes (e.g. Richardson and Whitaker 1979; Marschall 1988; Menshenina and Melnikov 1995; Melnikov and Spiridonov 1996). Many amphipods as-

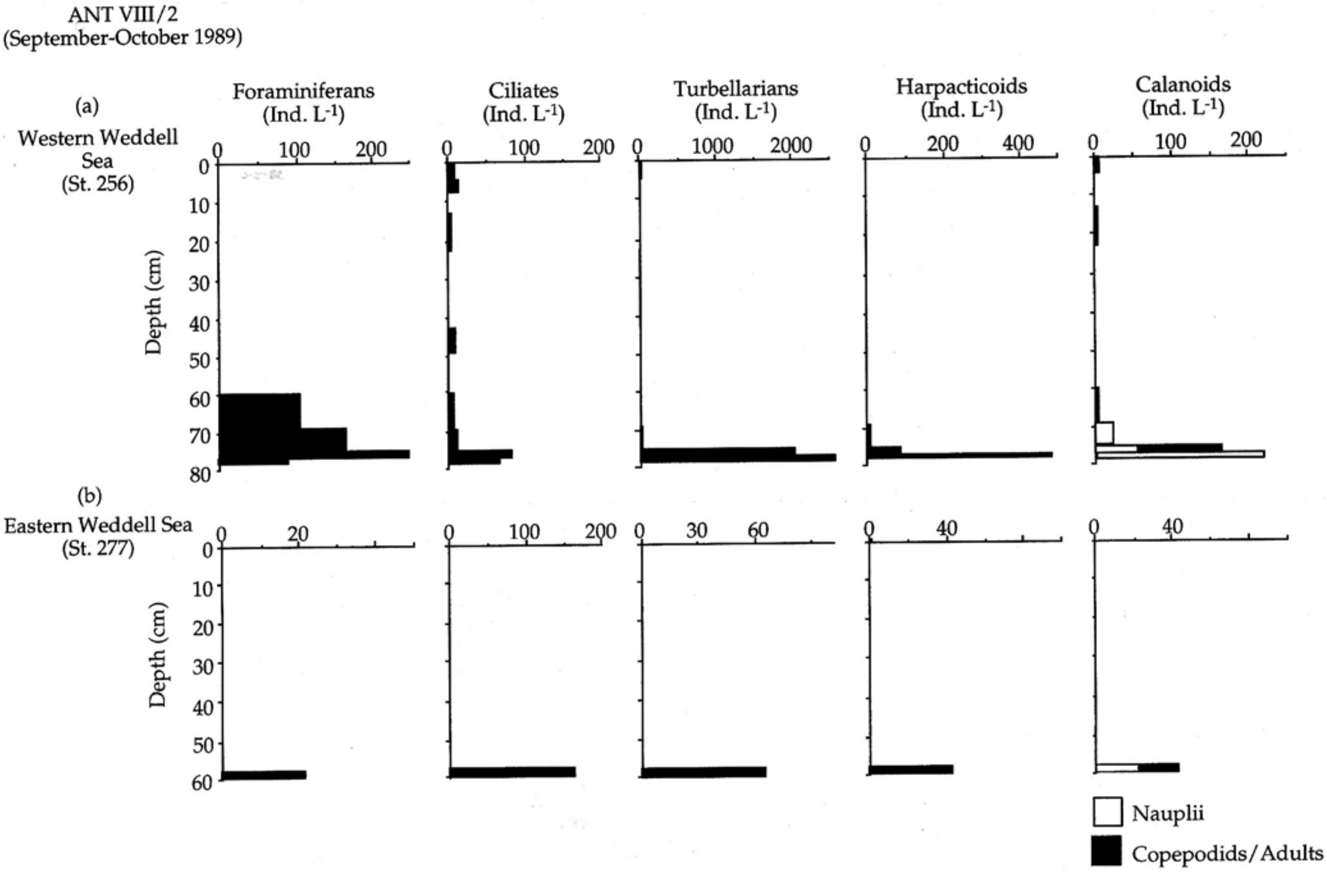

Fig. 2a, b Depth distribution of ice meiofauna taxa in sea-ice cores in late winter (September/October 1989) in the Weddell Sea

sociated with Antarctic sea ice are benthic species that appear to seasonally colonize the undersides of the floes from the benthos below. Moving along the bottom of the ice, they feed directly on the bottom community and use brine channels and pressure ridges between the floes as shelter against possible predators such as fish and birds (Richardson and Whitaker 1979).

Many sympagic heterotrophs live permanently or temporarily within the sea ice or at the ice/water interface. For example, the two dominant ice-associated copepod species in the Weddell Sea, *Drescheriella glacialis* and *Stephos longipes* (Dahms et al. 1990; Kurbjeweit et al. 1993; Schnack-Schiel et al. 1995; Günther et al. 1999), appear to differ in their life-cycle strategies. The harpacticoid, *D. glacialis*, seems to spend most of its life in the ice (Dahms et al. 1990). In contrast, the life-cycle of the calanoid, *S. longipes*, is strongly associated with the seasonal fluctuation of sea-ice cover. In late winter/early spring and autumn, when sea ice predominates,

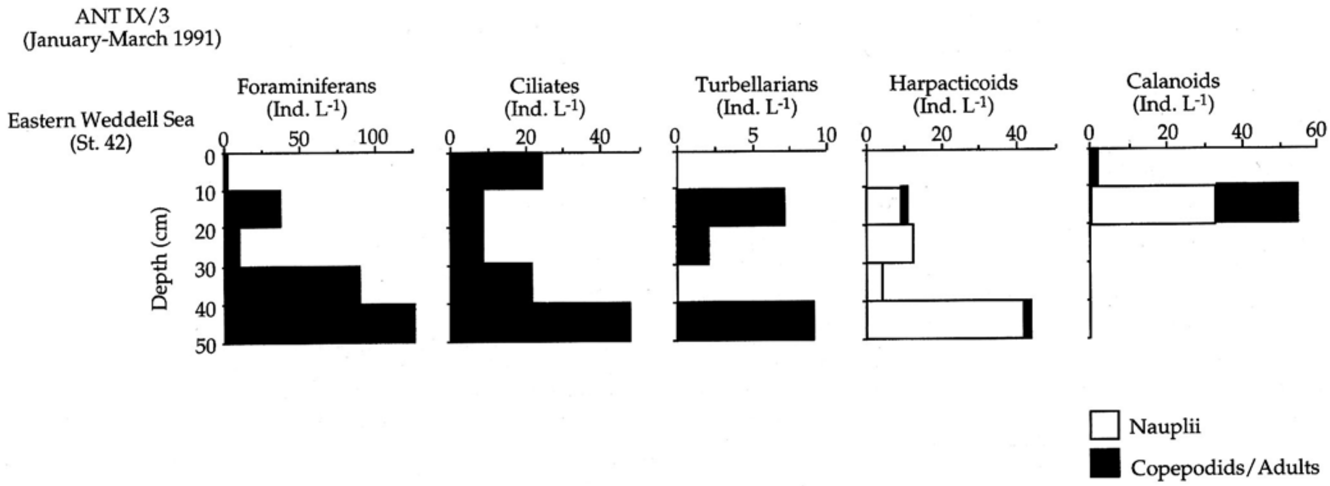

Fig. 3 Depth distribution of ice meiofauna taxa in a sea-ice core in summer (January/March 1991) in the eastern Weddell Sea

S. longipes was seldom found in the water column, whereas high numbers occurred in the sea ice and in the ice/water interface (Menshenina and Melnikov 1995; Schnack-Schiel et al. 1995). In summer, when ice cover was minimal, *S. longipes* was very abundant in the water column particularly in the surface layers. According to Schnack-Schiel et al. (1995), *S. longipes* seems to have two alternative strategies for overwintering: a young population overwinters in and just below the sea ice, while an older population migrates deep into the water column and may reach the sea bed. At some stations in the Weddell Sea, the calanoid species *Paralabidocera antarctica*, a typical sympagic species in east Antarctic coastal areas (Hoshiai and Tanimura 1986; Tanimura et al. 1996), may also reach high concentrations in the sea ice and in platelet-ice layers. Platelet layers underlying fast ice adjacent to ice shelves generally attain high algal standing stocks (e.g. Arrigo et al. 1995) and, hence, are an important food source for herbivorous zooplankton over the continental shelf.

The seasonal ice melt in spring/summer has a pronounced effect on biological processes as ice algae are released to the water column where they seed phytoplankton blooms or sink to the sea bed. Ice algae also provide an important food source for a variety of heterotrophic organisms in the water column (Garrison and Mathot 1996). By release of faecal pellets to the water, the zooplankton serves as mediator for particulate organic matter from the sea ice to the water column and contributes to the particle flux in ice-covered seas.

Acknowledgements This is contribution no. 1812 of the Alfred-Wegener-Institut für Polar- und Meeresforschung, Bremerhaven.

References

Ackley SF, Buck KR, Taguchi S (1979) Standing crop of algae in the sea ice of the Weddell Sea region. Deep Sea Res 26A: 269–281

Arrigo KR, Dieckmann GS, Gosselin M, Robinson DH, Fritsen CH, Sullivan CW (1995) A high resolution study of the platelet ecosystem in McMurdo Sound, Antarctica: biomass, nutrient and production profiles within a dense microalgal bloom. Mar Ecol Prog Ser 127:255–268

Bartsch A (1989) Die Eisalgenflora des Weddellmeeres (Antarktis): Artenzusammensetzung und Biomasse sowie Ökophysiologie ausgewählter Arten. Ber Polarforsch 63:109

Blome D, Riemann F (1999) Antarctic sea ice nematodes, with description of *Geomonhystera glaciei* sp. nov. (Monhysteridae). Mitt Hamb Zool Mus Inst 96:15–20

Dahms HU, Bergmann M, Schminke HK (1990) Distribution and adaptations of sea ice inhabiting Harpacticoida (Crustacea, Copepoda) of the Weddell Sea (Antarctica). Mar Ecol 11: 207–226

Daly KL (1990) Overwinter development, growth and feeding of larval *Euphausia superba* in the Antarctic marginal ice zone. Limnol Oceanogr 35:1564–1576

Dieckmann GS, Eicken H, Haas C, Garrison DL, Gleitz M, Lange M, Nöthig E-M, Spindler M, Sullivan CW, Thomas DN, Weissenberger J (1998) A compilation of data on sea ice algal standing crop from the Bellingshausen, Amundsen, and Weddell Seas from 1983 to 1994. Antarct Res Ser 73:85–92

Fukuchi M, Tanimura A, Hoshiai T (1979) "NIPR-I": a new plankton sampler under sea ice . Bull Plankton Soc Jpn 26: 104–109

Garrison DL, Buck KR (1986) The biota of Antarctic pack ice in the Weddell Sea and Antarctic Peninsula regions. Polar Biol 10:211–219

Garrison DL, Close AR (1993) Winter ecology of the sea-ice biota in Weddell Sea pack ice. Mar Ecol Prog Ser 96:17–31

Garrison DL, Mathot S (1996) Pelagic and sea ice microbial communities. Antarct Res Ser 70:155–172

Golden KM, Ackley SF, Lytle VI (1998) The percolation phase transition in sea ice. Science 282:2238–2240

Gradinger R (1999) Integrated abundance and biomass of sympagic meiofauna in Arctic and Antarctic pack ice. Polar Biol 22:169–177

Günther S, George KH, Gleitz M (1999) High sympagic metazoan abundance in platelet layers at Drescher-Inlet, Weddell Sea, Antarctica. Polar Biol 22:82–89

Horner R (1985) Sea ice biota. CRC Press, Boca Raton, Fla

Hoshiai T, Tanimura A (1986) Sea ice meiofauna at Syowa Station, Antarctica. Mem Natl Inst Polar Res Spec Issue 44:118–124

Kurbjeweit F, Gradinger R, Weissenberger J (1993) The life cycle of *Stephos longipes* – an example for cryopelagic coupling in the Weddell Sea (Antarctica). Mar Ecol Prog Ser 98:255–262

Marschall P (1988) The overwintering strategy of Antarctic krill under the pack-ice of the Weddell Sea. Polar Biol 9:129–135

Melnikov IA, Spiridonov VA (1996) Antarctic krill under perennial sea ice in the western Weddell Sea. Antarct Sci 8:323–329

Menshenina LL, Melnikov IA (1995) Under-ice zooplankton of the western Weddell Sea. Proc NIPR Symp Polar Biol 8:126–138

Richardson MG, Whitaker TM (1979) An Antarctic fast-ice food chain: observations on the interaction on the amphipod *Pontogeneia antarctica* Chevreux with ice-associated micro-algae. Br Antarct Surv Bull 47:107–115

Schnack-Schiel SB, Thomas D, Dieckmann GS, Eiken H, Gradinger R, Spindler M, Weissenberger J, Mizdalski E, Beyer K (1995) Life cycle strategy of the Antarctic calanoid copepod *Stephos longipes*. Prog Oceanogr 36:45–75

Schnack-Schiel SB, Thomas D, Dahms HU, Haas C, Mizdalski E (1998) Copepods in Antarctic sea ice. Antarct Res Ser 73:173–182

Schnack-Schiel SB, Thomas D, Haas C, Dieckmann GS, Alheit R (in press) The occurrence of the copepods *Stephos longipes* (Calanoida) and *Drescheriella glacialis* (Harpacticoida) in summer sea ice in the Weddell Sea, Antarctica. Antarct Sci

Scott P, McMinn A, Hosie G (1994) Physical parameters influencing diatom community structure in eastern Antarctic sea ice. Polar Biol 14:507–517

Spindler M, Dieckmann GS, Lange MA (1990) Seasonal and geographical variations in sea ice community structure of the Weddell Sea, Antarctica. In: Kerry KR, Hempel G (eds) Antarctic ecosystems, ecological change and conservation. Springer, Berlin Heidelberg New York, pp 129–135

Stretch JJ, Hamner PP, Hamner WM, Michel WC, Cook J, Sullivan CW (1988) Foraging behavior of Antarctic krill *Euphausia superba* on sea ice microalgae. Mar Ecol Prog Ser 44:131–139

Swadling KM, Gibson JAE, Ritz DA, Nichols PD (1997) Horizontal patchiness in sympagic organisms of the Antarctic fast ice. Antarct Sci 9:399–406

Tanimura A, Hoshiai T, Fukuchi M (1996) The life cycle strategy of the ice-associated copepod *Paralabidocera antarctica* (Calanoida, Copepoda), at Syowa Station, Antarctica. Antarct Sci 8:257–266

Thomas DN, Lara RJ, Haas C, Schnack-Schiel SB, Dieckmann GS, Kattner G, Nöthig EM, Mizdalski E (1998) Biological soup within decaying summer sea ice in the Bellingshausen Sea. Antarct Res Ser 73:161–171

Weissenberger J, Dieckmann GS, Gradinger R, Spindler M (1992) Sea ice: a cast technique to examine and analyze brine pockets and channel structure. Limnol Oceanogr 37:179–183