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Horizontal patchiness in sympagic organisms of the Antarctic fast ice

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Abstract: Patchiness in the horizontal distribution of sympagic organisms was studied at an Antarctic coastal site during autumn. A hierarchical sampling design (nested ANOVA) was used to assess variation in the biota on scales from metres to kilometres. Metazoan abundance, chlorophyll concentration and salinity were measured in 54 sea ice cores. The metazoan fauna was dominated by nauplii of the copepod *Paralabidocera antarctica* (6×10^4 to 4×10^5 m^{-2}). Other copepods present included *Stephos longipes*, *Oncaea curvata*, *Oithona similis*, *Ctenocalanus citer*, and unidentified harpacticoid copepods. Chlorophyll *a* concentrations were generally much higher than values recorded at other sites at the same time of the year, reaching a maximum of 78 mg m^{-2}. Metazoan abundances did not correlate strongly with chlorophyll or salinity. Significant variability in abundance of *P. antarctica* and *O. similis*, and chlorophyll concentration occurred at the scale of kilometres, whereas salinity and other metazoan abundances were not significantly variable at any of the scales examined. Considerable variation was evident at scales of less than one metre.

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Introduction

The study of spatial and temporal variation in organisms in nature often forms the basis for posing questions and hypotheses about important ecological processes occurring at the individual, population and community levels (see reviews by Barry & Dayton 1991, Levin 1992). While temporal variation in organisms is often observed, studies specifically aimed at unravelling spatial patterns have become common only recently (e.g. Chapman *et al.* 1995, Harvey & Miller 1996, Thomson *et al.* 1996). In comparison with more accessible habitats, such as temperate forests and intertidal areas, ecological studies of Antarctic sea ice systems are in their infancy. Attempts to calculate the contribution from sea ice to annual Antarctic primary production (e.g. Knox 1990, Legendre *et al.* 1992), for example, are hindered both by lack of data from seasons other than late spring/summer and by lack of comprehensive geographical coverage.

The heterogeneous nature of the Antarctic sea ice environment is the result of complex interactions between such factors as ice structure, light penetration, temperature and salinity gradients, nutrient regimes and water circulation. Large scale seasonal changes in the environment, especially the annual cycle of growth and decay of sea ice and the extreme seasonality in light and temperature at high latitudes, strongly influence the biology of organisms which depend on sea ice for part or all of their life cycles (sympagic organisms, Horner *et al.* 1992). Furthermore, localized differences, such as thickness of snow cover on the ice, will affect recruitment and subsequent survival of sympagic populations. Abundance and distribution of sympagic biota have been shown to vary on scales from days (Melnikov 1995) to years (Hoshiai 1985), and from less than one metre (Spindler & Dieckmann 1986, Eicken *et al.* 1991) to many kilometres (Garrison & Close 1993, Scott *et al.* 1994). However, a systematic approach to quantifying spatial variation in sea ice is rare and Spindler (1994) notes that ice cores for study have generally been taken at random during different times and at different locations.

This paper discusses a study designed to examine patchiness in sympagic biota at scales from metres to kilometres. Quantifying spatial variation is important because:

a) it provides a framework within which discrete samples of the type taken with ice corers can be interpreted in relation to their near surroundings;

b) it increases confidence in the extrapolation of data from a few cores to large scale production, and other, estimates; and

c) it permits a cost-benefit analysis of those scales at which sampling effort is best directed.

Materials and methods

Study site and experimental design

Horizontal patchiness in sea ice biota was examined in the fast ice near Australia's Davis Station, East Antarctica (68°35'S, 77°58'E; Fig. 1) on 17 April 1994. Fast ice in the area is annual, persisting for up to 11 months of each year and usually reaching maximum thickness in mid November. Once formed, the ice is held in place by numerous offshore islands. Breakout generally does not occur until December or January, when the internal ice structure has destabilized sufficiently to be broken up by wind and wave action. Ice at the study site had broken out on 23 December 1993 and began reforming in early March 1994, growing at an average rate of 1 cm d^{-1} for the next two months (C. Blobel, personal communication 1994). There was no snow cover on the sea ice until the end of April 1994.

The hierarchical sampling design incorporated four spatial scales, ranging from less than one metre to several kilometres (Fig. 2). The advantages of hierarchical sampling designs are that they enable assessment of patchiness over multiple spatial scales (Kotliar & Wiens 1990, Lindegarth *et al.* 1995), and the partitioning of variances associated with each scale allows for unconfounded comparisons between the variables at any of the chosen scales (Morrisey *et al.* 1992). At the largest scale, three Locations, each 1 km apart, were selected in areas that appeared to be typical of the sea ice offshore from Davis. Within each Location, three Sites of 20 m diameter were placed so that they were at least 100 m apart. Two Quadrats (2 m x 2 m in area), at least 10 m apart, were nested within each Site. Finally, for each Quadrat, three replicate ice cores were collected, 0.5–1 m apart. All factors (Location, Site, Quadrat) in the analysis were random.

The linear model used for this analysis was:

$$Y_{ijk} = \beta_o + \beta_1 L_i + \beta_2 S(L)_{j(i)} + \beta_3 Q(S(L))_{k(j(i))} + e_{ijkl} \quad (1)$$

where: Y_{ijk} is the variable under consideration (e.g. chlorophyll *a*, metazoans, salinity), β_o is the overall mean, $\beta_1 L_i$ is the effect of the i^{th} Location, $\beta_2 S_{j(i)}$ is the effect of the j^{th} Site nested within Location, $\beta_3 Q_{k(j(i))}$ is the effect of the k^{th} Quadrat nested within Site within Location, and e_{ijkl} represents individual error associated with the cores themselves (e.g. microhabitat differences).

Sampling methods and processing of samples

Sea ice cores were collected over an 8 h period using a 76 mm diameter motorized SIPRE corer. On the day of collection the air temperature was *c.* -15°C and the day was clear and sunny. The 54 cores were wrapped in opaque black plastic immediately on collection, and transported to Davis, where they were stored at -20°C until further processing within three weeks of sampling date. Cores were stored horizontally to prevent leaching of brine from the ice. Algae in stored ice cores can continue to photosynthesize at very low light levels and temperatures (A. McMinn, personal communication

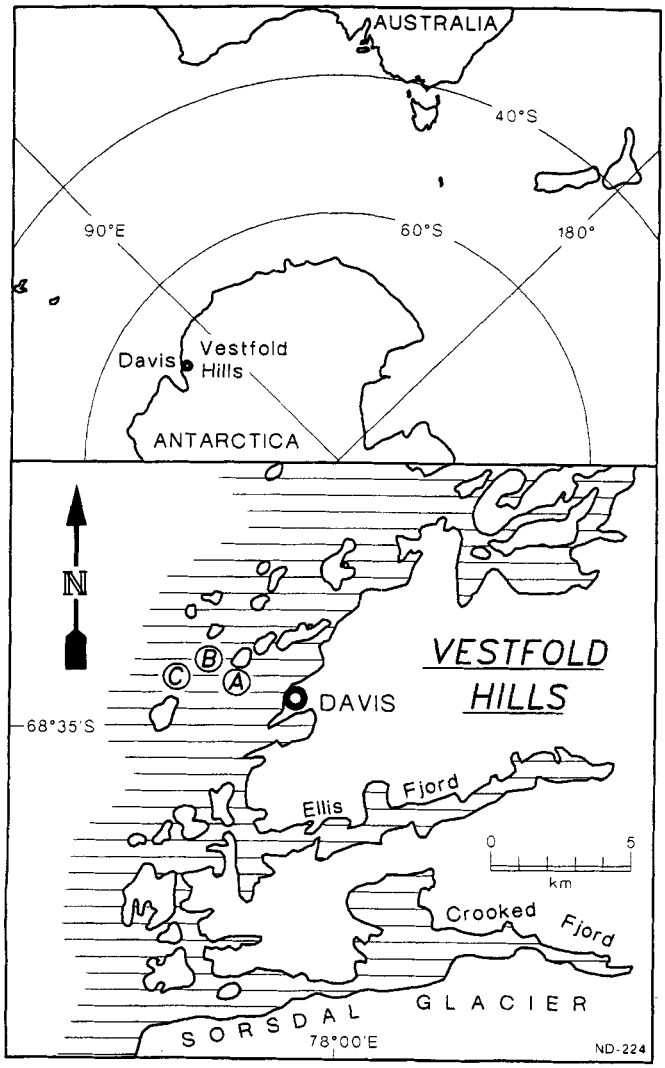

Fig. 1. Map of study site (68°35'S, 77°58'E) showing Locations A, B and C.

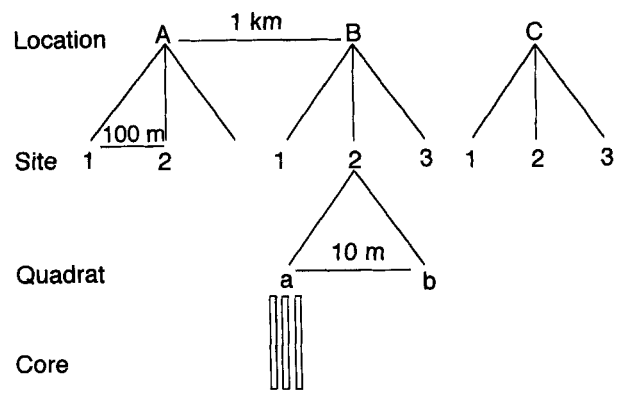

Fig. 2. Hierarchical sampling design used in study.

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1996), so variable storage times might have affected chlorophyll readings. As there was no correlation between chlorophyll concentration and length of storage, it was believed that storage-related effects were negligible. Loss of the fragile bottom ice community is possible when sampling with a SIPRE corer (Horner *et al.* 1992). However, a distinct, 2–4 cm thick, dark brown layer at the bottom of each core suggested that cores were being collected intact. The thickness of the sea ice through each hole and the depth of the water column (Humminbird Echosounder) at each site were recorded.

In the laboratory, entire cores were melted in 5 l opaque plastic containers at less than 8°C. Each core yielded between 1800–2000 ml of water on melting. As cores were to be subsampled for salinity measurements, they were not melted into prefiltered seawater, a procedure suggested by Garrison & Buck (1986) to prevent the loss of soft-bodied protists through osmotic stress. Therefore, it is possible that chlorophyll concentrations measured in this study were somewhat underestimated. However, chain-forming diatoms dominate the ice algal community offshore from Davis (A. McMinn, personal communication 1996) so, as all cores were processed in the same manner, it is believed that the trends in chlorophyll concentrations shown below are reflections of true differences between the ice cores. Metazoans, which form a large part of this study, were unlikely to have been affected by the lack of additional seawater.

The melted water from each core was mixed, then subsampled for salinity and chlorophyll measurements, and metazoan counts. Density of the salinity samples was measured at 20°C (to ± 0.00001 kg m^{-3}) using an Anton Paar DMA55 density meter, and salinity calculated using the following equation:

$$S = -2085.6 + 2776.6 \times \rho_{20} - 689.64 \times \rho_{20}^{2} \qquad (2)$$

where S is salinity in practical salinity units (psu) and ρ_{20} is density at 20°C (S. Stark, personal communication 1995). A 200 ml subsample from each core was filtered onto a Whatman GF/F filter and the photosynthetic pigments extracted from the samples with 90% acetone. Concentrations of chlorophyll *a* (chl *a*) and chlorophyll *b* (chl *b*) were determined by spectrophotometry (Parsons *et al.* 1984). The remaining water from each core was washed through a 53 μm mesh sieve and the contents of the sieve preserved in 5% borax buffered formaldehyde/seawater. Identification and enumeration of metazoans were performed under a stereomicroscope (Wild M7) at 60x magnification. Eight metazoan taxa or categories were recorded: three species of calanoid copepods, one species of cyclopoid copepod, one species of poecilostomatoid copepod, unidentified harpacticoid copepods, harpacticoid nauplii and unidentified copepod eggs.

Statistical analysis

Eight of the 11 variables recorded were present in enough cores to perform a 3-factor nested analysis of variance (ANOVA) (SYSTAT version 5.03): salinity; chl *a*; chl *b*; *Paralabidocera antarctica*; *Ctenocalanus citer; Oithona similis*; harpacticoids and harpacticoid nauplii. Two important assumptions underlying the use of any ANOVA procedure are that:

a) the data are normally distributed, and

b) there is no direct relationship between variances and the means (i.e. there is homogeneity of variances) (Underwood 1981).

The first assumption was verified via normal probability plots of the standardized residuals and the second assumption was checked by examining residual scatter plots. In several cases the capacity of the data to meet the above assumptions was improved considerably after $\log_{10}(x + 1)$ or square root transformation. The relative contribution of each spatial scale (Location, Site, Quadrat) towards the total variance was calculated from the mean squares (McPherson 1990). These variance components were calculated from the untransformed data, and negative estimates were assumed to be zero (Underwood 1981). A Pearson correlation matrix was constructed for all variables measured during the study.

Results

All cores consisted predominantly of congelation ice with large columnar crystals. Length of the ice cores ranged from 420–450 mm. Water depth was around 23 m at Locations A and B, although at Site B3 the water depth was only 10 m due to the presence of an underwater shelf. Water depth at Location C was around 32 m.

There was considerable variation in the variables measured. Bulk salinity in the cores ranged from 7.44–10.76 psu, with salinities at Location A slightly higher than those at the other two Locations (Fig. 3). Chl *a* and chl *b* concentrations ranged from 1.76–78.7 mg m^{-2} and from 0.38–7.33 mg m^{-2} respectively. Overall, concentrations were highest at Location A and lowest at Location B (Fig. 4). The metazoan fauna was dominated numerically by nauplii of *Paralabidocera antarctica* (Fig. 5), which ranged in numbers from 6×10^4 to 4×10^5 individuals m^{-2}. No copepodite stages of this species were observed. *Paralabidocera antarctica* life stages were identified using Tanimura (1992). Other taxa, such as *Stephos longipes*, *Ctenocalanus citer*, harpacticoid copepods, *Oithona similis*, *Oncaea curvata* and unidentified eggs and nauplii, were present in much smaller numbers (Fig. 5). Visual examination of the data indicated that there were few clear trends in the distributions of animals between Locations, Sites or Quadrats.

Nested ANOVA revealed statistically significant variation at the scale of Location (km) for four of the eight variables

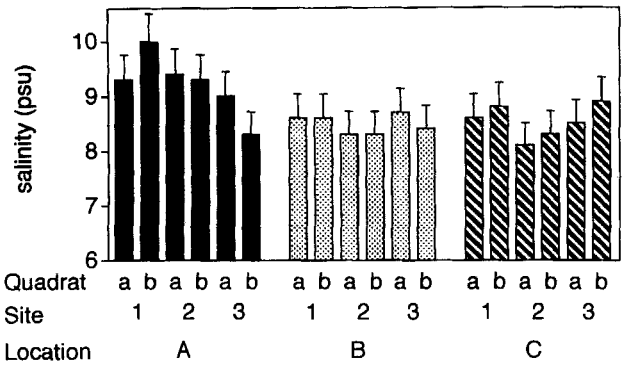

Fig. 3. Salinity of sea ice cores. Bars represent the mean (± s e) of three cores within a quadrat.

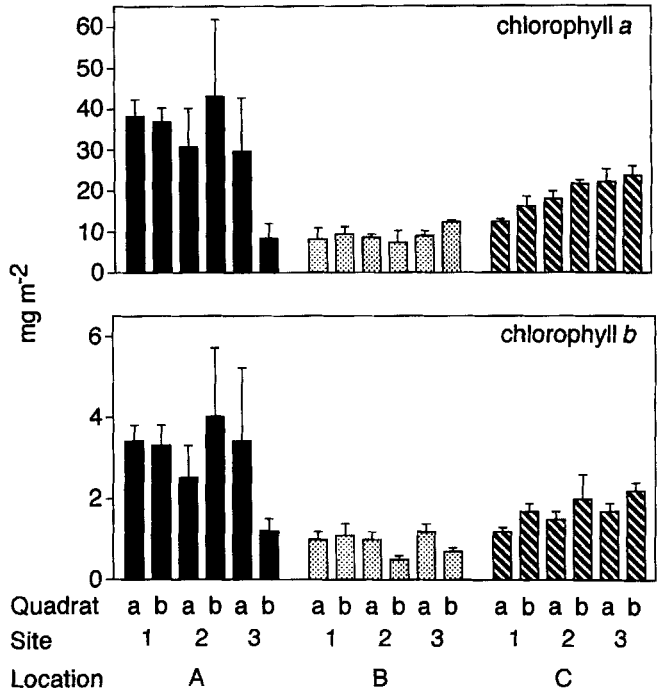

Fig. 4. Chlorophyll concentrations. Bars represent the mean (± s e) of three cores within a quadrat. Note that vertical scales are different.

tested: chl *a*, chl *b*, *P. antarctica* and *O. similis* (Table I). No other spatial scales had a significant effect. The contribution that each scale made to the total variance was calculated for each variable tested (Table II). Interpretation of variance components is not straightforward because the magnitude of the residual variance can influence the size of the contribution made by the other spatial scales to the total variance (Morrisey *et al.* 1992). However, it is nevertheless important to note that residual variance accounted for between 46–100% of the total variance. High residual variance indicates that considerable patchiness was present in the sea ice habitat at spatial scales smaller than Quadrat, i.e. between cores.

Pairwise Pearson correlation coefficients between all eleven variables revealed only one strong relationship, that between chl *a* and chl *b* (Table III, Fig. 6a). The ratio of chl *a*: *b* was approximately 10:1, indicating a low but consistent contribution from green algae. Further exploration of the data via bivariate scatter plots showed that in some cases there was stronger correlation at the level of Location. For example, at Location A *P. antarctica* and chl *a* did have a fairly strong positive correlation (Fig. 6b). However, no such trend was observed for other bivariate plots, such as chl *a* and salinity (Fig. 6c) or *P. antarctica* and salinity (Fig. 6d).

Table I. Summaries of analyses of variance for selected variables. Significant values (p = 0.05) are shown in **bold**.

Source of variation	df	Salinity MS	F	*P*	Chlorophyll *a*[1] MS	F	*P*	Chlorophyll *b*[1] MS	F	*P*
Location	2	2.81	3.85	0.084	0.89	6.36	**0.030**	0.36	18.00	**0.005**
Site	6	0.73	3.32	0.052	0.14	2.33	0.104	0.02	1.00	0.419
Quadrat	9	0.22	0.69	0.722	0.06	1.50	0.151	0.02	1.00	0.224
Residual	36	0.32			0.04			0.02		

Source of variation	df	*Paralabidocera antarctica*[1] MS	F	*P*	*Ctenocalanus citer*[2] MS	F	*P*	*Oithona similis*[2] MS	F	*P*
Location	2	0.44	8.80	**0.016**	64.79	0.19	0.832	1950.0	11.34	**0.009**
Site	6	0.05	0.83	0.599	341.38	2.28	0.129	171.9	0.97	0.494
Quadrat	9	0.06	1.20	0.232	149.95	0.75	0.658	176.5	1.22	0.312
Residual	36	0.05			198.92			144.4		

Source of variation	df	Harpacticoids[2] MS	F	*P*	Harpacticoid nauplii MS	F	*P*
Location	2	302.99	4.47	0.065	46359	0.51	0.626
Site	6	67.78	0.61	0.717	91546	0.83	0.576
Quadrat	9	110.76	0.69	0.715	110521	0.93	0.509
Residual	36	161.07			118532		

[1]$Log_{10}(x+1)$ transformation
[2]Square root transformation

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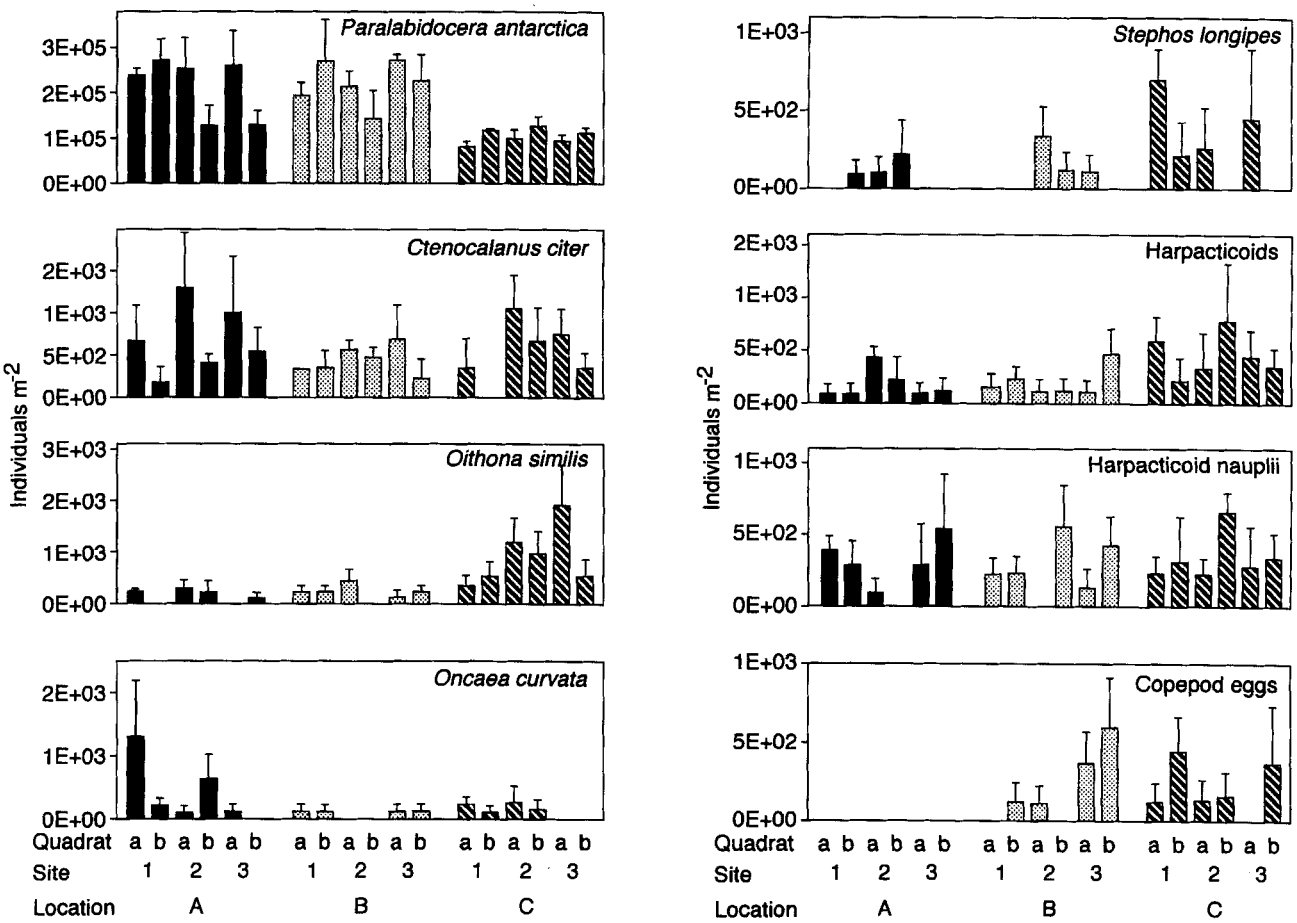

Fig. 5. Abundances of sympagic metazoans. Bars represent the mean (± s e) of 3 cores within a quadrat. Note that vertical scales are different.

Table II. Variance components (percentage) calculated from the analyses of variance.

Source of variation	Salinity	Chl *a*	Chl *b*	*Paralabidocera antarctica*	*Ctenocalanus citer*	*Oithona similis*	Harpacticoids	Nauplii
Location	21.9	42.5	49.3	36.7	0	36.7	12.5	0
Site	16.3	10.7	0	0	1.9	0.2	0	0
Quadrat	0	0.	1.4	7.7	0	9.6	0	0
Residual	61.8	46.8	49.3	55.6	98.1	53.5	87.5	100

Table III. Pearson correlation matrix for all variables measured in the study.

	Sal	Chl *a*	Chl *b*	*P. ant*	*C. cit*	*O. sim*	*O. cur*	*S. lon*	Harp	Naup	Eggs
Sal	1.00										
Chl *a*	0.59	1.00									
Chl *b*	0.53	0.93	1.00								
P. ant	0.29	0.22	0.29	1.00							
C. cit	0.06	0.31	0.26	0.29	1.00						
O. sim	-0.24	0.01	-0.09	-0.26	0.26	1.00					
O. cur	-0.02	0.15	0.23	0.10	-0.19	-0.05	1.00				
S. lon	-0.09	-0.09	-0.11	-0.18	0.08	0.35	0.05	1.00			
Harp	-0.09	-0.04	-0.10	-0.11	0.06	0.27	-0.11	0.08	1.00		
Naup	0.14	0.09	0.08	0.02	0.07	0.10	-0.16	-0.29	0.04	1.00	
Eggs	-0.14	-0.19	-0.19	-0.08	-0.22	0.01	-0.01	-0.09	-0.16	-0.02	1.00

Abbreviations are: *P. ant* = *Paralabidocera antarctica*; *C. cit* = *Ctenocalanus citer*; *O. sim* = *Oithona similis*; *O. cur* = *Oncaea curvata*; *S. lon* = *Stephos longipes*; Harp = harpacticoids; Naup = harpacticoid nauplii; Eggs = unidentified copepod eggs.

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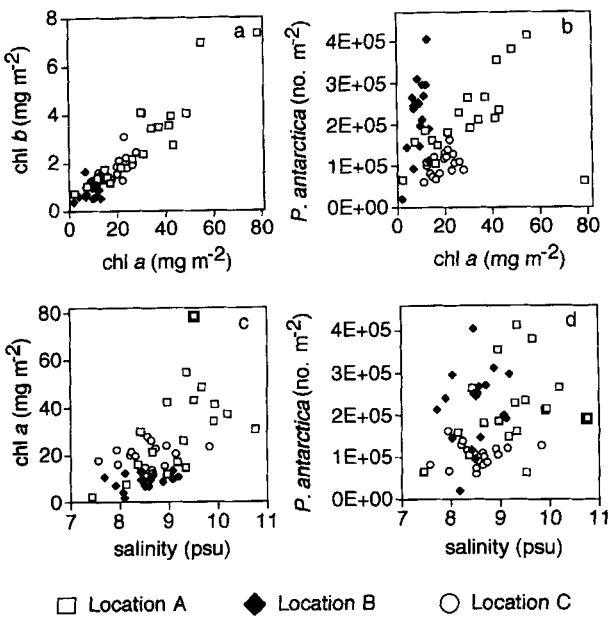

Fig. 6. Bivariate scatterplots. **a.** Chlorophyll *b* and chlorophyll *a*, **b.** *Paralabidocera antarctica* and chlorophyll *a*, **c.** Chlorophyll *a* and salinity, **d.** *Paralabidocera antarctica* and salinity.

Discussion

Autumn abundances of sympagic biota

Chl *a* concentrations were highly variable, averaging 31.0, 9.12 and 18.9 mg m^{-2} at Locations A, B and C respectively. The highest value recorded on 17 April 1994 (78.7 mg m^{-2}) was close to integrated chl *a* measurements made at the same site during November 1993 (Archer *et al.* 1996), and was much higher than concentrations recorded from single cores by Perrin *et al.* (1987), at a site close to Location A in 1982 (0.30 mg m^{-2} in April and 4.36 mg m^{-2} in May). Although less than the maximum chl *a* recorded for McMurdo Sound fast ice during November and December (up to 150 mg m^{-2}; Palmisano *et al.* 1988), our results nevertheless provide further evidence for a substantial autumn contribution to total ice algal production. These results also underscore Hoshiai's (1985) suggestion that the extent of the autumn contribution must be assessed to arrive at accurate estimates of annual production of ice algae in the Antarctic Ocean. Hoshiai (1985) summarized data collected from fast ice near Syowa Station over three different autumns and concluded there was a high degree of temporal variability that resulted from differences in the rate of ice growth during the three years. However, all of Hoshiai's chl *a* values measured during the three years fall within the total range of values measured in the present study, and so an equally plausible interpretation of Hoshiai's data is that it might reflect spatial, rather than interannual, variability.

Abundances of *Paralabidocera antarctica* nauplii were an order of magnitude greater than those recorded by Hoshiai & Tanimura (1986) during autumn near Syowa Station, and the numbers indicate the importance of sea ice to the life cycle of *P. antarctica*, as shown recently by Tanimura *et al.* (1996). Low abundances of *Stephos longipes*, another species known to associate with sea ice, indicate that this species appears to prefer deeper waters such as those of the Weddell Sea (Kurbjeweit *et al.* 1993). The life cycle of *Ctenocalanus citer* is poorly known, although Tucker & Burton (1990) recorded it during the year in the water column near Davis Station. It is likely that *Oncaea curvata* and *Oithona similis*, which were present in very high densities in the water column (K. Swadling, unpublished data), did not occur in the ice but were sampled fortuitously by collection of the ice/water interface and they will not be considered further here. Several species of harpacticoid copepods do have a close association with sea ice during their life cycles (Dahms *et al.* 1990). In our study, harpacticoid nauplii, copepodites and adults with egg sacs were recorded from the cores, although generally in low numbers (from 0–5 per core). There was considerable patchiness in their distribution, a finding similar to that of Dahms *et al.* (1990) who recorded numbers of 0, 1 and 116 *Drescheriella glacialis* in three cores *c.* 1 m apart.

Degree of horizontal patchiness and possible causes

Of the spatial scales measured in this study only Location (1–2 kms) contributed significant variation to the variables measured. Intermediate scales of hundreds of metres (Site) and tens of metres (Quadrat) did not add significantly to the variation in the data. Partitioning of variance components revealed that between 50–100% of the total variance came from residual or "unexplained" variance, thus highlighting the fact that horizontal patchiness of sympagic biota can vary as much at scales of less than one metre as it can at scales of several kilometres. Therefore, to maximize the coverage of Antarctic fast ice biota it is recommended that effort be directed towards sampling at the scale of kilometres rather than at tens or hundreds of metres. Within each location sampled, replicate ice cores should be taken as close together as practicable. Given the degree of variability between closely spaced cores, all planned analyses should be performed on each of the cores whenever possible.

An advantage of using fast ice in a study of this kind is that the past history of the ice is usually known and physical processes, such as growth rate of ice, light and temperature regimes, patterns of snow cover and water circulation, can be described. In contrast, interpretation of data from pack ice can be hindered by the lack of knowledge about past deformational events such as rafting, ridging and crushing. However, pack ice represents by far the greatest coverage (approx 90%; Lizotte & Sullivan 1992) of the Southern Ocean sea ice and so the applicability of these types of studies should be assessed. Eicken *et al.* (1991) measured nutrients, salinity and chl *a* at scales from 0.25–20 m from three pack ice floes in the Weddell Sea and concluded there was as much variability at scales of less than 1 m as there was in cores

collected over their entire sampling area. Thus it appears that small scale patchiness is a property of both fast and pack ice, and that the factors influencing settlement of sympagic organisms might be similar in both habitats.

While this study has clearly shown a high degree of variability at small spatial scales, the source of the variability is not clear. Snow cover, which can be important in structuring sea ice communities (Sullivan *et al.* 1985), was not a feature of this study as there was no snow on the sea ice from the time of freezing until after the sampling date. Nevertheless, in the absence of snow cover, irregularities in sea ice crystals will affect absorption and scattering of light particles, thus resulting in variable light penetration to the under ice surface. This, in turn, will influence growth and development of under ice algae, resulting in the patchy distribution shown in this study. It is reasonable to hypothesize that herbivorous species, such as *Paralabidocera antarctica*, will accumulate in areas of high algal density. However, a clear correlation between chl*a* and *P. antarctica* was shown only at Location A. Brine channels might branch for some distance across the ice but the extent of movement of individual organisms within them is unknown.

Particles are incorporated into the sea ice via scavenging by frazil ice crystals as they form and rise to the surface, or by advection in open water areas (Ackley & Sullivan 1994). Rate of ice growth, snow cover, daily illumination, water currents, extent of brine channels and pockets, differential brine drainage and grazing activity (Eicken *et al.* 1991) then interact to influence settlement and subsequent development of ice organisms. To elucidate the mechanisms responsible for horizontal patchiness in the sympagic community it might be necessary to measure these features at very small scales, such as centimetres and millimetres.

Acknowledgements

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