INFLUENCE OF SEASONAL ICE FORMATION ON LIFE CYCLE STRATEGIES OF ANTARCTIC COPEPODS

by

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Declaration

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Kerrie M. Swadling

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Abstract

Zooplankton from inshore marine and marine-derived lacustrine Antarctic habitats were studied over two summers and the intervening winter from December 1993 to March 1995 at two sites in the Vestfold Hills region, East Antarctica. Particular emphasis was placed on the interaction between fast ice and the underlying water column, and the effect of this on the ecology of dominant copepod species. The overwintering strategies of commonly found copepods were investigated.

The sea ice habitat was characterised by high abundance and low diversity of metazoans. *Paralabidocera antarctica* dominated the metazoan assemblage, reaching densities of up to 500,000 individuals m^{-2}. Other taxa present included *Drescheriella glacialis*, unidentified harpacticoids, *Stephos longipes* and *Ctenocalanus citer*. Horizontal patchiness of the sympagic biota varied as much on scales of less than one metre as it did at scales of several kilometres. Metazoan density was not clearly correlated with chlorophyll concentration, salinity or particulate organic carbon.

The zooplankton assemblage at the inshore marine site was numerically dominated by *Oncaea curvata* and *Oithona similis* throughout the sampling period. Diversity was highest in the summer when the break-out of the fast ice, coupled with the phytoplankton bloom, encouraged the development of meroplanktonic larvae of benthic species. Other copepod species present included *Paralabidocera antarctica*, *Calanoides acutus*, *Ctenocalanus citer*, *Stephos longipes*, and unidentified harpacticoids. Grazing impact by the copepod assemblage on primary productivity during the 1994-5 summer was consistently low, ranging between 1 and 5 %.

The life cycle of *Paralabidocera antarctica* was strongly associated with the growth and development of ice algae. Lipid storage by this species was predominantly in the form of triacylglycerols, indicating that copepods were feeding throughout the year. In

contrast, *Oithona similis* and *Oncaea curvata* predominantly stored wax esters, and their life cycles were not linked strongly to the summer phytoplankton bloom.

A lacustrine population of *Paralabidocera antarctica* was also found to store triacylglycerols, suggesting that the copepods were able to graze throughout the year. This species, the only planktonic metazoan consumer present in the lake, reached abundances of up to 35,000 m^{-3}. The life cycle of this population had become much less tightly regulated than at the coastal site, and specimens were rarely found living within the lake ice. The lack of predators and competitors, along with measurable quantities of phytoplankton present in the lake throughout the year, has resulted in the decoupling of the life cycle of this population from the growth cycle of the ice algae.

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Abbreviations

Standard SI unit and prefix abbreviations are used, and are not listed except for some less common units.

µCi	microcurie
chl *a*	chlorophyll *a*
chl *b*	chlorophyll *b*
Bq	becquerels
DOC	dissolved organic carbon
dpm	disintegrations per minute
FFA	free fatty acid
HC	hydrocarbon
MeA	methylamine hydrochloride
MIZ	marginal ice zone
PAR	photosynthetically active radiation
PL	polar lipid
POC	particulate organic carbon
psu	practical salinity unit
ST	sterol
TAG	triacylglycerol
WE	wax ester

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Chapter 1
Introduction

1.1 The Polar Marine Environment

Variable coverage by ice characterises marine environments at high latitudes. At its maximum extent, sea ice covers 8% of the southern hemisphere and 5% of the northern hemisphere (Horner et al. 1992). The high albedo of sea ice gives it a pivotal role in the global energy balance as it influences important interactions between the ocean and the atmosphere. For example, heat flux, gas exchange and transmission of photosynthetically active radiation (PAR) are all moderated by the presence of sea ice (Spindler 1990, Nicol and Allison 1997). The cycle of growth and decay of sea ice further influences ocean circulation and structure. As the sea ice forms salt is rejected into the underlying ocean, which causes denser, salty water to sink, and encourages deep ocean mixing and the subsequent upwelling of nutrients. Conversely, when ice melts, a layer of fresh, less dense water is trapped at the top of the water column, which enhances vertical stratification (Nicol and Allison 1997).

Although superficially similar, there are substantial differences between the Arctic and Antarctic oceans. The former, a deep basin surrounded by continents, has limited water exchange with other oceans via several narrow passages. Conversely, the Southern Ocean, about half of which is influenced by ice cover, consists of generally much deeper water circulating around a large, ice-covered continent. It has the capacity to exchange with all other global oceans except the Arctic (Johnson 1990). Sea ice coverage at both poles is seasonal in its extent. In Antarctica it undergoes a five-fold increase in area from a summer minimum of 4×10^6 km^2 to a winter maximum of 20×10^6 km^2. In contrast, sea ice coverage of the Arctic Ocean undergoes only a doubling in area from a summer minimum of 7×10^6 km^2 to a winter maximum of 14×10^6 km^2 (Maykut 1985).

Together the biota of the polar oceans produce from 0.50 to 0.57 gigatonnes of biogenic carbon per year (Legendre et al. 1992), which represents approximately 5 % of that produced in surface oceans worldwide (Siegenthaler and Sarmiento 1993). When partitioned among the various sources, about 25 % of the total primary production coming from polar oceans was attributed to that occurring within the sea ice (Legendre et al. 1992). In the Southern Ocean a further 60% of primary production was associated with the highly dynamic ice edge, and 15 to 20% with water column production under the ice cover. In the Arctic Ocean 50% of the total primary production was estimated to arise in shelf waters, and another 25% was attributed to production in offshore waters (Legendre et al. 1992).

The dynamic nature of the ice coverage has important implications for organisms that live at high latitudes. Therefore, in the following section an overview is given of the physical nature of sea ice, including its formation, growth and decay. In section 1.3 various biological communities associated with sea ice are presented, with discussion of how animals and plants colonise the niches that it offers. Section 1.4 considers the responses adopted by organisms which enable them to thrive in the polar environment. Finally, the broad objectives of this thesis and the structure of the remaining chapters are presented in section 1.5.

1.2 Physics and Chemistry of Sea Ice

1.2.1 Growth

When the surface of seawater cools below its freezing point (≈ -1.86 °C), minute spheres of pure ice form on the surface and grow rapidly into frazil crystals. These are thin, hexagonal discs that are 2 to 3 mm in diameter. Frazil crystals also form at depth in supercooled water and rise to the surface (Horner et al. 1992). As temperatures

continue to decrease frazil ice crystals agglomerate to form grease ice, a soupy, grey slush with a matte-like appearance (Weeks and Ackley 1982). Under quiescent conditions grease ice will thicken vertically and form into a single sheet of nilas, elastic ice up to 25 mm thick. Alternatively, under wind and wave action, the young ice will break up into pancakes, irregularly rounded masses of unconsolidated slush that have thickened rims and are between 0.3 and 3.0 m in diameter (Spindler 1990). The pancakes collide and eventually freeze together to form a solid ice sheet. In coastal regions the resultant ice sheet tends to grow outwards from the shore (Weeks and Ackley 1982). After the ice sheet consolidates a strong temperature gradient develops between the ice-air interface and the ice-water interface. As the ice thickens the flow of heat from the water to the atmosphere decreases, thus reducing the rate of ice formation. Growth continues to occur by accretion of ice on the underside of the sheet and is largely a function of how rapidly heat is conducted through the ice to the surface (Maykut 1985).

As sea ice continues to grow it will take one of two main forms. Quiescent conditions favour the formation of congelation ice that forms by the growth of large, elongated (columnar) crystals perpendicular to the underside of the ice sheet (Horner et al. 1992). Alternatively, turbulent conditions promote consolidation of agglomerations of frazil ice crystals into sheets of granular ice (Eicken and Lange 1989). A series of intermediates between these two ice types is also recognised (Eicken and Lange 1989). Congelation ice of columnar texture is the primary type of Arctic sea ice (Spindler 1990), and is usually the dominant form in Antarctic fast ice (i.e. that attached along the shore) (Palmisano and Sullivan 1983). In contrast, the majority of pack ice (i.e. that floating freely), which in the southern hemisphere accounts for approximately 90% of the total sea ice cover, consists mainly of granular ice. Finally, large accumulations of loose platelet ice, sometimes several metres in thickness, have been observed under fast ice in McMurdo Sound (Palmisano and Sullivan 1985) and the

Weddell Sea (Dieckmann et al. 1986), but have not been observed in the Arctic (Spindler 1990).

1.2.2 Brine in sea ice

As seawater freezes brine is excluded from the matrix of freshwater ice crystals. The excluded brine has the effect of depressing the freezing point to a temperature where no more freezing can occur. The brine then accumulates into pockets and channels which form along the boundaries between ice platelets and between ice grains (Wakatsuchi and Kawamura 1987). The majority of pockets form in the initial stages of ice growth, and the frequency of formation depends on the ice growth rate. Brine pockets in sea ice result in a more complex crystal structure than that observed in freshwater ice (Weeks and Ackley 1982).

The salinity of brine is a function of temperature. At very cold temperatures brine is highly concentrated, with salinities as high as 70 to 144 practical salinity units (psu) (Spindler 1990). At approximately -20 °C brine pockets are constricted and have a mean diameter of 10^4 to 2 x 10^4 μm^2, and a length of 100 to 200 μm (Nicol and Allison 1997). When temperatures reach approximately -5 °C, the brine pockets link up to form channels. Brine channels are tree - shaped in structure, with a main branch linking several smaller tributary branches (Wakatsuchi and Kawamura 1987). Brine channels, while typically about 200 μm (Weissenberger et al. 1992), can be up to 4 mm in diameter (Maykut 1985).

As temperatures warm, brine pockets and channels enlarge and brine is flushed through the system via the mechanisms of gravity drainage, brine channel migration, brine expulsion and flushing. Flow through channels is oscillatory, with the duration of the downward flow usually shorter than that of the upward flow (Weeks and Ackley

1982). Flushing of brine through sea ice is of biological importance as substances essential for the growth of algae and bacteria, such as nutrients and dissolved gases, are replenished (Dieckmann et al. 1991).

Brine expelled into the ocean influences convective processes in the water column, which, in turn, affects primary production. In spring, melting sea ice releases less saline water into the surface layer of the ocean at the edge of the disintegrating ice pack. A lens of fresher, less dense water is separated from the rest of the water column by a pycnocline. Algae released into this lens are trapped by the pycnocline in nutrient rich water that receives large amounts of incoming PAR. The result is a phytoplankton bloom that typically follows the retreating ice edge as it moves southwards. Thus, the productivity of the marginal ice zone (MIZ) was generally believed to be far higher than that in open water or under fast or pack ice (Smith and Nelson 1986, Legendre et al. 1992). However, a recent re-assessment of the productivity of the MIZ has suggested that the dense phytoplankton blooms observed in earlier studies might not be applicable to all regions, and thus the importance of this system to overall primary productivity may be overestimated (Savidge et al. 1996).

1.2.3 Light

Input of solar radiation to high latitudes is extremely seasonal. Hours of daylight can range from 24 per day for several weeks in the summer to none during the winter. Furthermore, the ice and snow that cover the ocean strongly attenuate the amount of light that actually reaches the water column. Two to five times more incoming radiation is reflected by ice-covered ocean than by ice-free ocean (Spindler 1990). In McMurdo Sound the under-ice irradiance during a spring phytoplankton bloom was typically less than 1 %, and often less than 0.1 %, of the surface irradiance (Palmisano et al. 1985). Snow cover on the sea ice attenuates light more strongly than ice itself because of

different light extinction co-efficients (Maykut and Grenfell 1975). For example, there was an inverse relationship between chlorophyll *a* (chl *a*) and thickness of snow cover in McMurdo Sound (Sullivan et al. 1985). However, ice algae can continue to photosynthesise at very low irradiances and many studies have documented the photoadaptive abilities of algae growing at the under-ice surface (e.g. Cota 1985, Palmisano and Sullivan 1985, Barlow et al. 1988).

Inclusions trapped in the ice, such as air bubbles, brine and particulate matter, affect absorption and scattering of light particles. Light spreads heterogeneously and anisotropically (along an axis) through sea ice, largely as a result of scattering by vertically oriented brine channels. Therefore, sunlight falling on ice at relatively low angles will still propagate through the ice with a radiance that is strongly oriented in the vertical direction (Buckley and Trodahl 1987).

Penetration of light through sea ice varies with season. For example, penetration of ultraviolet radiation (UV) through ice may be stronger in spring, when transparency is greater, than in summer. As this is also the period when ozone depletion in the atmosphere is most severe (Trodahl and Buckley 1989), there may be important consequences for organisms living near the under-ice surface. Antarctic zooplankton sustained significant DNA damage during periods of increased UVB flux (Malloy et al. 1997), and it is believed that enhanced levels of UVB contribute to reduced rates of photosynthesis and changes in the photosynthetic pigmentation of algae (El-Sayed et al. 1990). On the other hand, whether increased UVB has caused a decline in species diversity has led to some debate (McMinn et al. 1994).

1.3 Sea Ice Communities

Sea ice plays a pivotal role in the life cycles of many species. Seals, seabirds and penguins use the surface as breeding habitat and as a platform from which to forage. Crevices in the under-surface of the ice provide refuge from predation for fish and large crustaceans such as krill and amphipods. Niche space is also found within the interstitial brine channels. These spaces are occupied by a diverse range of organisms including bacteria, algae, unicellular zooplankton, and small metazoans such as copepods, turbellarians and nematodes. These organisms are broadly defined as the sympagic ("with ice") biota (Horner et al. 1992).

Several distinct habitats, with their associated biota, have been described for sea ice. At the surface 'snow ice' results when snow loading reaches a point where it depresses the ice below sea level, thereby becoming infiltrated with sea water. Snow ice, which covers much of the Weddell Sea, is characterised by a mixed diatom-flagellate community (Burkholder and Mandelli 1965), and supports high concentrations of chl *a* (100 to 400 mg m^{-3}) (Ackley and Sullivan 1994). Deformation communities, also described from the Weddell Sea, arise via seawater infiltration of pressure ridges, or when ice deflected below the surface is flooded by seawater that then collects into ponds. A diverse range of autotrophic and heterotrophic microorganisms has been described from these habitats (Garrison and Buck 1991). Finally, melt pool communities form via flooding and/or thawing of the surface. These communities, often consisting of diatoms, flagellates and ciliates, are particularly common in the Arctic where they may cover up to 50 to 60 % of the sea ice (Maykut 1985).

Freeboard communities develop in the ice, just below sea level, when surface temperatures warm the ice and cause partial brine drainage from the upper layers. At the same time algal growth increases, heat is trapped and the ice melts (Horner et al. 1992). Solid layers of ice occur above and below the freeboard layer. The salinity of

this layer is often much higher than observed in other sections of the ice, and chl *a* concentrations up to 425 mg m^{-3} have been reported (Ackley and Sullivan 1994). The brine channel systems that branch throughout the ice constitute the most common interior habitat. Organisms are either concentrated in narrow bands or spread diffusely throughout the ice (Horner et al. 1992).

Bottom ice communities have been the most studied to date. The lower layers of congelation ice have high stability, a high probability of colonisation and free exchange of nutrients with underlying seawater. Approximately 99 % of the primary productivity of congelation ice in McMurdo Sound was measured in the bottom 20 cm, where chl *a* concentrations of 310 mg m^{-2} were recorded (Palmisano and Sullivan 1983). Furthermore, the highest densities of sympagic metazoans are usually found in these bottom layers (Hoshiai and Tanimura 1986, Dahms et al. 1990). The sub-ice platelet layer is also a region of high algal growth and accumulation. High concentrations of chl *a* (2120 mg m^{-2}) were measured in the platelet layer in McMurdo Sound (Ackley and Sullivan 1994). An extension of these under-ice communities is the strand communities (McConville et al. 1985, Watanabe 1988), largely composed of chains of diatoms, which form in spring and are possibly derived from melting of the platelet layer (McGrath-Grossi et al. 1987).

As the base of the ice continues to melt, ice algae are released into the water column. The fate of this material is equivocal. In Antarctic pack ice the algae might play a substantial role in seeding the spring phytoplankton bloom (Garrison et al. 1987, Garrison and Buck 1989). However, in a coastal study, algae released from fast ice made little contribution to subsequent phytoplankton growth (McMinn 1996). Therefore, this material must either sediment to the benthos (Knox 1990, Legendre 1990), be removed via zooplankton grazing (Legendre et al. 1992, Michel et al. 1996), or moved away by currents.

1.3.1 Incorporation of particulate matter into sea ice

The quality and quantity of habitable space in sea ice vary considerably and are a function of physical, chemical and biological processes that act on the ice during its development. Organisms become incorporated into the ice via active colonisation or passive harvesting. They, in turn, may influence ice structure as they affect heat absorption and promote loss of ice strength (Eicken et al. 1991a).

Scavenging and nucleation are two mechanisms proposed to explain passive incorporation of particles into sea ice. Nucleation results from frazil ice crystals preferentially forming on suspended particles, such as algal cells, and carrying them to the surface. Scavenging occurs when ice crystals rising through the water collide with particles and sweep them upwards. Garrison et al. (1983) postulated that scavenging was the dominant concentrating mechanism as neither nucleation nor *in situ* growth could account for observed cell densities in ice. Furthermore, substantial amounts of nucleation occur only at air temperatures of less than -10 °C (Parker et al. 1985).

Granular ice formations commonly support a higher concentration of organisms than found in congelation ice (Horner et al. 1992, Ackley and Sullivan 1994). For example, in the Weddell Sea the highest densities of the foraminiferan *Neogloboquadrina pachyderma* were encountered in sea ice cores composed primarily of frazil ice. No *N. pachyderma* were found in cores consisting predominantly of congelation ice (Spindler et al. 1990). Frazil ice crystals form continuously at depth in supercooled water in the Weddell Sea, promoting continual scavenging of particles by ice crystals as they rise to the surface. Furthermore, the brine volume of granular ice is about twice that of congelation ice (Weissenberger et al. 1992), thus available habitat space is likely to be greater in the former. Congelation ice grows by accretion at the ice-water interface and thus enrichment by scavenging is less common.

Although physically mediated harvesting as described above may be the primary mechanism for incorporating small cells into sea ice, active colonisation by macrofauna is also likely. In the Arctic, ice in coastal regions often has contact with the sea floor and benthic species can crawl directly into the brine channels (Spindler 1990). Other organisms, including krill, amphipods and larval fish, must be efficient swimmers to maintain their position at the ice-water interface. Furthermore, adaptations such as spines and 'stickiness' will facilitate incorporation of particles. Algal cells released from Weddell Sea ice during a melting experiment showed a strong propensity to form aggregations, suggesting the cells were 'inherently sticky', probably as a result of production of extracellular polysaccharide mucilages (Riebesell et al. 1991).

1.3.2 Sympagic macrofauna

As it became accepted that substantial primary production was occurring within sea ice (Bunt 1963, Bunt and Wood 1964), attention turned to establishing the presence of an ice-associated fauna. Twelve species, including polychaetes, copepods, amphipods and fish, were described as having strong association with the bottom layers of Antarctic fast ice near Mirny Station (Andriashev 1968). Subsequent studies of Arctic and Antarctic fauna have added turbellarians, nematodes and euphausiids to this list (Kern and Carey 1983, Grainger and Hsaio 1990, Garrison 1991). The complex physical structure of sea ice provides these animals with a refuge from predation. Furthermore, the extended growing season of ice algae as compared to phytoplankton (e.g. Garrison and Buck 1989) means that the foraging potential provided by the former is prolonged. Some species of macrofauna live and feed within the interstitial brine channels (Kern and Carey 1983, Hoshiai et al. 1987, Kurbjeweit et al. 1993), whereas others concentrate to feed at the ice-water interface (Conover et al. 1986, Runge and Ingram 1988, Daly 1990).

Sympagic macrofauna have been classified as those species that complete their entire life cycle within the sea ice (autochthonous fauna), or those which spend only part of their life cycle associated with ice (allochthonous fauna) (Gulliksen and Lønne 1991). Autochthonous species have rarely, if ever, been recorded from the Antarctic, as over 90 % of Antarctic sea ice is seasonal (Spindler 1990) and must be colonised anew each year. In contrast, Arctic sea ice is mainly perennial (Spindler 1990) and, therefore, there is a higher probability that autochthonous species will have evolved. These species rely on year-round ice cover and a drift pattern of ice that maintains the floe within the perennial ice zone. However, as ice is eventually advected out of this zone, autochthonous species must be able to spread laterally from floe to floe (Gulliksen and Lønne 1991). Arctic ice can support species with life spans of greater than one year. For example, the amphipod *Gammarus wilkitzkii*, an autochthonous Arctic species, can live for at least 6 years (Gulliksen and Lønne 1991). In contrast, most species that associate with Antarctic sea ice have life spans of one year or less (Dahms et al. 1990, Schnack-Schiel et al. 1995, Tanimura et al. 1996).

The sea ice cover of polar oceans often supports high densities of metazoans (e.g. Kern and Carey 1983, Hoshiai and Tanimura 1986, Smetacek et al. 1990). However, there remains a lack of information about the importance of their role in the polar marine food web. Data on biogeographical diversity, *in situ* grazing rates, physiological tolerances and overwintering strategies are necessary to assess fully the impact of these species on the sea ice ecosystem.

1.4 Adapting to the Polar Marine Environment

Living at high latitudes imposes constraints on a species' life cycle in terms of growth, life span and reproductive output. Behavioural and physiological responses to these constraints include migration to more favourable habitats during winter, delayed

reproduction and development, extended brooding of larvae, dietary switching, diapause, and the accumulation of lipids as an energy reserve.

Large vertebrates, such as whales, seals and birds, migrate considerable distances during winter and can forage well away from the sea ice zone. However, smaller, less mobile species cannot easily escape the influence of sea ice and this is reflected in their life history strategies. Timing reproduction to take advantage of the summer phytoplankton bloom is a common trait amongst polar organisms. Algal cells that sediment out of the water column provide a pulse of production that triggers the release of larvae of benthic species. For example, an Antarctic echinoid, *Sterechinus neumayeri*, spawns from October to December to coincide with the beginning of the spring bloom (Bosch et al. 1987, Pearse et al. 1991). Other benthic species, including many amphipods, commonly brood their larvae throughout the winter and then release them at an advanced stage in late spring (Tucker 1988).

Timing peak reproductive activity to coincide with the phytoplankton bloom is also common among some Antarctic copepods. The life cycle of herbivorous polar copepods is typified by *Calanoides acutus*. Briefly, mating occurs at depth during winter, then females ascend to shallow waters in spring-summer, feed and spawn. Development to copepodite stages CIV and CV is rapid and, after accumulating extensive lipid stores, these stages descend to deep waters in autumn where they overwinter in a state of diapause. During this time development is arrested and metabolism is dramatically reduced (reviewed by Atkinson et al. 1997). Alternatively, some species remain in surface waters and undergo a dietary switch from herbivory to a more opportunistic feeding mode. For example, *Calanus propinquus*, while feeding predominantly on phytoplankton in the summer, is capable of catching and ingesting the small poecilostomatoid copepod *Oncaea curvata* (Metz and Schnack-Schiel 1995). Inferences about the dietary modes of copepods can be made from examination of their lipid stores, and this topic is discussed below.

1.4.1 Lipids in polar copepods

The presence of oil sacs in copepods has long been acknowledged as a means of surviving unfavourable periods (Collin et al. 1934, Lovern 1935; cited in Marshall and Orr 1972). The main constituents of oil sacs are wax esters, which are long-chain fatty alcohols esterified with long chain fatty acids (Sargent and Falk-Petersen 1988). However, some copepods, along with terrestrial plants and animals, store triacylglycerols as their primary energy source. Triacylglycerols consist of three molecules of fatty acids esterified with one molecule of glycerol (Sargent and Falk-Petersen 1988).

Based on an extensive survey of lipids in copepods, Lee and co-workers (Lee et al. 1971, Lee and Hirota 1973) hypothesised that the highest levels of wax esters would be found in copepods that experienced short periods of abundant food followed by long stretches of food scarcity. The corollary of this was that the ability to accumulate wax esters would be most highly evolved in herbivorous copepods living near the poles, and those that live in the deep ocean. Furthermore, Hakånson (1984) showed that triacylglycerols were mobilised first after a period of starvation, whereas wax esters were metabolised over a longer period. Thus the relative proportions of these lipids can be used to make inferences about the feeding history of a species.

Lipid stores have been studied in copepods collected from the Arctic (Tande and Henderson 1988, Graeve and Kattner 1992, Graeve et al. 1994) and the Antarctic (Hagen 1988, Hagen et al. 1993, 1995). While wax esters were the predominant storage lipid in many of the species examined, a more complex picture has emerged. *Calanoides acutus*, an important component of Antarctic zooplankton, behaved as a 'typical' herbivore by storing large amounts of lipids in the form of wax esters and overwintering at depth in a state of diapause. In contrast, *Calanus propinquus*, another common species, primarily stored triacylglycerols (Hagen et al. 1993), providing

further evidence that this species switched to a more opportunistic feeding mode in winter (e.g. Bathmann et al. 1993, Schnack-Schiel and Hagen 1994). Another omnivorous species, *Euchirella rostromagna*, also stored more triacylglycerols than wax esters (Hagen et al. 1995).

The type and concentration of lipid that is stored by polar copepods vary with age, season, developmental stage, reproductive state and depth distribution (Båmstedt 1986). Hagen and Schnack-Schiel (1996) concluded that four important copepod species of the Southern Ocean stored lipids primarily to fuel reproduction in spring, rather than as a means of surviving the winter. However, while lipid storage in the larger oceanic species has received some attention there is little, if any, information concerning lipids in smaller, coastal species. There is also a paucity of data on the lipid stores of sympagic species. In particular, there is no information on changes in lipids with season and developmental stage.

1.5 Objectives of this Investigation

Copepods are an important component of the Antarctic marine ecosystem and often dominate zooplankton abundance and biomass (Atkinson 1991, Conover and Huntley 1991). Their role in the marine food web is gradually being elucidated, however many questions remain. In particular, responses of individual species to the demands of the polar winter are still poorly understood. One difficulty in studying polar copepods is that their life cycles are long, usually taking at least one year to complete. Furthermore, polar research often involves a trade-off between the good spatial but poor temporal coverage provided by ship-based research, and good temporal but less rigorous spatial coverage of station-based research. One advantage of the present 15 month long study was that the biology of copepods could be examined in conjunction with changes to

their physical environment over a full annual cycle. The following objectives were developed:

1. Documentation of the diversity of sympagic macrofauna in coastal fast ice, and examination of temporal and spatial patchiness in the distribution and abundance of this assemblage.

2. Investigation of the relationship between sea ice formation and decay, the cycle of primary production, and the abundance and distribution of zooplankton and sympagic macrofauna.

3. Examination of the range of overwintering strategies employed by copepods living at high latitudes. Emphasis was placed on lipid storage, and timing of reproduction and development.

4. Determination of the impact of grazing by the copepod assemblage on a summer phytoplankton bloom in the presence and absence of sea ice.

5. Comparison of the life history strategy of a common neritic copepod with that of a population that had been isolated in a lacustrine environment for approximately 5,000 years.

The study described in this thesis was carried out close to Australia's Davis Station in the Vestfold Hills, East Antarctica. Two major sampling sites were used, one of which was located in the nearshore marine environment, and another in a marine-derived lake. Furthermore, sea ice along the coast and in three of the nearby fjords was sampled to establish the distribution of sympagic macrofauna. Chapter 2 of this thesis describes the sampling sites and reviews previous studies from the region. Chapters 3 and 4 discuss spatial patchiness in the distribution of sympagic organisms. The annual

cycle of abundance and distribution of zooplankton and the sympagic fauna is summarised in Chapter 5. Chapter 6 describes grazing by common coastal copepods during a summer phytoplankton bloom. Chapter 7 provides a detailed comparison of lacustrine and neritic populations of the calanoid copepod *Paralabidocera antarctica*. Finally, Chapter 8 summarises the study and presents an appraisal of the direction that future studies could take. Appendix A provides details of sampling protocols and analytical methods used. Lipid class composition and content of phytoplankton and sea ice algae are presented in Appendix B.

Chapter 2
Description of Study Sites

2.1 Introduction

This chapter provides a description of the Vestfold Hills and surrounding coast-line, where the field work for this thesis was undertaken. The two primary sampling sites were Ace Lake on Long Peninsula and offshore at O'Gorman Rocks. In addition, sea ice cores were collected from several other localities during the study, and these sites are also described. Physical characteristics are outlined, and previous studies from the area are reviewed. A brief discussion of the climate of the region is also provided.

2.2 Vestfold Hills

The Vestfold Hills, a triangular-shaped region of exposed rock approximately 410 km^2 in area, is situated on the eastern boundary of Prydz Bay in the Indian Ocean sector of the Southern Ocean (Figure 2.1). It is bounded to the east by the continental ice sheet and to the south by the Sørsdal Glacier. The Vestfold Hills were exposed approximately 8,000 years ago, when retreat of the ice cap resulted in isostatic uplifting of submerged rock, and an associated lowering of relative sea level. The topography of the region consists of low hills with a maximum relief of approximately 200 m. The ice free area is maintained because the low albedo of the exposed rock leads to greater absorption of solar radiation which, in turn, warms the rock and prevents ice from forming (Adamson and Pickard 1986). The bedrock of the hills is Archaean gneiss (3,000 Ma) bisected by younger dolerite dykes (1,000 Ma). Invasion by the sea into depressions of the hills has resulted in the formation of several fjords and marine-derived lakes throughout the area. Along the coast are many islands which are of similar topography to the hills themselves.

Figure 2.1. Location of the study area. A. A map of the Antarctic continent showing Prydz Bay and Davis Station, along with several other locations mentioned in this thesis. Ice sheets are indicated by stippling.
B. A map of the Prydz Bay region, showing Davis Station and depth contours (m) of Prydz Bay.

A.

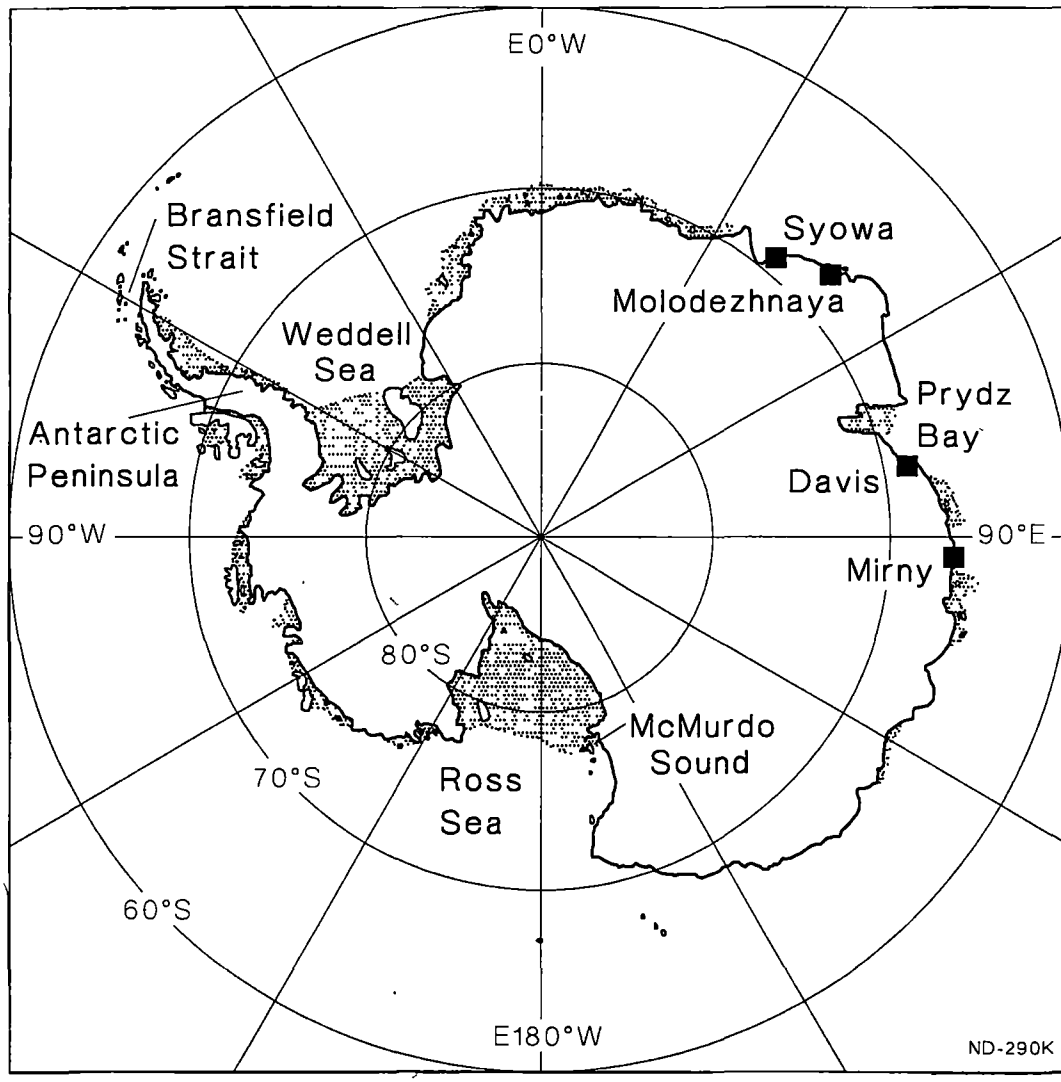
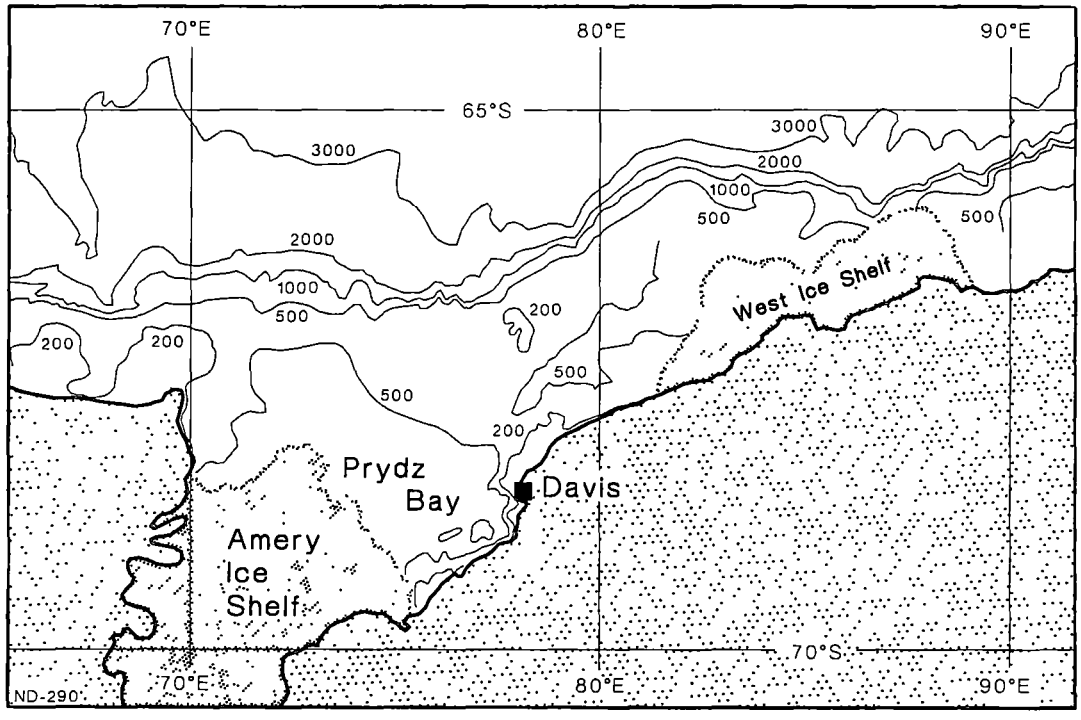


Figure 2.1. B. A map of the Prydz Bay region, showing Davis Station and depth contours (m) of Prydz Bay.



The Vestfold Hills were first discovered in 1935 (Mikkelsen 1935), but it was not until 1957 that Davis Station was established. Except for the period from 1965 to 1968 Davis Station has operated continuously. The station now supports a well-equipped scientific laboratory where much of the analytical work described in this thesis was undertaken.

2.3 Weather Conditions at the Vestfold Hills

Meteorological records have been kept by staff of the Australian Bureau of Meteorology since 1957. Measurements are predominantly from the vicinity of Davis Station, which is situated on the coast, and are therefore not always representative of weather conditions closer to the continental ice sheet. For example, strong katabatic winds, typical of the Antarctic coastline, usually dissipate before reaching Davis (Lied 1963, 1964). For this reason, Davis experiences mean average wind speeds of only 5 m sec^{-1}, which is significantly less than at other continental sites (Streten 1986). In general, the climate of the area is similar to that experienced along the Antarctic coastal belt, with the large expanses of exposed rock producing some distinctive local features (Streten 1986).

2.3.1 Air temperature

There is a strong seasonal variation in the long-term average air temperature, ranging from -17.7 °C in July to +1.0 °C in January (Figure 2.2). Temperatures below -40 °C have been recorded in winter and summer temperatures occasionally exceed 10 °C. Absorption and re-radiation of incoming solar radiation by the dark rock of the hills results in slightly warmer temperatures than those recorded at other Antarctic sites (Burton and Campbell 1980).

Air temperatures during this study were close to the long term average for most of the sampling period, with the monthly mean temperature ranging from -20.6 °C in August 1994 to 2.9 °C in February 1995 (Figure 2.2). Departures from this trend occurred in May and August 1994, when substantially colder temperatures than average were recorded, and in June 1994 and February 1995 which were warmer than average.

2.3.2 Sunlight

There is extreme seasonal variation in the amount of incoming solar radiation measured at the Vestfold Hills (Burton and Campbell 1980, Streten 1986). At a site of similar latitude to the Vestfold Hills, Oasis Station in the Bunger Hills (66°17'S, 100°47'E), global radiation varied from 21 MJ m^{-2} $month^{-1}$ in June to 749 MJ m^{-2} $month^{-1}$ in December (Rusin 1964, quoted in Streten 1986).

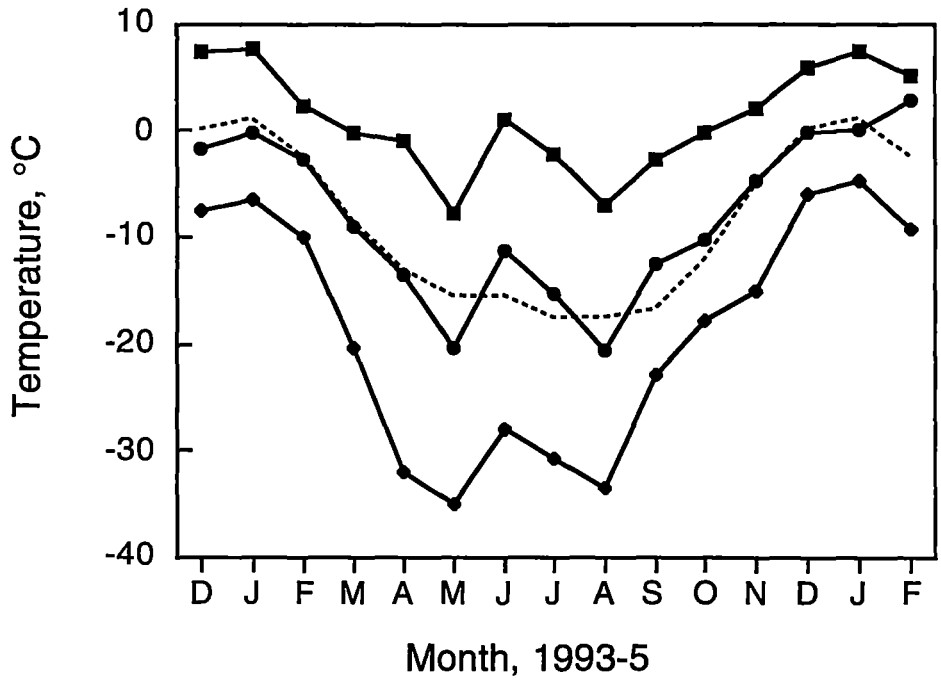


Figure 2.2. Monthly maximum (squares), minimum (diamonds) and average (circles) temperatures (°C) at Davis Station, December 1993 to February 1995. Long term average monthly temperatures are indicated by the dashed line (Data provided by the Australian Bureau of Meteorology).

The average number of sunlight hours per day followed the expected cycle, with the longest period of light in summer and no sunlight when the sun did not rise above the horizon for six weeks in winter (Figure 2.3). In December 1993 and November and December 1994 the hours of sunlight per day were higher than the long term average. Water column irradiances would not necessarily follow the same trend as shown in Figure 2.3, because irradiance is also a function of the angle of the sun above the horizon.

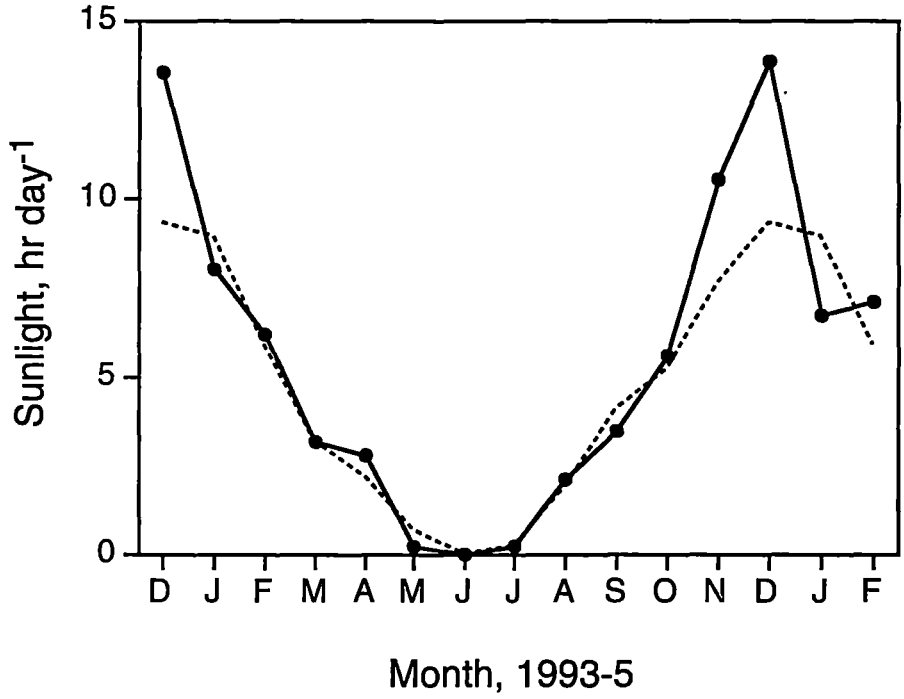


Figure 2.3. Average sunlight (hr day^{-1}) at Davis Station, December 1993 to February 1995. Long term average monthly sunlight hours are indicated by the dashed line (Data provided by the Australian Bureau of Meteorology).

2.4 Fast Ice

Sea ice along the edge of Prydz Bay persists for up to 11 months of each year. Break-out of the fast ice in front of Davis Station occurs any time from early December to late January, usually as a result of the combination of strong offshore winds and onshore

swells. Re-freezing begins in late February as first frazil ice, then pancake ice, forms along the coast. Consolidation of the ice sheet occurs rapidly, and by late March the nearshore ice is usually traversable by pedestrian traffic. Maximum thickness of 1.5 to 2 m is reached in November. The fast ice reaches its maximum area in late winter and can extend offshore for between 10 and 30 kilometres. Beyond this the pack ice extends for many hundreds of kilometres.

Congelation ice is the dominant ice type in the area around the Vestfold Hills (Scott et al. 1994). Large (≈ 1 cm), columnar crystals are interspersed with vertical brine channels. Accumulations of loose ice crystals in the form of 'stalactites' have been observed at the under-ice surface in the autumn (Tucker 1983, Perrin et al. 1987), but not in the summer (McConville and Wetherby 1983, Archer et al. 1996a).

2.5 Primary Sampling Sites

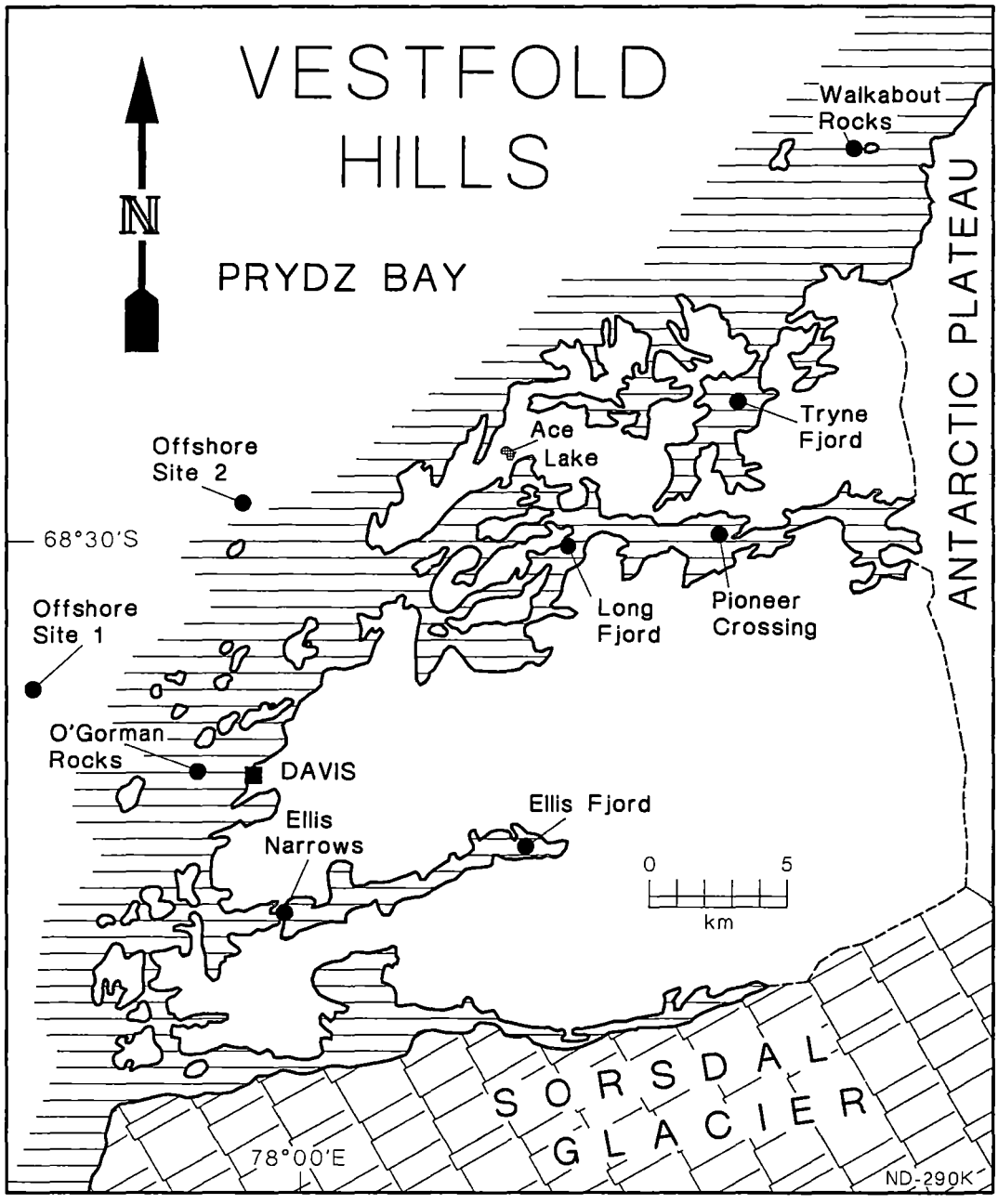
O'Gorman Rocks (68°34'S, 77°56'E; Figure 2.4) was selected as a sampling site representative of the inshore marine ecosystem for two main reasons:

(i) Sea ice at the site is traversable for much of the year and, once broken out (usually within a 24 hour period), the site can be reached easily by boat, thus increasing the period of accessibility; and

(ii) Several aspects of the ecology of the inshore marine environment at or near the site have been studied over the last fifteen years and a substantial body of literature therefore exists.

Ace Lake (68°28'S, 78°10'E; Figure 2.4) provided a site for a comparative life history study as it supports an isolated population of *Paralabidocera antarctica*, a calanoid copepod that is common in the nearshore marine environment. *Paralabidocera*

Figure 2.4. A map of the Vestfold Hills region. The locations of Davis Station, the O'Gorman Rocks sampling site, Ace Lake and the other sampling sites are indicated.



antarctica was the dominant planktonic metazoan present in the lake and represented the highest trophic level. Ace Lake is the most studied marine-derived lake in the Vestfold Hills and, as for O'Gorman Rocks, there is a considerable amount of information available concerning the ecology of the site.

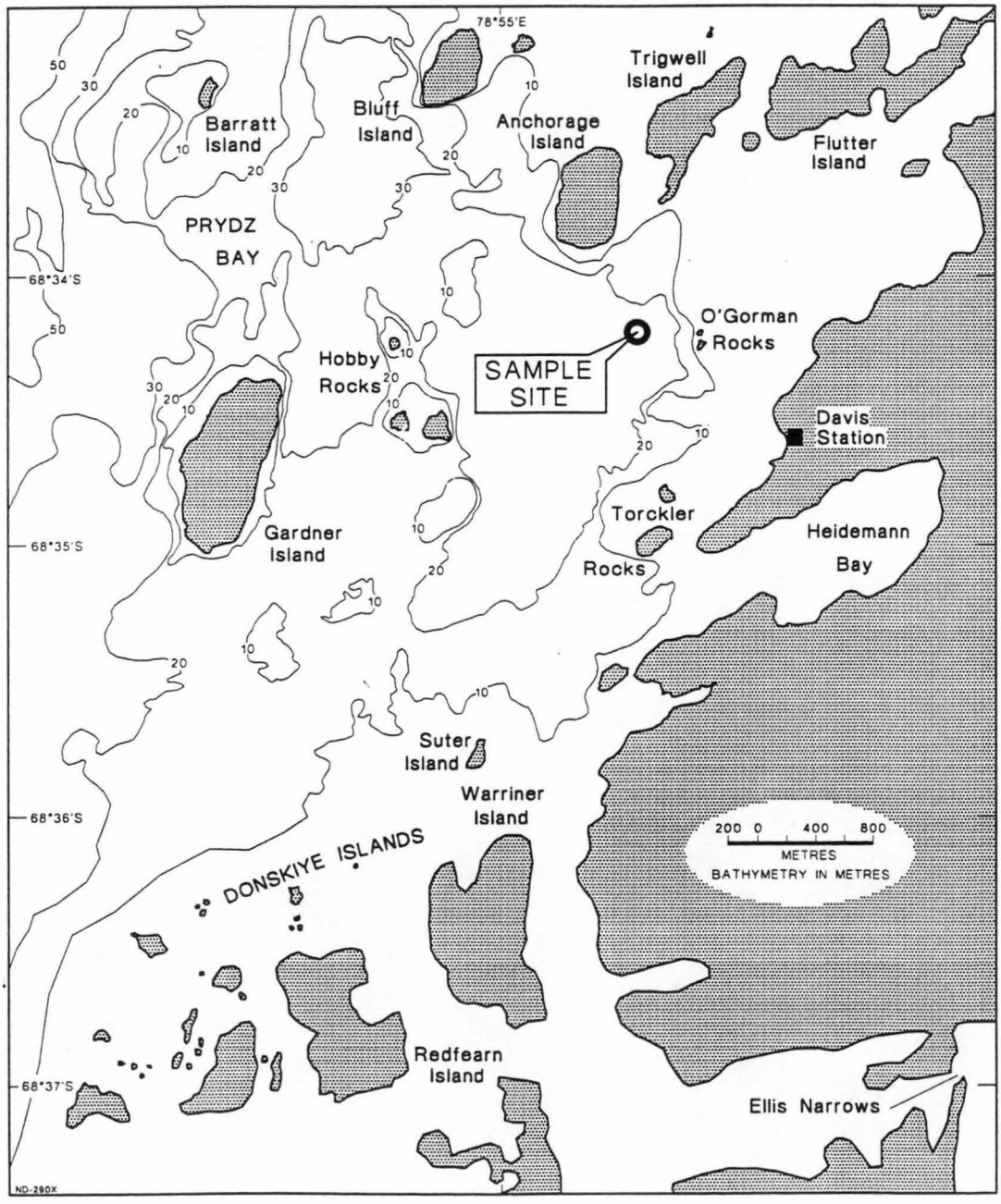
2.5.1 O'Gorman Rocks

2.5.1.1 Habitat description

The O'Gorman Rocks site was situated in the middle of a flat underwater plain that averages approximately twenty metres in water depth (Figure 2.5). The water depth at the sampling site was 23 m. The sediments of the area consist of fine silt with a high organic content (Gibson 1997).

Water flow through the inshore waters around the sampling site has not been studied. However, observations during periods of open water suggest that water enters the area from between Gardner and Anchorage Islands, and exits between Gardner Island and the Donskiye Group (Figure 2.5) (J. Gibson, personal communication 1997). The average tidal range at Davis Station is approximately 1 m (Gallagher et al. 1989). Water that flows through the site is part of the East Wind Drift that flows along the coastline of Antarctica into Prydz Bay, where it interacts with the more northerly West Wind Drift to form the Prydz Bay Gyre (Smith et al. 1984). The average velocity of water flow in the East Wind Drift is 13 to 20 cm s^{-1}, but considerably higher velocities (up to $\approx$ 60 cm s^{-1}) have been recorded in waters offshore from the Vestfold Hills (Maksimov 1958).

Figure 2.5. A bathymetric map of the waters offshore from Davis Station showing the position of the O'Gorman Rocks site. The depth contours are in metres.



Physical characteristics of the water column have been measured during several studies (e.g. Perrin et al. 1987, Davidson and Marchant 1992, Gibson 1997). Over an annual cycle water temperature increased from a winter minimum of -1.85 to -1.90 °C to a summer maximum of 0 to 1 °C. Salinity showed a similar, but inverted, trend. It reached a maximum of 34.2 to 34.5 practical salinity units (psu) at the end of winter then fell to ≈ 33 to 33.5 psu in summer, as a result of freshwater input from the melting of the sea ice, icebergs and ice shelves.

2.5.1.2 Previous studies

The inshore marine environment near Davis Station has been the site of several year-round (Tucker 1983, Perrin et al. 1987, Gibson 1990a, 1990b, Marchant and Perrin 1990, McTaggart 1994, Gibson 1997), and many summer-based research programs (Davidson and Marchant 1992, Skerratt et al. 1995, Archer et al. 1996a, 1996b, Leakey et al. 1996). The phytoplankton and bacterial assemblages present are similar, both in species distribution and seasonal cycles, to those found at other inshore Antarctic sites (e.g. Krebs 1983, Holm-Hansen et al. 1989, Knox 1990). Phytoplankton growth begins in spring in the bottom few centimetres of the sea ice, then spreads to the water column in late November or early December. The bloom in the water column continues until mid to late February. Phytoplankton that occur regularly in the area include diatoms of the genera *Entomoneis*, *Nitzschia*, *Fragilariopsis*, *Thalassiosira* and *Chaetoceros*, as well as the flagellates *Phaeocystis* and *Cryptomonas*. Phytoplankton biomass (estimated as chl *a*) is often much greater than that found further out in Prydz Bay (e.g. Hosie and Cochran 1994). However, there is a great deal of interannual variation, both in biomass and species composition, of the phytoplankton (Gibson et al. 1997a). Bacterial abundance has been shown to parallel the biomass of phytoplankton (Gibson et al. 1990b). The protozoan assemblage includes several heterotrophic dinoflagellates (Archer et al. 1996b),

nanoflagellates (Leakey et al. 1996), ciliates and choanoflagellates (Marchant and Perrin 1990).

Increased biological activity and dilution by meltwater during summer has the effect of lowering concentrations of the nutrients nitrate, phosphate and silicate (Perrin et al. 1987, Gibson 1997). As is common for other inshore Antarctic marine environments (Fukui et al. 1992, Holm-Hansen et al. 1994, McMinn et al. 1995), there is a greater reduction in the concentrations of nutrients than is usually found at deep water sites (Nelson and Tréguer 1992). In particular, nitrate is reduced to less than 0.5 μM at the height of the phytoplankton blooms (Perrin et al. 1987, Gibson 1997).

There have been two year-long studies of the abundance and distribution of zooplankton in the inshore region near Davis. Tucker (1983) and Tucker and Burton (1988, 1990) reported that the fauna was dominated numerically by small copepods, predominantly *Oncaea curvata* and *Oithona similis*. In nearby Ellis Fjord (Figure 2.4), the numerically dominant copepod species were also *O. curvata* and *O. similis*, however a higher number of non-copepod species, in particular the ctenophore *Callianira antarctica* and the hydromedusa *Rathkea lizzioides*, was recorded (Kirkwood 1993).

The inshore marine environment of the Vestfold Hills supports a well developed benthic community that includes several species of macrophytes (Thomas and Jiang 1986, Dhargalkar et al. 1988), and crustaceans, polychaetes and echinoderms (Everitt et al. 1980, Tucker and Burton 1987). Fish collected from the area include *Pagothenia bernacchii*, *Chionodraco hamatus* and the sea-ice associated *Pagothenia borchgrevinki* (Williams 1988). Commonly sighted higher predators are Weddell, elephant and leopard seals, Adélie penguins, cape petrels, snow petrels and Wilson's storm petrels.

Sea ice studies of the area near Davis are sparse and, apart from those of Lu et al. (1986) and Perrin et al. (1987), have been limited to the summer months. One hundred and thirty-five psychrophilic bacterial strains have been isolated from the fast ice and include isolates of the genera *Cytophaga*, *Vibrio*, *Shewanella* and *Psychrobacter* (Bowmen et al. 1997). The diatoms of the bottom ice algal community are characteristic of those found in fast ice at other localities. Commonly recorded genera include *Navicula*, *Nitzschia*, *Pleurosigma*, *Entomoneis* and *Cocconeis* (Perrin et al. 1987, Scott et al. 1994, Skerratt et al. 1995, Archer et al. 1996a). The interior ice community is dominated by a small dinoflagellate, *Gymnodinium* sp., and heterotrophic protozoa, including ciliates, dinoflagellates and euglenoids, are common throughout (Archer et al. 1996a). Thick algal strands hanging from the undersurface of the ice have been observed in the summer months (McConville and Wetherby 1983, McConville, et al. 1985). The strands largely consist of *Berkeleya* sp. and chains of *Entomoneis kjellmanni.*

Ice algal biomass recorded over an annual cycle (Perrin et al. 1987) reached a maximum in early May 1982 of 4.35 mg chl *a* m^{-2}, and thereafter declined to approximately 1.6 mg m^{-2} for the remainder of the year. However, Lu et al. (1986) also measured chl *a* in the sea ice at the same times and sites as Perrin et al. (1987) and they recorded a maximum concentration of 122.5 mg m^{-2} in mid-November. Archer et al. (1996a) measured up to 73.1 ($\pm$ 69.9) mg chl *a* m^{-2} in mid November 1993, which then decreased to 5.5 ($\pm$ 3.3) mg chl *a* m^{-2} by early January 1994. Large standard deviations in the data of Archer et al. (1996a) indicate a great deal of variability within replicate sets of ice cores and highlight the patchiness inherent in fast ice communities.

Tucker (1983) collected samples from the ice-water interface and found them to be dominated by the small calanoid copepods *Stephos longipes* and *Paralabidocera antarctica*, and the amphipod *Paramoera walkeri.* Kirkwood's (1993) study of Ellis Fjord described large numbers of *P. antarctica* associated with the under-ice surface

during the summer months. The life cycle of this species has been shown to be highly dependent on sea ice, with nauplii and young copepodite stages overwintering in brine channels within the ice (Hoshiai and Tanimura 1986, Hoshiai et al. 1987, Tanimura et al. 1996).

2.5.2 Ace Lake

Some 300 lakes and ponds are scattered throughout the Vestfold Hills. They range from glacier fed freshwater lakes (e.g. Lake Druzhby, salinity < 0.1 psu) to hypersaline lakes (e.g. Deep Lake, salinity > 250 psu). The saline lakes (defined as having salinity of greater than 3 psu, Burton 1981) were generally formed when pockets of seawater were trapped as the hills emerged after the retreat of the ice cap, and subsequent isostatic uplift of the land. Many of these lakes have undergone complex cycles of flushing by freshwater, and decrease of the water level by evaporation, to reach their current state. The sediments of the lakes often record the history of their formation and cores have been taken to trace their evolution (Bird et al. 1991, Fulford-Smith and Sikes 1996).

Approximately 10% of the lakes are meromictic (i.e. permanently stratified) (Gibson and Burton 1996). They form when fresher water flows onto the lake surface and is prevented from mixing by the layer of ice on the surface (Burton 1981). Stratification is then maintained by a strong salinity gradient which results in an increase in density with depth. Meromixis can be destroyed by wind mixing of the surface waters. However, as many of the lakes are ice free for only short periods, this mechanism is sometimes insufficient to mix even the surface waters.

2.5.2.1 Habitat description

Ace Lake is a saline, meromictic lake that has a maximum depth of 25 m (Figure 2.4). It has an area of 18 hectares and drains a small catchment that is approximately three times the size of the lake (J. Gibson, personal communication). There is very little allochthonous input to the lake as the catchment is free of any permanent bird colonies, and the only plant life present are small and sparse lichens and mosses. The ice cover on the lake persists for at least 11 months each year and the period of open water is short. During winter, small snow banks develop in the catchment. These banks melt during summer, leading to some meltwater input. The oxycline in the lake is at approximately 11 m and below this the water is anoxic. The oxylimnion (in the top 11 m) is the site of most of the biological activity. However, as mentioned below, anaerobic bacteria are found in the anoxic waters and sediments of the lake.

2.5.2.2 Previous studies

Ace Lake is the most intensively studied saline lake in the Vestfold Hills. Detailed investigations of the bacteria in the lake have revealed the presence of several bacterial strains including photosynthetic sulphur bacteria, *Chlorobium* spp., photosynthetic purple bacteria (Rhodospirillaceae), *Chromatium* sp (Burke and Burton 1988, Volkman et al. 1988, Mancuso et al. 1990), anaerobic bacteria of the genus *Carnobacterium* (Franzmann and Dobson 1992), and an unidentified obligately anaerobic, coiled bacterium (Franzmann and Rohde 1991). A picocyanobacterium, tentatively identified as *Synechococcus* sp. is particularly abundant just above the oxycline at 11 m (Rankin et al. 1997).

The protistan assemblage of the lake is characterised by low species diversity and strong vertical zonation. *Pyramimonas gelidicola*, a small flagellate, was found in

highest numbers just above the oxycline (Burch 1988, Volkman et al. 1988), and was sparsely distributed in waters closer to the surface. A cryptophyte of the genus *Cryptomonas* was common in surface waters during winter but migrated downwards in spring as light intensity increased, reaching its maximum abundance at 5 m (Burch 1988). *Mesodinium rubrum*, an autotrophic ciliate, was present just below the ice during winter where it may have taken advantage of the limited light available (Gibson et al. 1997b). This species reached peak abundance at 5 m in December. An unidentified prymnesiophyte, dinoflagellates, diatoms, and unidentified ciliates are also present in the lake.

In 1974 a calanoid copepod was collected from the lake and was described as a lacustrine form of *Paralabidocera antarctica* (Bayly 1978). It differed from the coastal population by being considerably smaller (about 60 % of the total length of the oceanic form), and by several minor morphological differences in the fifth leg of the male. At the same time Bayly (1978) reported a small number of *Acartia* sp. in the collections. However, as that genus has never been collected again in the lake, those specimens are now believed to have been a contaminant (Bayly and Burton 1987).

Benthic algal mats are found in the oxic waters around the edges of the lake. They support a community *inter alia* of rotifers, a harpacticoid copepod, *Idomene scotti*, and turbellarians (Dartnall 1992). There is very little known about this assemblage and to what extent it might interact with the planktonic community.

2.6 Other Sampling Sites

Three marine-derived fjords bisect the hills, with two of them running from the polar plateau to the sea and one in a northerly direction (Figure 2.4). Of the three, Ellis Fjord is by far the most intensively studied (Gallagher and Burton 1988, Kirkwood and

Burton 1988, Gallagher et al. 1989, McMinn et al. 1995, McMinn 1996, Kirkwood 1996). Ellis Fjord is 10 km long and separated from the sea by a narrow, 2 m deep sill (shown on Figure 2.4 as Ellis Narrows). The fjord has a maximum depth of 117 m and there are up to six major basins along its length separated by shallow sills (Gallagher and Burton 1988, Gallagher et al. 1989). At the time of the present study, ice in the fjord, except at Ellis Narrows, had not broken out for at least two years. The strong currents (up to 2 m s^{-1}; Kirkwood 1993) and shallow depth of Ellis Narrows keep that area ice free for much of the year.

Long Fjord is 18.5 km long and has a complex structure, with numerous bays and islands found along its length. During summer the fjord provides habitat for breeding Weddell Seals. Several narrow channels pass around three large islands that are situated at the seaward end. These narrower regions are probably of shallower depth and greater current flow than other parts of the fjord (Anderson 1993), however, no detailed bathymetric or hydrographic studies have been undertaken in this fjord. Tryne Fjord is approximately 5 km in length and has limited exchange with Tryne Bay via a narrow channel that is deeper than Ellis Narrows. To the best of my knowledge the only sampling undertaken in Tryne Fjord has been limited to the collection of a sea ice core to test for the presence of hydrocarbons (Green et al. 1992).

Chapter 3
Horizontal Patchiness of Sympagic Organisms in the Fast Ice near O'Gorman Rocks[1]

3.1 Introduction

The study of spatial and temporal variation of 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 and Dayton 1991, Levin 1992). While temporal variation in biological processes is often observed, studies specifically aimed at unravelling spatial patterns have become common only recently (e.g. Chapman et al. 1995, Harvey and Miller 1996, Thomson et al. 1996). In comparison with more accessible habitats, such as temperate forests and intertidal regions, studies of patchiness in Antarctic sea ice ecosystems are in their infancy.

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 and Dieckmann 1986, Eicken et al. 1991b) to many kilometres (Garrison and Close 1993, Scott et al. 1994). However, a systematic approach to quantifying spatial variation in sea ice is rare and Spindler (1994) noted that ice cores for study have generally been taken at random during different times and at different locations.

This chapter discusses a study designed to examine patchiness in sympagic biota at scales from metres to kilometres. Quantifying spatial variation in the sympagic biota early in this study was important because:

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[1] Published in part as: Swadling, K.M., Gibson, J.A.E., Ritz, D.A., and Nichols, P.D. 1997. Horizontal patchiness of sympagic organisms in the Antarctic fast ice. Antarctic Science, 9: 399-406. Authorship acknowledges field assistance by J.A.E. Gibson and thesis supervision by D.A. Ritz and P.D. Nichols.

a) it allowed apparent temporal changes in the ice community (Chapter 5) to be assessed in light of possible confounding effects from spatial patchiness;

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

c) it permitted a cost-benefit analysis of those scales at which further sampling effort was best directed.

3.2 Methods

3.2.1 Experimental design

The hierarchical sampling design used in this study incorporated four spatial scales, ranging from less than one metre to several kilometres (Figure 3.1). The advantages of hierarchical sampling designs are that they enable assessment of patchiness over multiple spatial scales (Kotliar and 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 near the O'Gorman Rocks site. 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, 3 replicate ice cores were collected, 0.5 to 1 m apart. All factors (Location, Site, Quadrat) in the analysis were random. Note that Location A, Site 1, Quadrat a corresponded to the O'Gorman Rocks site.

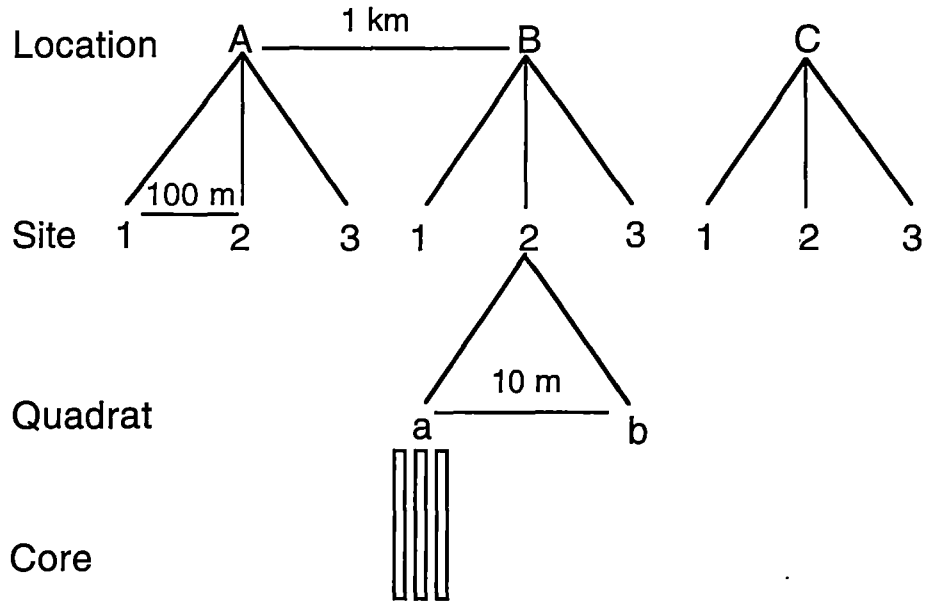


Figure 3.1. Hierarchical sampling design used in study.

The linear model used for this analysis was:

$$Y_{ijk} = ß_o + ß_1L_i + ß_2S(L)_{j(i)} + ß_3Q(S(L))_{k(j(i))} + e_{ijkl} \qquad (3.1)$$

where: Y_{ijk} is the variable under consideration (e.g. chl *a*, metazoans, salinity), $ß_o$ is the overall mean, $ß_1L_i$ is the effect of the i^{th} Location, $ß_2S_{j(i)}$ is the effect of the j^{th} Site nested within Location, $ß_3Q_{k(j(i))}$ 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)

Fifty-four sea ice cores were collected over an 8 hour period on 17 April 1994. Coring was done with a 76 mm diameter motorised SIPRE corer. On the day of collection the air temperature was approximately -15 °C, and the day was clear and sunny. The ice was cored through its entire thickness (420 to 450 mm), and each core was wrapped in opaque black plastic and returned to the laboratory. The thickness of the sea ice through each hole and the depth of the water column (Humminbird Echosounder) at each site were recorded. There was no snow cover on the ice at the time of sampling.

In the laboratory entire cores were melted (without the addition of prefiltered seawater) in 5 L opaque plastic containers at less than 8 °C. Each core yielded between 1,800 and 2,000 mL of water on melting. The melted water from each core was well mixed, then subsampled for salinity and chlorophyll measurements, and metazoan counts (Appendix A provides details of methods). 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.

3.2.2 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*; chlorophyll b (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 standardised 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.

3.3 Results

All cores consisted predominantly of congelation ice with large columnar crystals. The length of the ice cores ranged from 420 to 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 to 10.76 psu, with salinities at Location A slightly higher than those at the other two Locations (Figure 3.2). Chl *a* and chl *b* concentrations ranged from 1.76 to 78.7 mg m^{-2} and from 0.38 to 7.33 mg m^{-2} respectively. Overall, concentrations were highest at Location A and lowest at Location B (Figure 3.3). The metazoan fauna was dominated numerically by nauplii of *Paralabidocera antarctica* (Figure 3.4), which ranged in numbers from 6 x 10^4 to 4 x 10^5 m^{-2}. No copepodite

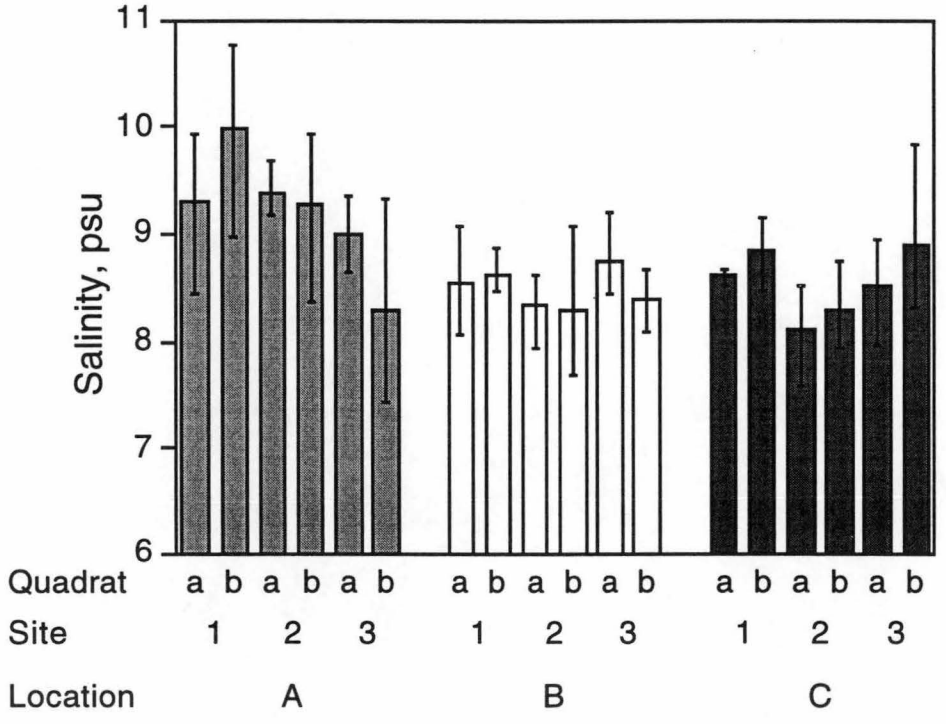


Figure 3.2. Bulk salinity (psu) of sea ice cores. Bars show the mean of three cores within a quadrat. The range of the values for each quadrat is also shown.

stages of this species were observed in the samples. 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 (Figure 3.4). Graphical 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 tested: chl *a*; chl *b*; *Paralabidocera antarctica* and *Oithona similis* (Table 3.1). 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 3.2). 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 and 100 % of the total variance. High residual variance indicated that considerable patchiness was present in the sea ice habitat at spatial scales smaller than Quadrat, i.e. between cores.

Pairwise Pearson correlation co-efficients between all eleven variables revealed only one strong relationship, that between chl *a* and chl *b* (Table 3.3, Figure 3.5A). The ratio of chl *a* : chl *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 *Paralabidocera antarctica* and chl *a* did have a fairly strong positive correlation (Figure 3.5B). However, no such trend was observed for other bivariate plots, such as chl *a* and salinity (Figure 3.5C), or *P. antarctica* and salinity (Figure 3.5D).

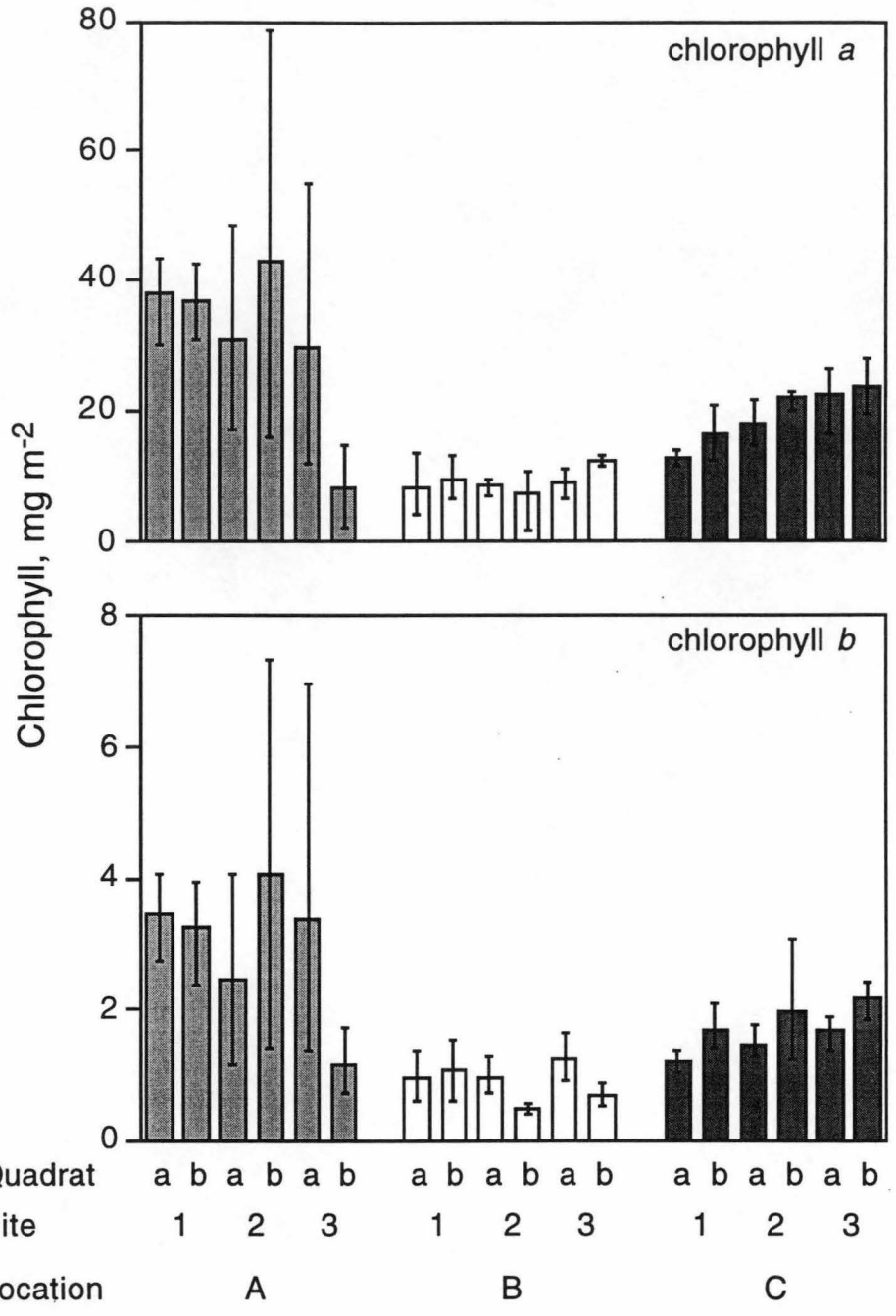


Figure 3.3. Chlorophyll concentrations (mg m^{-2}). Bars show the mean of three cores within a quadrat. The range of the values for each quadrat is also shown. Note that vertical scales are different.

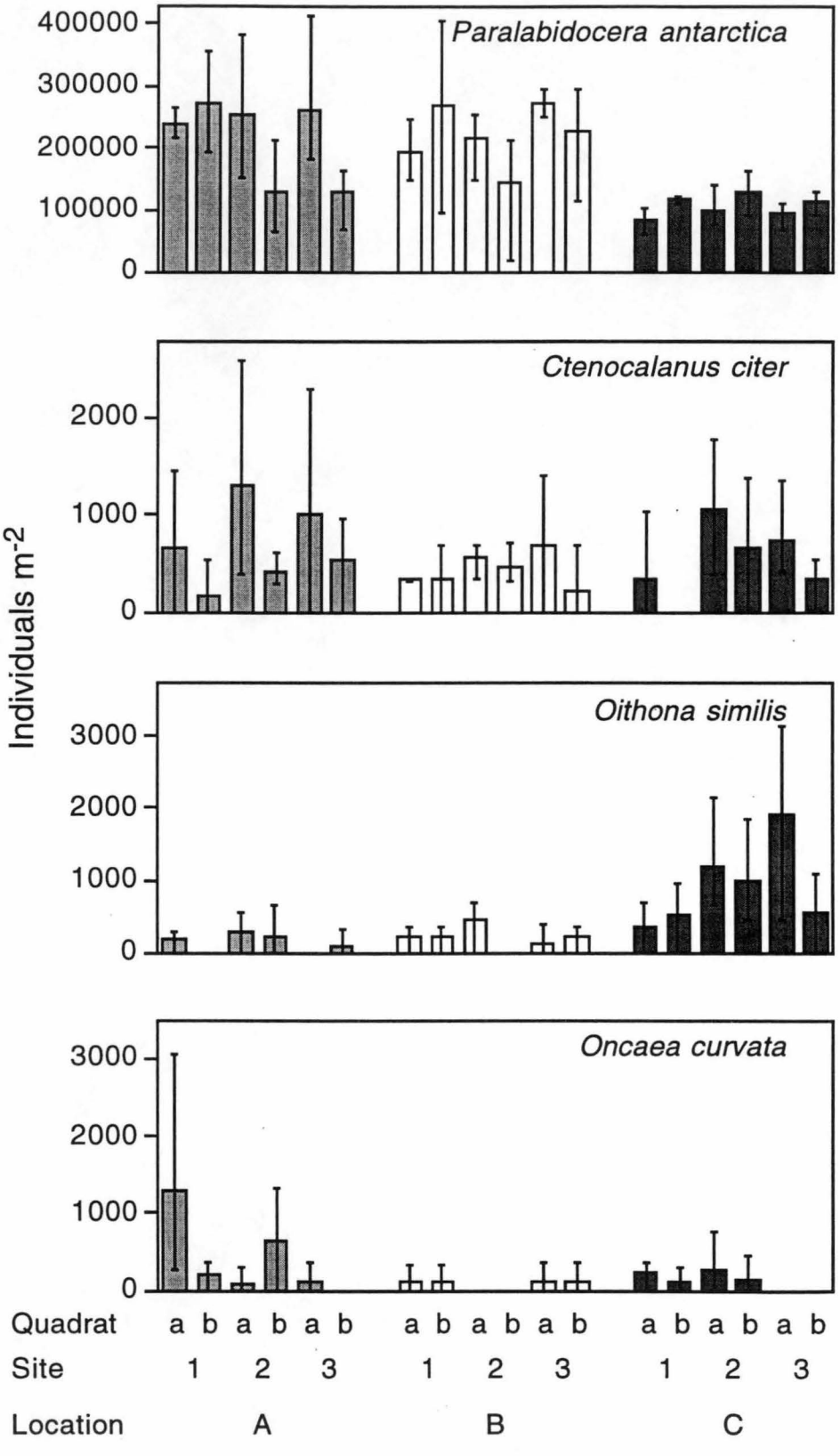


Figure 3.4. Abundance (individuals m^{-2}) of sympagic metazoans. Bars show the mean of three cores within a quadrat. The range of the values for each quadrat is also shown. Note that the vertical scales are different.

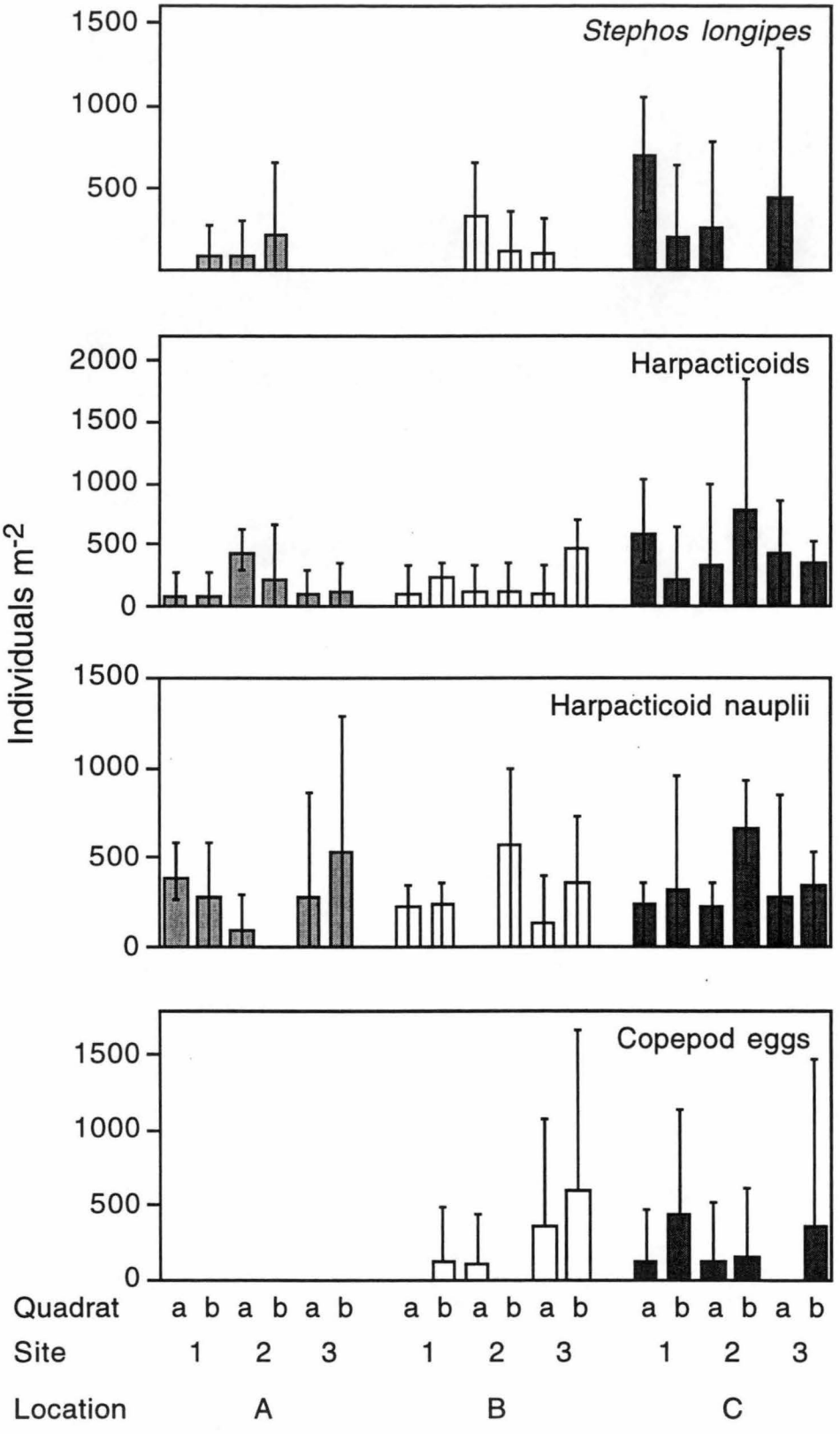


Figure 3.4. continued

Table 3.1. Summaries of analyses of variance for selected variables. Significant values ($\alpha = 0.05$) are shown in bold.

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

Source of		Chlorophyll *b*[1]			*Paralabidocera antarctica*[1]		
variation	df	MS	F	p	MS	F	p
Location	2	0.36	18.00	**0.005**	0.44	8.80	**0.016**
Site	6	0.02	1.00	0.419	0.05	0.83	0.599
Quadrat	9	0.02	1.00	0.224	0.06	1.20	0.232
Residual	36	0.02			0.05		

Source of		*Ctenocalanus citer*[2]			*Oithona similis*[2]		
variation	df	MS	F	p	MS	F	p
Location	2	64.79	0.19	0.832	1950.0	11.34	**0.009**
Site	6	341.38	2.28	0.129	171.9	0.97	0.494
Quadrat	9	149.95	0.75	0.658	176.5	1.22	0.312
Residual	36	198.92			144.4		

Source of		Harpacticoids[2]			Harpacticoid nauplii		
variation	df	MS	F	p	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

Table 3.2. Variance components (percentage) calculated from the analyses of variance.

Source of variation	Salinity	Chlorophyll *a*	Chlorophyll *b*	*Paralabidocera antarctica*
Location	21.9	42.5	49.3	36.7
Site	16.3	10.7	0	0
Quadrat	0	0	1.4	7.7
Residual	61.8	46.8	49.3	55.6

Source of variation	*Ctenocalanus citer*	*Oithona similis*	Harpacticoids	Nauplii
Location	0	36.7	12.5	0
Site	1.9	0.2	0	0
Quadrat	0	9.6	0	0
Residual	98.1	53.5	87.5	100

Table 3.3. Pearson correlation matrix for all variables measured in the study. Abbreviations are: Sal=salinity; Chl *a* = chlorophyll *a*; Chl *b* = chlorophyll *b*; 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.

	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

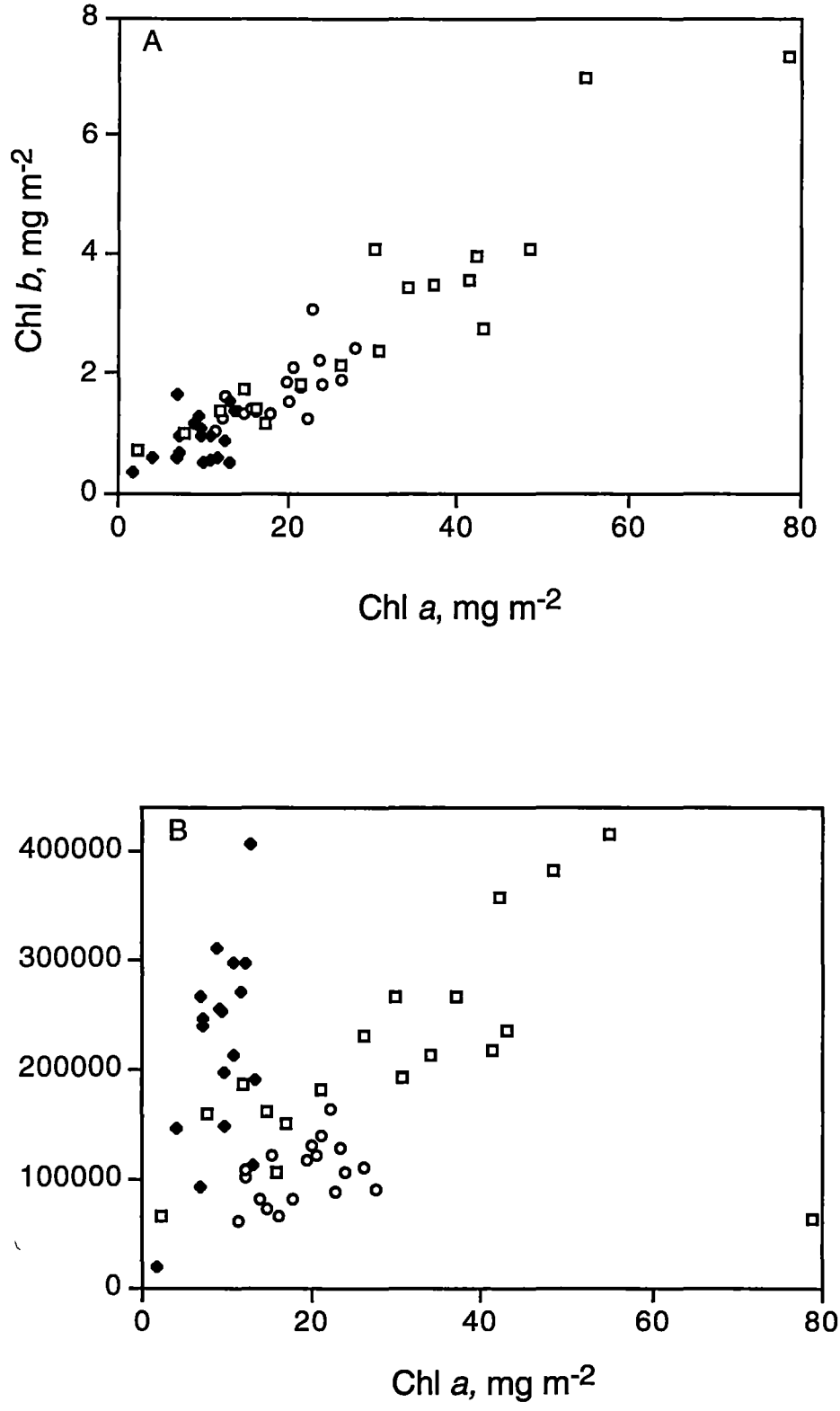
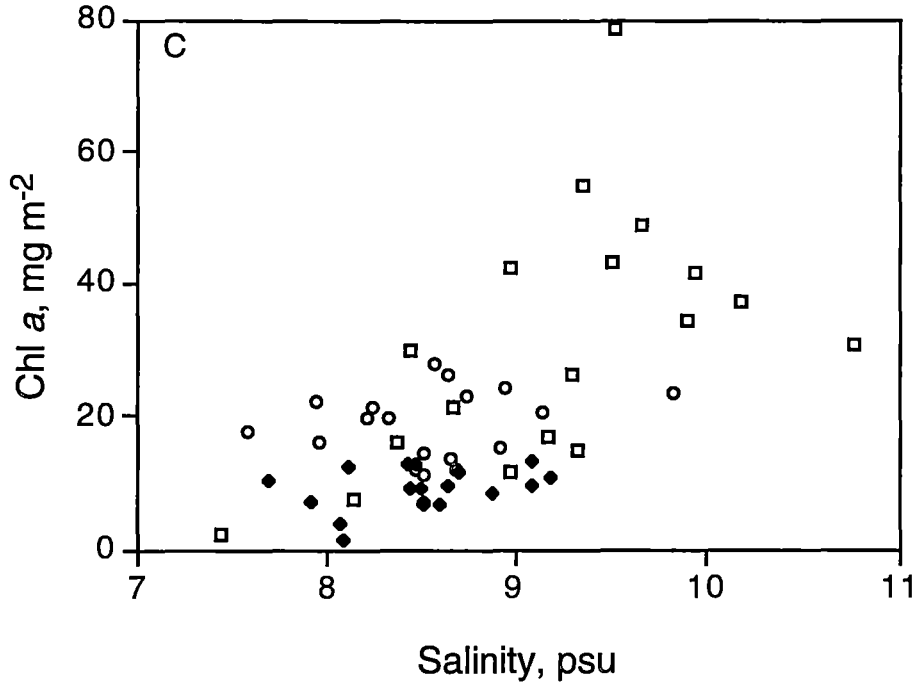


Figure 3.5. Bivariate scatterplots. A. Chlorophyll *b* and chlorophyll *a*, B. *Paralabidocera antarctica* and chlorophyll *a*, C. Chlorophyll *a* and salinity, D. *Paralabidocera antarctica* and salinity. Symbols show Location A (squares), Location B (diamonds) and Location C (circles).



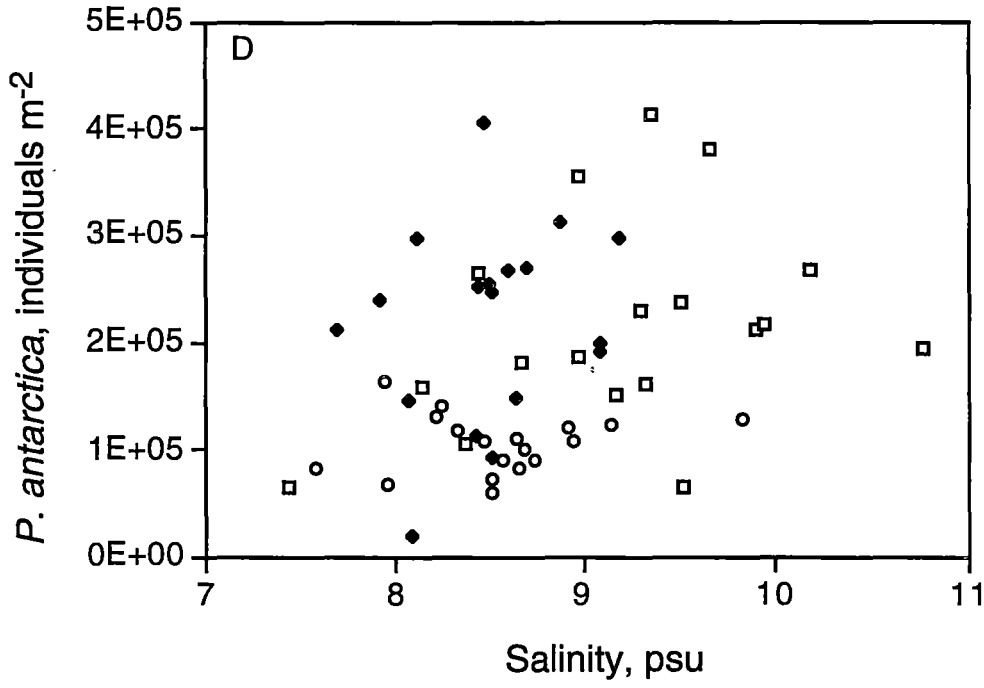


Figure 3.5. continued

3.4 Discussion

3.4.1 Autumn abundances of sympagic biota

Chl *a* concentrations, integrated over the entire ice thickness, 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 April 17 1994 (78.7 mg m^{-2}) was close to integrated chl *a* measurements made near O'Gorman Rocks during November 1982 (Lu et al. 1986) and November 1993 (Archer et al. 1996a). In contrast, the chl *a* concentrations measured during April 1994 were generally much higher than concentrations recorded from single cores by Perrin et al. (1987), at a site close to O'Gorman Rocks in 1982 (0.30 mg m^{-2} in April and 4.36 mg m^{-2} in May). The results from the present study 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) summarised 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 his study 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 sometimes up to an order of magnitude greater than those recorded during autumn near Syowa Station (Hoshiai and Tanimura 1986). Low abundances of *Stephos longipes*, another species known to associate with sea ice, reflect 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 and Burton (1990) recorded it during the year at the ice-water interface near Davis Station and it was recorded from some ice cores during

the present study (Chapter 5). It is likely that *Oncaea curvata* and *Oithona similis*, which were present in very high densities in the water column (Chapter 5), 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 the present study, harpacticoid nauplii, copepodites and adults with egg sacs were recorded from the cores, although generally in low numbers (from 0 to 5 per core). There was considerable patchiness in their distribution, a finding similar to that of Dahms et al. (1990) who recorded 0, 1 and 116 *Drescheriella glacialis* in three cores approximately one metre apart.

3.4.2 Degree of horizontal patchiness and possible causes

Of the spatial scales measured in this study only Location (1 to 2 km) contributed significant variation to the variables measured. Intermediate scales of hundreds of metres (Site) and tens of metres (Quadrat) did not contribute significantly to the variation in the data. Partitioning of variance components revealed that between 50 and 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, the results of this study suggested that future sampling regimes designed to examine spatial patchiness should be directed 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 deformation events such as rafting, ridging and crushing. However, pack ice represents by far the greatest coverage (approx. 90 %; Lizotte and Sullivan 1992) of the Southern Ocean sea ice and so the applicability of these types of studies should be assessed. Eicken et al. (1991b) measured nutrients, salinity and chl *a* at scales from 0.25 m to 20 m from three pack ice floes in the Weddell Sea and concluded there was as much variability at scales of less than one metre 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 hypothesise 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 and so movement of sympagic biota between food patches is likely. Unfortunately, the extent of movement of individual organisms within brine channels is unknown.

A further explanation is that small scale differences in the distribution of the biota are the result of the physical characteristics of the sea ice itself, such as the size and connection of brine channels, and differential brine drainage. One result of higher salinities in sea ice is greater porosity (Eicken et al. 1991b), which, in turn, implies greater area for settlement and attachment of organisms. While the present study did not reveal strong correlations between the variables measured, some results did support this concept. Location A had somewhat higher salinities than the other two Locations and also had higher densities of *Paralabidocera antarctica* and higher concentrations of chl *a*. However, given that salinity can vary greatly on scales of mm or less, these results should only be considered as a trend. 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. 1991b) probably all interact to influence settlement and subsequent development of ice-associated 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.

3.5 Conclusions

The sympagic macrofauna sampled in April 1994 near the O'Gorman Rocks site was characterised by high abundance and low taxonomic diversity, being dominated by one species of copepod. There was no clear correlation between the density of animals and chl *a*, except at Location A. Similarly, neither metazoan abundance nor chl *a* concentration strongly correlated with bulk salinity of the ice. Clearly the forces structuring the sympagic community are complex and likely to interact on a variety of scales, both in the vertical and horizontal planes. The question of whether the fast ice community near the O`Gorman Rocks site was representative of that of the wider Vestfold Hills region is discussed in the next chapter.

Chapter 4
Diversity and Abundance of Sympagic Biota in Fast Ice near the Vestfold Hills

4.1 Introduction

Low diversity and high abundance characterised the sympagic macrofauna of the sea ice near the O`Gorman Rocks site during autumn 1994 (Chapter 3). Nauplii of *Paralabidocera antarctica* dominated the assemblage, with other taxa occurring at substantially lower densities. These observations raised the following questions:

a) was the assemblage recorded from the ice near O'Gorman Rocks widespread throughout the fast ice of the region?;
b) did other species have a strong association with the sea ice during part of their life cycle?
c) were there differences in the sea ice habitat that could account for variations in the sympagic assemblage?

To answer these questions the abundance and distribution of metazoans living within the fast ice were examined from nine locations situated over approximately 35 kilometres of coastline. Physico-chemical properties of the ice were measured at each location, with the aim of identifying which environmental factors were important in structuring the metazoan communities. At the same time, the study provided an opportunity to investigate sea ice communities during winter, a comparatively poorly studied season in Antarctica. This chapter describes the study, which complements the investigation of patchiness of sympagic biota presented in Chapter 3.

4.2 Methods

Results from the study of spatial patchiness in sympagic biota (Chapter 3) suggested that sampling should be directed at the scale of kilometres rather than at scales of tens or hundreds of metres. Therefore, for the present study, sites were chosen at five fjord and four coastal locations that were from 5 to 35 km apart (Figure 4.1). The ice was sampled between 17 July and 12 August 1994. The locations were selected with the aim of sampling a range of fast ice habitats, e.g. annual or multi-year ice, coastal or fjord ice, and fast or slow water currents (Table 4.1). During this study the hours of sunlight increased from approximately 0.5 hr day^{-1} in mid-July to 3 hr day^{-1} in mid-August (Chapter 2; Figure 2.3). Air temperatures averaged between -15 and -20 °C, although temperatures as low as -30 °C were recorded. Sub-ice water temperatures were around -1.86 °C, and water column salinity ranged from approximately 33 to 35 psu.

Four cores were collected within a 4 m^2 area at each location. The entire ice thickness was cored at each site. However, as the ice thickness was greater than 1 metre at most locations the ice was cored in two or three sequential sections. Unfortunately the cutting edge of the SIPRE corer was such that it caused the core to fragment into small pieces. Therefore the structure of the cores was obscured and it was not possible to obtain reliable information on the vertical stratification. The thickness of the ice and the snow depth were measured at each hole left by the corer. Water depth (m) was measured at each location with a Humminbird Echosounder. The cores were wrapped in opaque black plastic and transported to the laboratory for processing.

As discussed above it was not possible to examine the vertical structure of the ice cores so entire cores were melted in 30 L opaque plastic fish boxes at temperatures of less than 4 °C. Each core yielded between 4,000 and 7,000 mL of water on melting. Three cores, used for the determination of chl *a*, particulate organic carbon (POC) and lipid

Figure 4.1. A map of the Vestfold Hills region showing the nine locations used in the study.

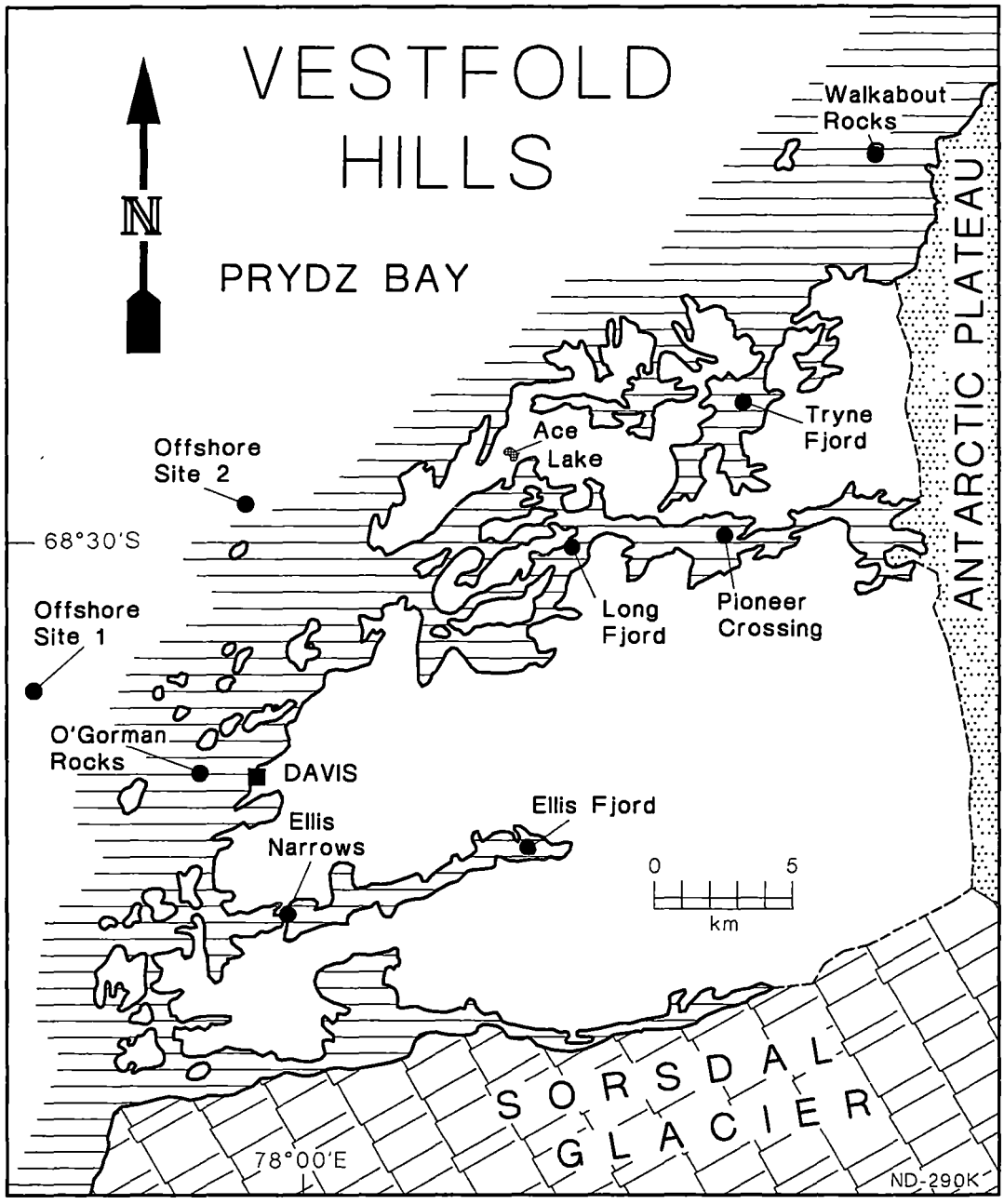


Table 4.1. Characteristics of the nine sea ice sampling locations. Abbreviations are: F = fjord location; C = coastal location. Ice thickness and snow depth show the range of values for four cores. Water depth is approximate.

Location	Date	Type	Age (years)	Ice (mm)	Snow (mm)	Water Depth (m)
Ellis Narrows	19.7.94	F	1	980-990	64-68	6
Ellis Fjord	19.7.94	F	>2	1300-1380	118-132	30
Long Fjord	12.8.94	F	1	1350-1360	174-180	20
Pioneer Crossing	24.7.94	F	1	1340-1380	148-157	20
Tryne Fjord	24.7.94	F	>1	1300-1350	84-87	65
O'Gorman Rocks	9.8.94	C	1	1270-1290	163-174	23
Offshore Site 1	17.7.94	C	1	1150-1190	49-52	>100
Offshore Site 2	12.8.94	C	1	1270-1290	130-149	60
Walkabout Rocks	25.7.94	C	1	1100-1140	76-81	> 100

concentrations, were melted in prefiltered seawater (GF/F) at dilution factors between 1:3 and 1:4 ice to seawater. The remaining core from each set of four was melted without the addition of filtered seawater. These cores were used for measurement of salinity, and macronutrient and dissolved organic carbon (DOC) concentrations. The melted core water was thoroughly mixed, then subsamples of approximately 2 L were extracted with plastic beakers. Subsamples were weighed to determine the exact dilution factor. Following the subsampling procedures water remaining from each core was filtered through a 53 μm mesh sieve, and material retained on the sieve was preserved in 10 % Borax-buffered Steedman's fixative (Appendix A.3). Details of methods are provided in Appendix A.

4.3 Results

4.3.1 Environmental parameters

Integrated nutrient concentrations and bulk salinities of the ice at each location are given in Table 4.2. Salinity of the ice cores ranged from 3 psu in Long Fjord to 11 psu at Ellis Narrows. Phosphate concentrations ranged from 0.19 to 1.43 μM and were substantially lower than those recorded in the water column throughout the year (Gibson 1997). Nitrate concentrations were lower than recorded in the water column during winter (Gibson 1997), and ranged from a minimum of 1.50 μM at Ellis Fjord

Table 4.2. Bulk salinity (psu) and integrated nutrient concentrations (μM) in the sea ice cores collected from the nine locations. Data from 2 m water depth at O'Gorman Rocks and a site in Ellis Fjord measured at the time of this study are shown for comparison.

Location	Salinity (psu)	Phosphate (μM)	Silicate (μM)	Nitrate (μM)
Ellis Narrows	11	0.77	12.9	5.91
Ellis Fjord	5	1.43	3.10	1.50
Long Fjord	3	0.34	2.24	3.42
Pioneer Crossing	4.5	0.64	2.20	2.90
Tryne Fjord	7	0.19	8.87	4.77
O'Gorman Rocks	5	0.31	6.66	2.53
Offshore Site 1	8	0.89	6.66	3.64
Offshore Site 2	7	0.61	5.27	3.04
Walkabout Rocks	8.5	0.98	7.45	3.70
[1]O'Gorman Rocks 9/8/94	32.7	1.9	63.8	26.7
[1]Ellis Fjord 8/7/94	34.2	2.1	47.7	21.1

[1]Gibson (1997)

to a maximum of 5.94 μM at Ellis Narrows. Pioneer Crossing had the lowest silicate concentration (2.20 μM), and concentrations at all sites (range: 2.20 to 12.9 μM) were much lower than recorded from the water column at O'Gorman Rocks (Gibson 1997).

Mean chl *a* concentrations, integrated over the entire ice thickness, ranged from 1.7 mg m^{-2} at Ellis Narrows to 13.5 mg m^{-2} at Tryne Fjord (mean: 7.0 mg m^{-2}) (Table 4.3), and were at least one order of magnitude higher than those of the water column at that time, indicating that substantial amounts of algae were present in the sea ice during the winter months. POC concentration showed little variation between locations,

Table 4.3. Integrated concentration of carbon (g m^{-2}) and chl *a* (mg m^{-2}) measured at the nine locations. DOC concentrations are from a single core at each location. POC and chl *a* are the mean of three determinations ± S.D. Chl *a* concentrations (μg L^{-1}) from 2 m water depth at O'Gorman Rocks and a site in Ellis Fjord measured at the time of this study are shown for comparison.

Location	Chl *a*		DOC	POC	POC : Chl *a*
	(mg m^{-2})	μg L^{-1}	(g m^{-2})	(g m^{-2})	(w/w)
Ellis Narrows	1.7 (0.6)	1.7	1.4	2.0 (0.8)	1421
Ellis Fjord	7.4 (9.4)	5.5	3.2	2.8 (0.3)	976
Long Fjord	3.8 (0.7)	2.8	2.8	2.9 (0.7)	778
Pioneer Crossing	3.8 (0.8)	2.8	1.9	1.6 (0.8)	439
Tryne Fjord	13.5 (7.4)	10.1	4.1	2.6 (0.8)	316
O'Gorman Rocks	12.4 (0.5)	9.8	6.0	2.3 (0.4)	181
Offshore Site 1	5.3 (0.7)	4.6	2.4	2.7 (1.7)	538
Offshore Site 2	11.4 (0.2)	8.5	2.7	2.1 (0.2)	184
Walkabout Rocks	3.4 (0.9)	3.1	1.8	2.4 (0.8)	690
O'Gorman Rocks		0.2			
[1]Ellis Fjord		0.3			

[1]Gibson (1997)

averaging 2.4 g m^{-2}. Chl *a* and POC were not strongly correlated (Pearson Correlation; n = 27, r^2 = 0.12), and the variation in POC : chl *a* mainly reflected variation in chl *a* concentrations between the locations. DOC concentrations were lowest at Ellis Narrows (1.4 g m^{-2}) and highest at O'Gorman Rocks (6.0 g m^{-2}), and were significantly higher than concentrations measured in the water column throughout the year at O'Gorman Rocks and Ellis Fjord (Gibson 1997).

Substantial input of biogenic carbon from non-algal sources, such as bacteria and microzooplankton, is further suggested by high lipid : chl *a* ratios (Table 4.4). Polar lipids were the major lipids in the ice cores, with lesser amounts of triacylglycerols, hydrocarbons and free fatty acids. No sterols were detected in the samples.

Table 4.4. Lipid content (g m^{-2}) and composition (%) of the sea ice at the nine locations. (Mean ± S.D; n = 3). Abbreviations are: HC = hydrocarbons, TAG = triacylglycerols, FFA = free fatty acids, PL = polar lipids. NA = no data available for those locations due to equipment malfunction.

Location	Lipid	Lipid : Chl *a*	HC	TAG	FFA	PL	TAG : PL
	(g m^{-2})	(w/w)			(%)		(w/w)
Ellis Narrows	3.3 (2.4)	1943	21	3	6	70	0.04
Ellis Fjord	NA						
Long Fjord	4.8 (1.4)	1281	11	9	3	77	0.12
Pioneer Crossing	NA						
Tryne Fjord	NA						
O'Gorman Rocks	2.2 (1.2)	176	9	29	2	60	0.48
Offshore Site 1	2.0 (0.6)	381	18	0	11	71	0
Offshore Site 2	4.1 (1.4)	358	17	0	12	71	0
Walkabout Rocks	NA						

4.3.2 Metazoan abundance and diversity

The sympagic macro-fauna was characterised by low taxonomic diversity and high abundance. Densities were highly variable, with mean abundances ranging from 30,400 m^{-2} at Tryne Fjord to 577,700 m^{-2} at Pioneer Crossing (Figure 4.2). Overall, the highest densities occurred at the two locations sampled in Long Fjord. One-way analysis of variance (ANOVA) was used to test for differences between mean total densities at each location. ANOVA was performed on individuals per litre, rather than per m^2, to account for differences in sea ice thickness. Prior to analysis abundances were $\log_{10}(x+1)$ transformed to remove the effect of the mean on the variance. As is evident from Figure 4.2, there was a significant difference between mean total densities at the nine locations (d.f. = 35, F = 4.31, p = 0.00).

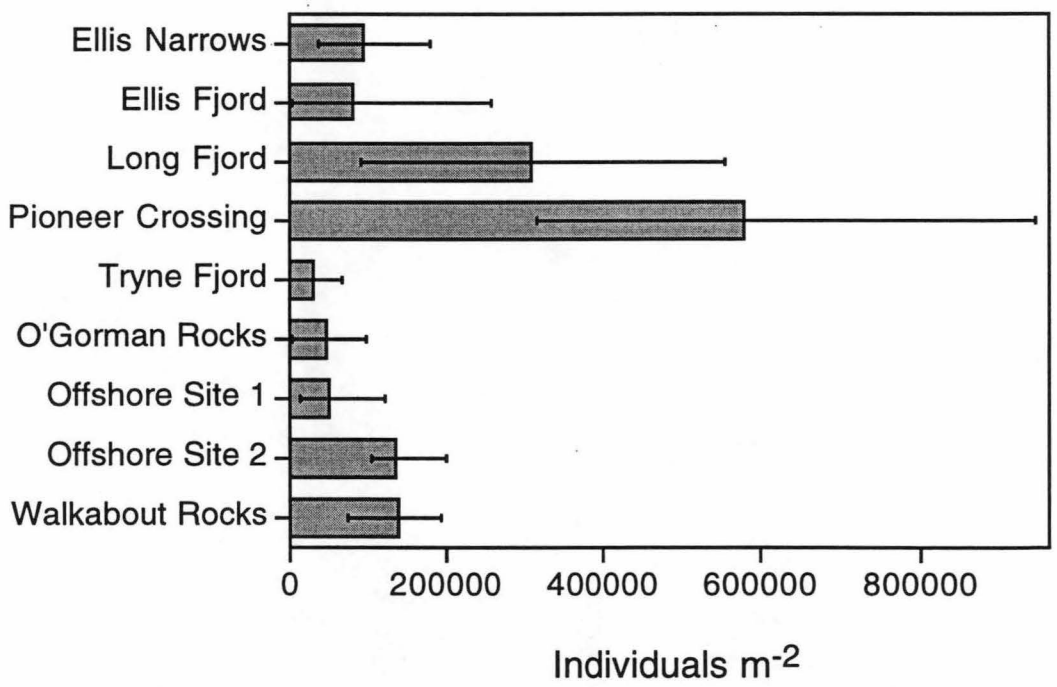


Figure 4.2. Total metazoan abundance (individuals m^{-2}) in sea ice from nine locations around the Vestfold Hills. Bars show the mean of four cores. The range of the values for each location is also shown.

Paralabidocera antarctica numerically dominated the metazoan assemblage at eight of the nine locations, accounting for at least 65 % of the total abundance (Table 4.5). In

contrast, a harpacticoid copepod, *Drescheriella glacialis*, accounted for 94 % of all specimens at Ellis Narrows. In general, other taxa, including *Stephos longipes*, *Oithona similis*, *Oncaea curvata*, cyclopoid-type nauplii, turbellarians and unidentified harpacticoids, contributed less than 5 % to the total. The exception was Tryne Fjord, where unidentified turbellarians comprised approximately 8 % of the total.

Table 4.5. Relative abundance (%) of each taxon recovered from the nine sea ice locations. Abbreviations are: P. ant = *Paralabidocera antarctica*; D. gla = *Drescheriella glacialis*; S. lon = *Stephos longipes*; O. cur = *Oncaea curvata*; O. sim = *Oithona similis*; Turb = unidentified turbellarians; Harp = unidentified harpacticoids.

Location	P. ant	D. gla	S. lon	O. cur	O. sim	Turb	Harp
Ellis Narrows	5	94	<1				<1
Ellis Fjord	98						2
Long Fjord	71	27			<1		<1
Pioneer Crossing	94	5	<1	<1			
Tryne Fjord	73	17	<1	<1		8	
O'Gorman Rocks	96			<1			3
Offshore Site 1	86	12	<1		<1		<1
Offshore Site 2	79	21					
Walkabout Rocks	65	34		<1			

The density of *Paralabidocera antarctica* was highest at Pioneer Crossing in Long Fjord and lowest at Ellis Narrows (Figure 4.3). Naupliar stages represented between 99 and 100% of the total abundance of this species at each location. Copepodites were present at only four of the nine locations, and then occurred in very low numbers (Figure 4.4). At Pioneer Crossing, Offshore Site 1 and Offshore Site 2 the copepodites came from only one of the four cores, while at O'Gorman Rocks copepodites were recovered from two of the four cores. *Drescheriella glacialis* was the dominant harpacticoid copepod at seven of the nine locations, reaching densities of up

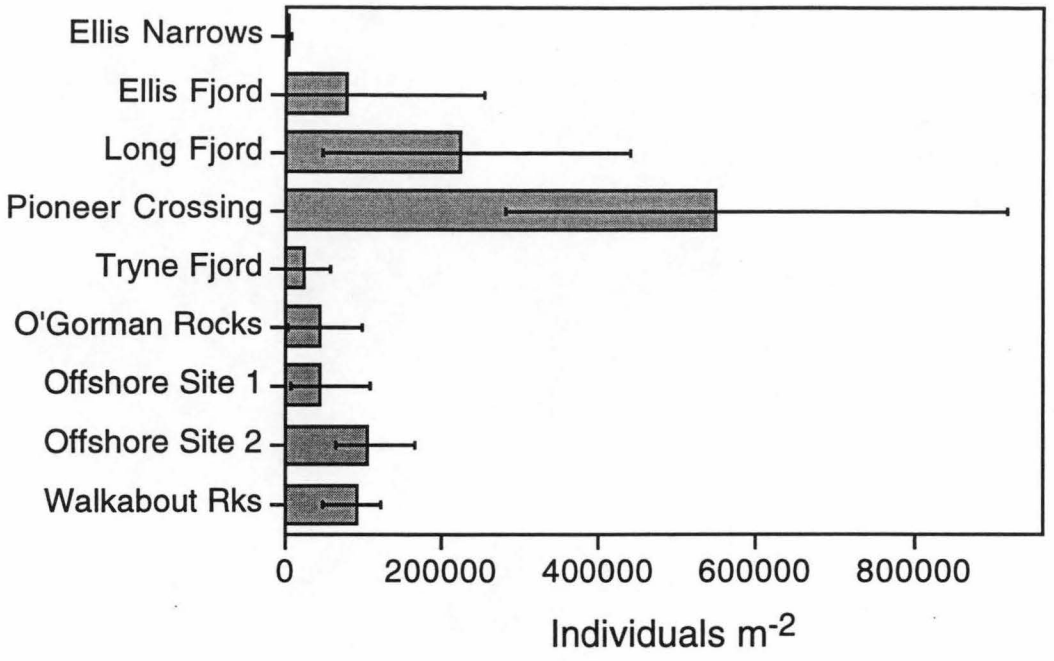


Figure 4.3. Mean density (individuals m^{-2}) of *Paralabidocera antarctica* at the nine sea ice locations. Bars show the mean of four cores. The range of the values for each location is also shown.

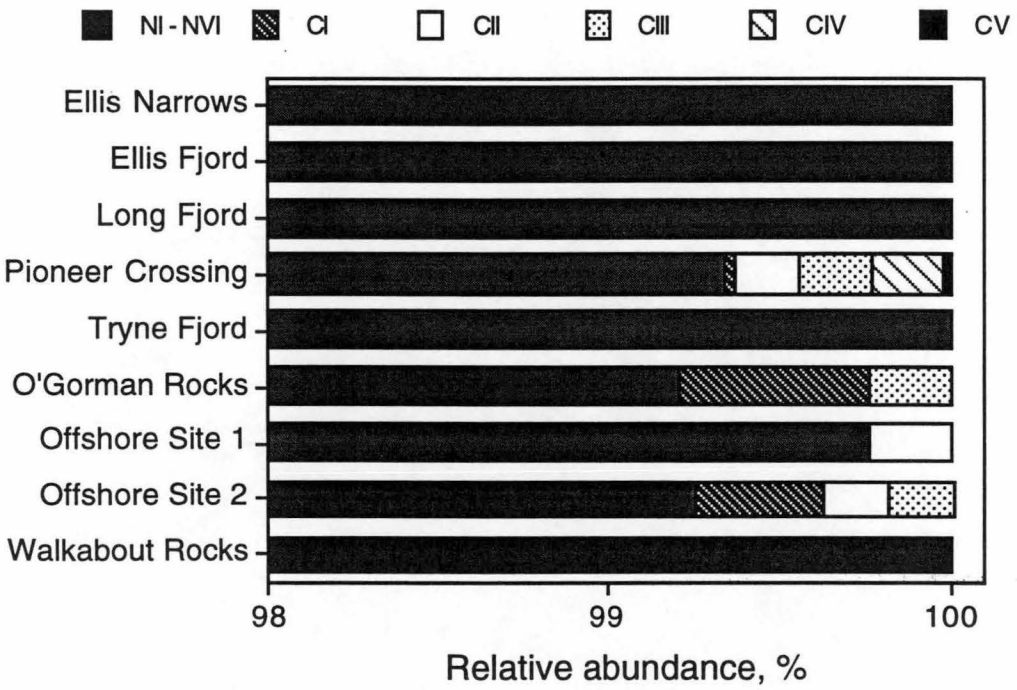


Figure 4.4. Relative abundance (%) of the developmental stages of *Paralabidocera antarctica* in sea ice cores from the nine locations. Note that the x-axis scale begins at 98 %.

to 100,000 m^{-2} at Ellis Narrows and Long Fjord (Figure 4.5). Nauplii and copepodites were recorded at each of those seven locations. Small numbers of adults, including several females with attached egg sacs, were observed from Ellis Narrows, Walkabout Rocks and Offshore Site 2 (Figure 4.6). A few unidentified harpacticoids, but no *D. glacialis*, were noted at O'Gorman Rocks and Ellis Fjord.

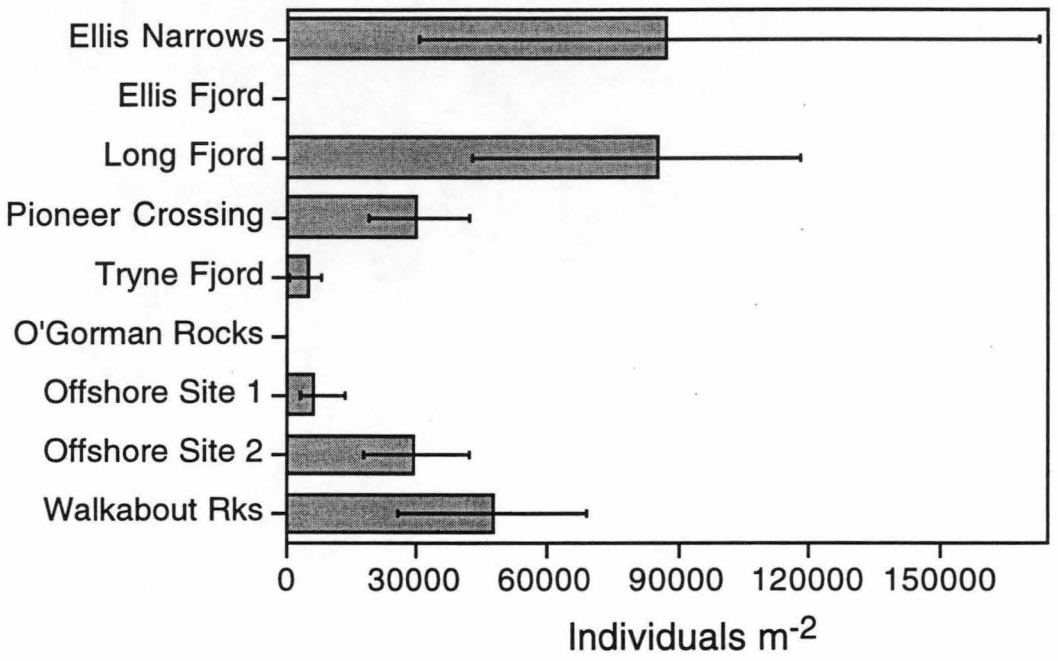


Figure 4.5. Mean density (individuals m^{-2}) of *Drescheriella glacialis* at the nine sea ice locations. Bars show the mean of four cores. The range of the values for each location is also shown. Note that no *D. glacialis* were recorded from O'Gorman Rocks or Ellis Fjord.

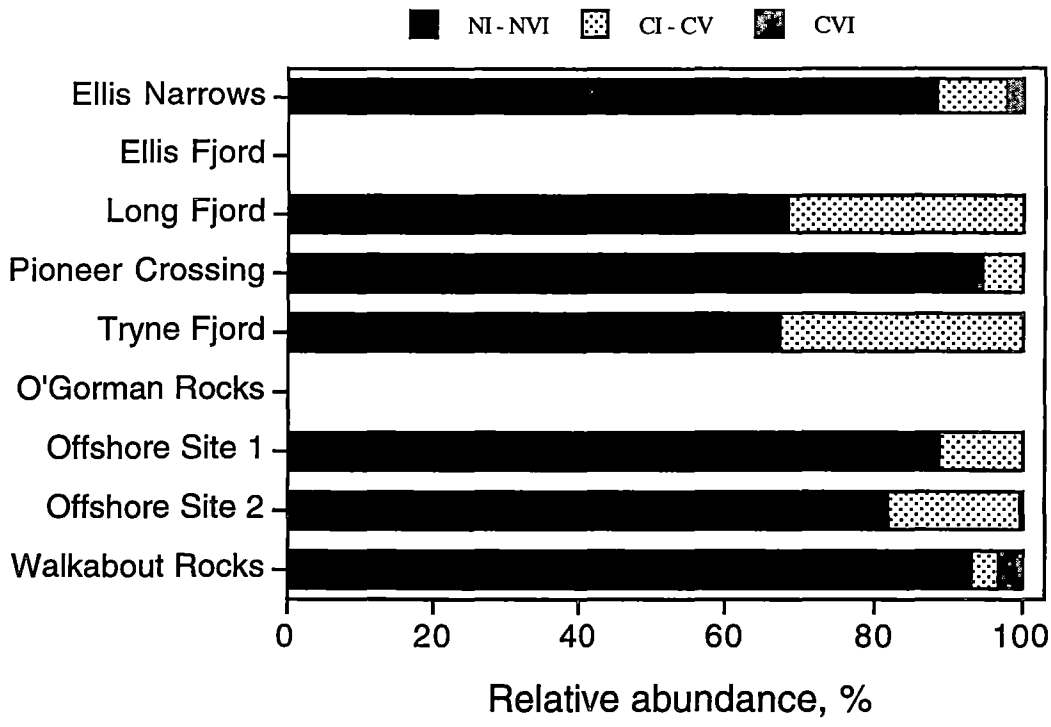


Figure 4.6. Relative abundance (%) of the developmental stages of *Drescheriella glacialis* in sea ice cores from the nine locations. Note that no *D. glacialis* were recorded from O'Gorman Rocks or Ellis Fjord.

4.3.3 Relationships between metazoans and environmental parameters

Analysis of complex multivariate data sets can take a variety of forms, and usually requires the application of more than one statistical technique. For example, clustering is commonly used in conjunction with ordination which, when there is agreement between results from these two approaches, strengthens belief in the adequacy of both (Clarke and Warwick 1994).

Densities of each taxon in each core (number per litre) were analysed by cluster analysis using the Bray-Curtis dissimilarity index (Bray and Curtis 1957), coupled with unweighted pair group average linkage (UPGMA). Prior to the calculation of dissimilarities data were $\log_{10}(x+1)$ transformed to downweight the importance of very

abundant taxa and to increase the weighting of rare or less abundant species (Clarke and Warwick 1994). The Bray-Curtis index was chosen because of its ability to deal with data sets with a high component of zero entries (Clarke and Warwick 1994).

The dendrogram resulting from the Bray-Curtis analysis revealed that cores were clustered more or less randomly with cores from every other site (Figure 4.7), indicating that within site variation was as great as between site variation. Clarke and Warwick (1994) state that when this situation occurs it could be dangerous to proceed with further statistical interpretation. Therefore, it was believed that to apply an ordination technique to this data set might subsequently lead to erroneous conclusions about the relative importance of environmental variables in structuring the assemblages. Furthermore, pairwise Pearson correlation co-efficients between the six variables that had been measured from three cores at each location (*Paralabidocera antarctica*, *Drescheriella glacialis*, chl *a*, POC, ice thickness, snow depth) did not reveal any strong correlations except that between ice and snow (Table 4.6).

Table 4.6. Matrix of Pearson correlation co-efficients for 6 variables measured from 27 sea ice cores from the nine locations. Abbreviations are: P. ant = *Paralabidocera antarctica*; D. gla = *Drescheriella glacialis*.

	P. ant	D. gla	Chl *a*	POC	Ice	Snow
P. ant	1.00					
D. gla	0.03	1.00				
Chl a	-0.11	-0.42	1.00			
POC	-0.06	0.13	0.12	1.00		
Ice	0.41	-0.49	0.36	-0.09	1.00	
Snow	0.44	-0.12	0.12	-0.33	0.72	1.00

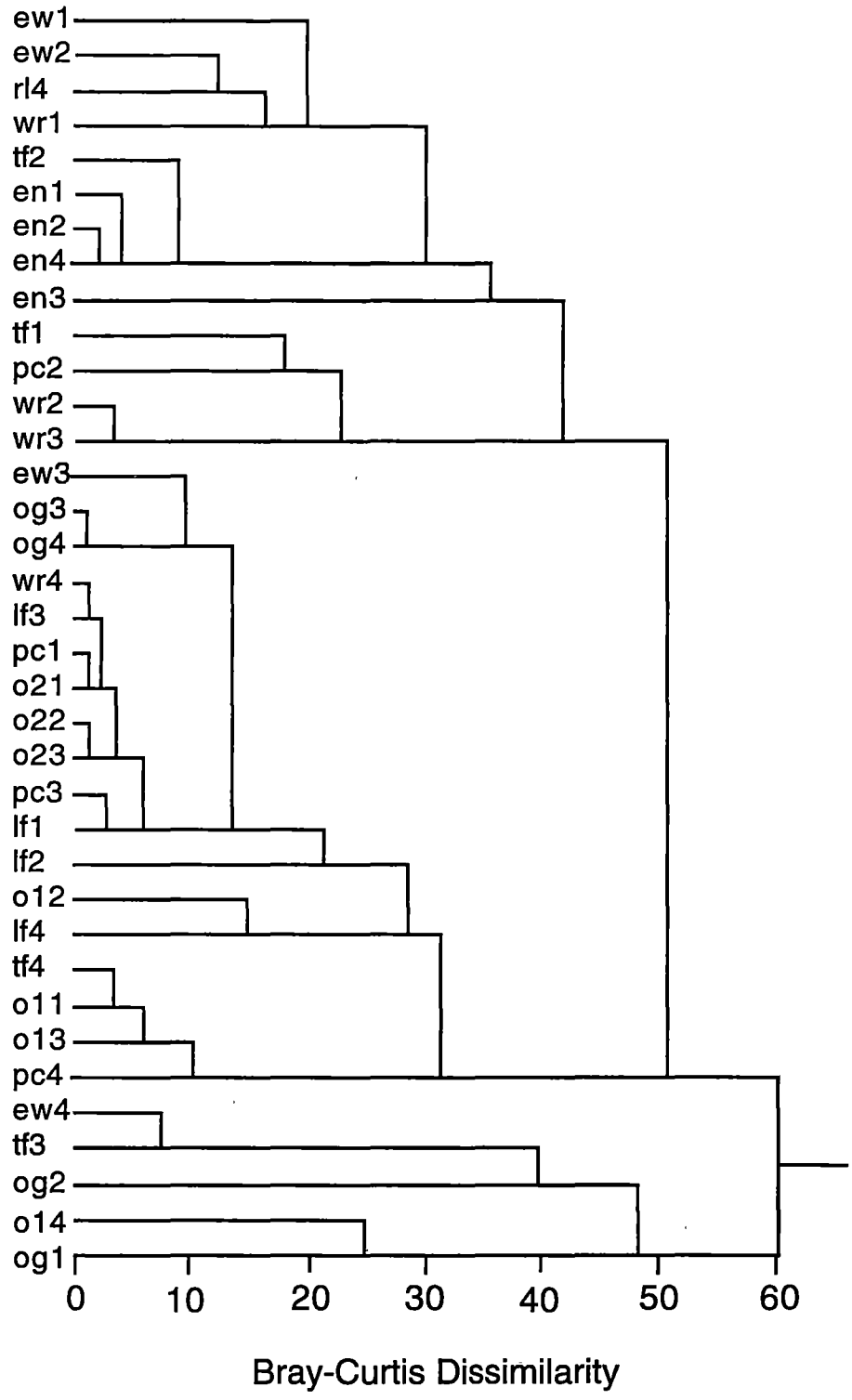


Figure 4.7. Dendrogram for hierarchical clustering of the 36 sea ice cores from nine locations, using UPGMA linking of Bray-Curtis dissimilarities calculated on $\log_{10}(x+1)$ data. Abbreviations are: ef = Ellis Fjord; en = Ellis Narrows; og = O'Gorman Rocks; tf = Tryne Fjord; pc = Pioneer Crossing; wr = Walkabout Rocks; lf = Long Fjord; o1 = Offshore Site 1; o2 = Offshore Site 2. Numerals 1 to 4 refer to the numbers of the cores at each site.

4.4 Discussion

4.4.1 Metazoan assemblages

Fast ice sampled from coastal and fjord sites near the Vestfold Hills in July and August 1994 was characterised by low macrofaunal diversity and high abundance of one or two dominant species. *Paralabidocera antarctica* was the most common metazoan sampled from all locations except Ellis Narrows, where *Drescheriella glacialis* was numerically dominant. Also present in the ice samples, albeit in low numbers, were *Stephos longipes*, *Oncaea curvata*, *Oithona similis*, at least two other species of harpacticoids, and turbellarians.

The above suite of species is typical of the sea ice assemblages that have been described to date. Copepods, turbellarians, nematodes and amphipods are the most common metazoans found in both Arctic and Antarctic sea ice. For example, the metazoan assemblage in fast ice near Syowa Station was dominated by *Paralabidocera antarctica*. Also common at that site were at least three different species of harpacticoids, however no attempt was made to identify them (Hoshiai and Tanimura 1986). To my knowledge no studies of the pack ice macrofauna have been made in the Indian Ocean sector of the Southern Ocean so it is not yet possible to determine whether a species assemblage similar to that in the fast ice is found further offshore.

In the Weddell Sea the sympagic macrofauna is dominated by a calanoid copepod, *Stephos longipes*, and several harpacticoid copepods, the most common of which is *Drescheriella glacialis* (Dahms et al. 1990, Spindler et al. 1990, Garrison 1991, Kurbjeweit et al. 1993). The foraminiferan *Neogloboquadrina pachyderma*, common in the Weddell Sea (Spindler and Dieckmann 1986, Spindler et al. 1990), has not been recorded from the eastern side of the continent (Hoshiai and Tanimura 1986, Chapter 5, this study). Furthermore, *S. longipes* was never found in the sea ice in large

numbers during the present study, although it occurred in reasonable abundance in the water column at different times (Chapter 5). It is possible that *S. longipes* occupies a similar ecological niche to *Paralabidocera antarctica* and replaces it in the Weddell Sea where conditions are more favourable for the existence of *S. longipes*. To my knowledge *Paralabidocera antarctica* has not been recorded from ice in the Weddell Sea (e.g. Kurbjeweit et al. 1993).

Arctic sea ice supports communities of turbellarians, nematodes, amphipods and both harpacticoid and cyclopoid copepods. In contrast to the Antarctic fast ice, no calanoid species have been found (Kern and Carey 1983, Grainger and Hsaio 1990). The Arctic sympagic fauna is dominated by meiobenthic species, especially over shallow areas, yet Kern and Carey (1983) noted no special adaptations for colonising the sea ice.

The low number of taxa inhabiting sea ice implies that comparatively few species possess the behavioural and physiological traits necessary for successful colonisation. For example, it would be expected that sea ice inhabitants all show strong degrees of euryhalinity. Salinity of interstitial brine channels probably changes frequently as brine is either concentrated by exclusion from the ice matrix or, alternatively, diluted as the ice melts. *Drescheriella glacialis* has been shown to survive in salinities from 18 to 90 psu, although it exhibited lethargic behaviour at both extremes of the range (Dahms et al. 1990). The euryhaline nature of *Paralabidocera antarctica* is indicated by its presence in hyposaline Antarctic lakes (10 to 20 psu) (Bayly 1978). Furthermore, 100 % survival rates have been recorded for nauplii of *P. antarctica* which were maintained for twelve days at salinities from 30 to 55 psu (G. Watson, unpublished data).

4.4.2 Variability in the fast ice environment

One aim of this study was to determine which environmental factors might play a significant role in structuring the fast ice assemblage. As discussed in Section 4.2 locations were selected with the goal of sampling as wide a range of fast ice habitats as practicable. Very little information existed about the sea ice in the region, and therefore the choice of sites was to some degree arbitrary. Including Ellis Narrows as a sampling site was fortuitous as it was the only location where *Drescheriella glacialis* was clearly dominant. Had this site not been sampled an erroneous assumption about the ubiquitous dominance of *Paralabidocera antarctica* could have been formed. The question of why *D. glacialis* replaced *P. antarctica* as the dominant metazoan species at Ellis Narrows is addressed in the forthcoming discussion.

4.4.2.1 Patchiness in food supply

Chl *a* concentrations (as an estimate of algal biomass) varied both between and within locations, but clearly indicated the presence of ice algae. As was also indicated by the study presented in Chapter 3, algae were patchily distributed on the under-surface of the fast ice. In the present study there was no clear correlation between chl *a* and the abundance and distribution of copepods. Patchiness in ice algae is dependent on snow cover thickness, light availability and nutrient supply. Light levels during the sampling period were very low (expressed as hr sunlight day^{-1}), yet it is known that under ice algae can continue to photosynthesise at irradiances as low as 0.1 % of the surface irradiance (Palmisano and Sullivan 1983). Chl *a* concentrations were not directly related to either sampling date or snow cover. This result is not surprising as chl *a* concentrations would largely reflect the past history of the ice. In particular, snow cover was very dynamic and would have fluctuated as a result of variation in wind speeds, precipitation and ablation.

There were sufficient nutrients for winter growth of ice algae yet the relationship between nutrients and chl *a* was not clear. The concentrations of nitrate and phosphate were lower than those measured in the water column at O'Gorman Rocks and Ellis Fjord. Silicate concentrations were substantially lower than in the water column, but were unlikely to have been limiting (Gibson, 1997). That nutrients were not limiting for algal growth was further suggested by the measurement of low levels of triacylglycerols relative to polar lipids at five of the nine locations. Accumulation of triacylglycerols by algae is indicative of physiological stress induced by environmental changes, such as nitrogen depletion, and may occur at the end of summer when ice algae are entering a quiescent phase (Nichols et al. 1989, Skerratt, et al. 1995).

In the absence of sufficient quantities of ice algae, detritus, in the form of faecal pellets, cadavers and exuviae of crustaceans, could provide a potential food source for sympagic heterotrophs. Concentrations of POC and DOC were high throughout the ice, and much higher than chl *a* concentrations, suggesting that there was a substantial input of biogenic carbon from non-algal sources. Once again, there was no clear correlation between POC concentration and the distribution of metazoans.

From this study it is suggested that, while food supplies may be patchy, there is a substantial potential supply available. However, the lack of a clear correlation between chl *a* or POC and metazoan densities suggests that food supply alone is not the main factor determining the distribution and abundance of metazoans. Rather it is likely that as the food supply waxes and wanes in the sea ice the heterotrophs move from one patch of food to another.

4.4.2.2 Water currents and formation of sea ice

Fast ice sampled during this study was composed primarily of congelation ice with very little frazil ice present. Although superficially similar, formation of the ice was likely to differ between coastal and fjord sites as a result of differences in bottom topography and water currents. At O'Gorman Rocks the ice began forming in early March 1994 and did not break out again until January 1995. While it is expected that ice formation along the coast would be similar to that observed at O'Gorman Rocks, it is not known whether the ice found further offshore broke out any time before the sampling dates.

Currents flow from north to south along the coast of the Vestfold Hills, bringing water down from the West Ice Shelf where it meets with water from the Prydz Bay Gyre. Current speeds up to 60 cm s^{-1} have been recorded in waters offshore from the Vestfold Hills (Maksimov 1958), however, there is no information available concerning current speed and direction at the particular locations of this study. The topography of the inshore regions of the Vestfold Hills, along with the numerous offshore islands, probably results in complex patterns of currents at small scales.

The topography of the fjords and local weather conditions result in variable growth and formation of the ice cover. The majority of the ice in Ellis Fjord had not broken out since the summer of 1991-2, and so was almost three years old by the time of sampling. The under-surface of the ice has been described as firm and relatively flat, with the ice towards the plateau end being harder and less opaque than the ice at the seaward end (Kirkwood 1993). In contrast to the remainder of the fjord, the ice cover at Ellis Narrows is highly dynamic and the area often remains ice free during the year. In 1994 a small area of open water was present directly over the Narrows throughout the year. The thin neck of Ellis Narrows is less than 3 m deep and current velocities up to 2 m s^{-1} have been measured in summer. In contrast, currents measured in a basin

near the landward end of the fjord reached a maximum velocity of 0.12 m s^{-1} (Kirkwood 1993).

Ice in Long Fjord had broken out in the summer of 1993-4, and so the ice sampled from the two locations was less than one year old. Nothing is known about the currents in Long Fjord but it is probable that they are fairly fast around the three large islands that restrict water flow to quite shallow (approximately 20 m) and narrow passages (Figure 4.1). Ice in Tryne Fjord did not break out in the summer of 1993-4 and it is not known when it was last free of ice. The entrance to Tryne Fjord is only 200 m across, but is of unknown depth. The fjord itself is relatively deep so rapid currents at the entrance might dissipate quite quickly as they flow out into the broad basin. There is no information about the degree of exchange between Tryne Fjord and the sea.

From the preceding discussion it is clear that the sampling location at Ellis Narrows differed from the other eight locations in the following ways: (i) shallow water depth; (ii) very strong water currents; and (iii) delayed formation of an ice cover. In some years the ice at Ellis Narrows might not form at all. It is the unpredictable nature of the ice at Ellis Narrows that is probably responsible for the dominance of *Drescheriella glacialis* at that site.

4.4.3 Life history characteristics of *Paralabidocera antarctica* and *Drescheriella glacialis*: strategies for the sea ice habitat

Some important life history characteristics of *Paralabidocera antarctica* and *Drescheriella glacialis* are presented in Table 4.7. Most developmental stages of *D. glacialis,* including nauplii, copepodites and females with egg sacs, were present in the ice during winter, a feature also noted by Dahms et al. (1990) from sea ice collections

in the Weddell Sea. The species is characterised by comparatively small size, year-round reproduction, production of a small number of relatively large egg sacs, and production of more than one generation per year (Dahms et al. 1990, Bergmans et al. 1991). It has been speculated that *D. glacialis* has no pelagic phase and completes its entire life cycle within the sea ice (Tanimura et al. 1996). If true, it may be the first autochthonous species, as defined by Gulliksen and Lønne (1991), recognised for the Antarctic (see Chapter 1).

The populations of *Paralabidocera antarctica*, on the other hand, were predominantly comprised of nauplii, with a very small number of copepodites observed in only five of the 36 cores. This species colonises the sea ice as early naupliar stages then remains in the ice over winter where subsequent development is reasonably synchronous (Tanimura et al. 1996). From late spring to early summer *P. antarctica* enters a pelagic phase. Reproduction is timed to take place over a short period in summer and one generation is produced per year (Tanimura et al. 1996). Furthermore, *P. antarctica* is considerably larger than *D. glacialis* and produces larger eggs.

Clarke (1979) suggested that most Antarctic benthic species exhibit an essentially *K*-selected life cycle, in that they display slow growth, deferred maturity, greater longevity, iteroparity, low fecundity and large, yolky eggs. At the other extreme *r*-selected species display fast growth, shorter longevity, semelparity, high fecundity and small eggs. In most cases the reality lies somewhere between these two extremes, along an *r*-*K* continuum as defined by Pianka (1970). Greenslade (1983) defined a third selection process, adversity selection (A-selection), whereby populations adapt to predictably severe environments. A-selected species display characteristics that are similar to *K*-selected species, such as slow growth, late maturity, low fecundity, and others that are associated with *r*-strategists, such as lack of specialisation or investment in defence mechanisms.

Table 4.7. Life history characteristics of the two dominant copepod species collected from the sea ice cores.

Paralabidocera antarctica	*Drescheriella glacialis*
Free spawning[1]	Carries egg sac[1]
Egg size 100 µm[1]	Egg size approximately 40 µm[1]
Spawns 50 - 80 eggs over 5 days[1]	Up to 80 eggs per sac[5]
One generation per year[2]	2 - 3 generations per year[6]
250 - 300 days generation time[2]	132 days minimum generation time[6]
Body length up to 2 mm[3]	Body length up to 900 µm[7]
Reproduction in summer[2]	Reproduction year round[5]
NI to CIV found in ice[2]	All stages found in ice[5]
Pelagic phase[2]	No pelagic phase?[2]
Begin feeding from NIV[4]	Begin feeding from NII[6]
Prolonged naupliar development[2]	Shorter naupliar development[6]

[1]this study, [2]Tanimura et al. (1996), [3]Tanimura (1992), [4]Hoshiai et al. (1987), [5]Dahms et al. (1990), [6]Bergmans et al. (1991), [7]Dahms and Dieckmann (1987)

Bergmans et al. (1991) described *Drescheriella glacialis* as a genuine *r*-strategist, particularly in relation to its fast growth, shorter longevity, high fecundity and small size (Table 4.7). These characteristics would enhance the ability of *D. glacialis* to colonise patches of sea ice which are unpredictable in formation and break-out, for example that at Ellis Narrows. Nauplii of *D. glacialis* are not strong swimmers (Dahms et al. 1990), therefore the copepodites and adults must be able to move efficiently between food patches as the concentration of under-ice algae fluctuates. The ability to reproduce year-round would mean that nauplii could be released from the egg sacs whenever favourable habitat became available.

Paralabidocera antarctica, in contrast, has a highly synchronised life cycle that ties in closely with the development of sea ice. The nauplii become incorporated in the ice in

early autumn, either in newly forming ice, or in multi-year ice such as in Ellis Fjord and Tryne Fjord. It is probable that, at the time that *P. antarctica* was undergoing its initial incorporation into the ice, Ellis Narrows was still open water. Thus the necessary habitat was not available at the required part of their life cycle. Similarly, if the ice at Ellis Narrows broke out unpredictably, catching *P. antarctica* at a critical point in its life cycle, then the local concentration of that species might disappear. The characteristics displayed by *P. antarctica* suggest that it is a *K*-selected species as defined by Clarke (1979). However, *K*-selection generally applies to habitats that are predictably favourable and highly diverse, thereby requiring species to evolve maximum competitive ability. As discussed earlier, the fast ice was characterised by low macrofaunal diversity and it is likely that interspecific competition was rare. Therefore, *P. antarctica* might be described as an A-selected species as defined by Greenslade (1983), as its life history strategy has responded to the physical demands of the sea ice environment rather than to pressures from competition.

4.5 Conclusions

The fast ice around the Vestfold Hills is variable in terms of age, formation and, consequently, physico-chemical characteristics. While none of the variables measured was strongly correlated with metazoan abundance and distribution, it is likely that complex interactions between biotic and abiotic factors were responsible for settlement and development of metazoans. Clearly, it would be useful to characterise the physical environment more fully, including information on current direction and speed, time of formation, type of ice, and bottom sediments, among other factors. In addition, as environmental variables will be distributed in a non-linear fashion in the ice column, it is essential that vertical sectioning of the ice cores also be undertaken.

The fast ice was characterised by low metazoan diversity with high abundances of one or two copepod species. In particular, *Paralabidocera antarctica* dominated the macrofaunal assemblage at all locations except Ellis Narrows, where it was replaced by *Drescheriella glacialis*. Life history responses might be dictated more by the physical environment than by biological interactions. Unpredictable break out of the sea ice might exclude *Paralabidocera antarctica* from forming dense populations at Ellis Narrows, thereby making way for *Drescheriella glacialis* to colonise those disturbed areas. Both nauplii of *P. antarctica* and copepodites and adults of *D. glacialis* are probably efficient foragers on ice algae and detritus, and thus it is the unpredictability of the sea ice, rather than the availability of food, which dictates which species will be successful colonisers.

Chapter 5
Temporal Patterns of Abundance of Zooplankton and Sympagic Fauna in Relation to Sea Ice Formation at O'Gorman Rocks

5.1 Introduction

The number of studies of Antarctic zooplankton has increased steadily during the last fifteen years. Combining ship-based sampling with information collected near coastal stations has improved our ability to make generalisations about the distribution and abundance of common species. Ship-based research has been especially prevalent near the island of South Georgia (Ward et al. 1995, Pakhomov et al. 1997), and in the Weddell Sea (Siegal et al. 1992, Kaufmann et al. 1995) and Prydz Bay (Zmijewska 1983, Hosie and Stolp 1989, Hosie and Cochran 1994). Those expeditions have provided good spatial coverage over large areas and, while the majority have been undertaken in late spring or early summer, there have been some winter voyages (Atkinson and Peck 1990, Lancraft et al. 1991). In contrast, shore based studies have been focused in the Indian Ocean sector, particularly at Davis, Mawson and Syowa Stations (Bunt 1960, Tucker 1983, Fukuchi et al. 1985, Tucker and Burton 1988, 1990, Kirkwood 1993, Tanimura et al. 1986, 1997). Logistical constraints on shore-based research generally mean that spatial coverage is limited to the fast ice zone that extends offshore for several kilometres. However, the potential for comprehensive temporal studies in these locations is strong, as it is often possible to sample nearshore sites on a regular basis throughout an entire annual cycle. Therefore, the behavioural and physiological responses of zooplankton can be examined in relation to seasonal changes in their environment.

The aim of the study described in this chapter was to examine the abundance of nearshore zooplankton and sympagic macrofauna over a 15 month period that

encompassed two consecutive summers and the intervening winter. Emphasis was on the relationship between growth and decay of sea ice and the cycle of primary production, and the role of these factors in structuring the zooplankton assemblage. This chapter includes comparisons with other studies of zooplankton from inshore sites around the Antarctic continent, and highlights the similarities and differences between the sites. The numerical dominance of Antarctic neritic zooplankton by small copepods is stressed. Seasonal changes in the ontogenetic distribution of the common copepods are examined, and inferences made about the overwintering strategies employed by these species.

5.2 Methods

This chapter discusses seasonal changes in the composition and abundance of zooplankton and sympagic macrofauna at the O'Gorman Rocks site from December 1993 to February 1995. The sampling site was visited 35 times during that period. Samples were collected approximately weekly in summer, monthly in autumn and winter, and biweekly in spring. Zooplankton were collected with a 2 m long, 100 µm mesh 'umbrella' net, fitted with a plastic cod-end as described in Appendix A.3. The sympagic fauna were sampled by coring the ice through its entire thickness with a 76 mm motorised SIPRE corer. Chl *a* concentration was measured in the sea ice and at five depths in the water column. Particulate lipid concentration was measured in the sea ice and at two depths in the water column. Specimens of *Oncaea curvata*, *Oithona similis* and *Paralabidocera antarctica* were collected on several occasions for lipid analysis. The animals were transported live to the laboratory and were sorted onto pre-weighed filters as soon as possible. The samples were kept frozen in liquid nitrogen or in a - 70 °C freezer until analysis. Temperature and salinity of the water column were measured on each sampling date with Platypus Submersible Data Logger. Methods are described in Appendix A.

5.3 Results

5.3.1 Habitat description of the O'Gorman Rocks site

5.3.1.1 Physical oceanography

At the beginning of this study in December 1993 ice thickness at O'Gorman Rocks was approximately 1.6 m. The ice broke out on 23 December 1993, and the site remained free of ice until the appearance of frazil ice in late February 1994. The ice thickness grew at a rate of $\approx$ 1 cm d^{-1} during March and April, thereafter growing more slowly until it reached a maximum thickness of 1.64 m in November (Figure 5.1). In early December 1994 increasing air temperatures caused the ice to begin decaying. Melting, and the subsequent enlargement of brine channels, destabilised the ice, and it was blown out on 13 January 1995 after a period of strong wind. Snow cover on the ice fluctuated between 0 and 280 mm (Figure 5.1). Note, however, that the dynamic nature of the snow cover meant that snow thickness between sampling dates might have varied somewhat from that displayed in the figure.

Bulk salinity of the ice cores ranged from 3 to 9 psu (Figure 5.2). Salinity averaged approximately 8 psu until July, then decreased to 3 psu in September as decreasing temperatures caused brine to be excluded from the ice matrix. The increase in salinity in October coincided with increasing air temperature. Brine channels began to expand in size, resulting in increased flushing of seawater through the ice. The decrease in salinity on the last two sampling dates reflects the observation that the ice had become very porous, resulting in much of the brine draining out as the core was extracted from the ice.

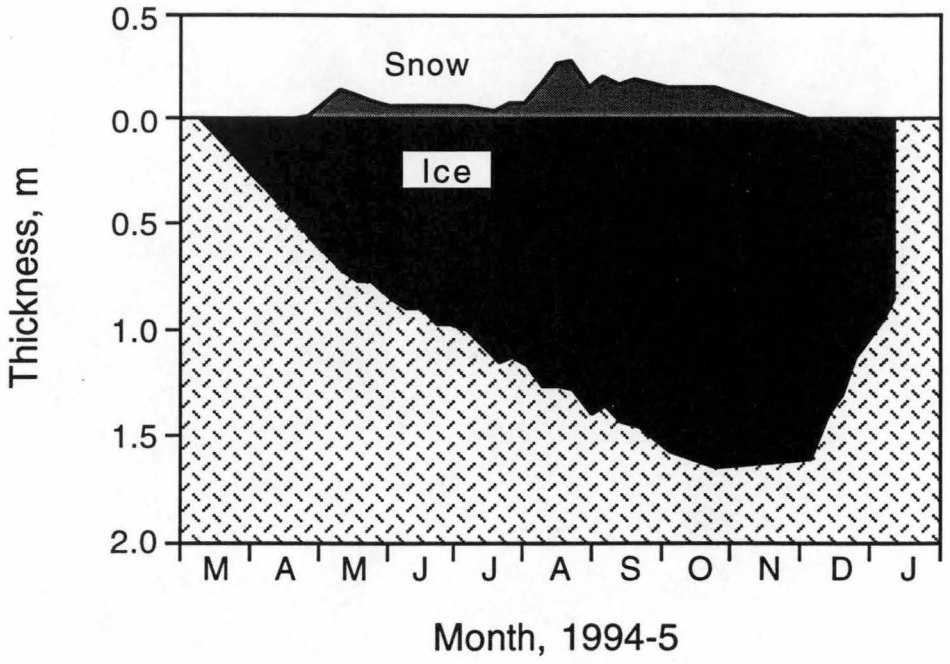


Figure 5.1. Ice and snow thickness (metres) at the O'Gorman Rocks site, March 1994 to January 1995.

Seasonal cycles of temperature and salinity in the water column are shown in Figures 5.3 and 5.4, respectively. Between late March and early November the water column was at its freezing point (about -1.9 °C) (Figure 5.3). Maximum water temperatures were 0.04 °C and 1.39 °C during the 1993-4 and 1994-5 summers respectively. During both summers higher temperatures were usually recorded when the sea ice was still present, as the ice insulated the water column from heat loss.

The water column was stratified during summer, with the temperature at the surface up to 1.5 °C warmer than that at 20 m. Exceptions occurred directly after periods of high winds (e.g. early January 1994), when the water column was homogenous. The continued stratification of the water column at times indicated that water flow alone through the area was incapable of mixing the water. Soon after the ice cover began to reform in March 1994, stratification disappeared. This was probably due to mixing caused by cooling of the surface water and the exclusion of brine from the rapidly forming ice cover.

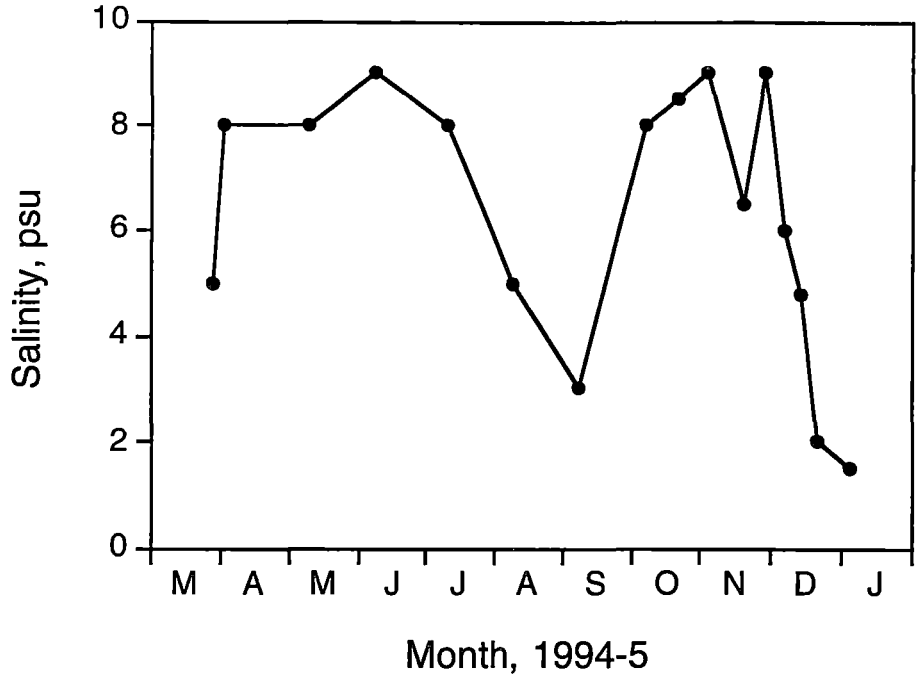


Figure 5.2. Bulk salinity (psu) of the ice cores collected from the O'Gorman Rocks site, March 1994 to January 1995.

Salinity of the water column exhibited trends (Figure 5.4) which mirrored those of the water temperature (Figure 5.3). Salinity was lowest during summer, when fresh water from melting ice diluted the surface waters. It increased steadily throughout winter to a maximum in October, as a result of brine exclusion during ice formation and entrainment into the winter mixed layer of more saline water.

Minimum salinities during both summers were recorded well after the break-out of the fast ice, indicating that it was not only melting of the local sea ice but also of icebergs, ice shelves and the Antarctic plateau that was decreasing the salinity of the water. After the beginning of ice formation in March 1994 salinity increased steadily, reaching a maximum at the end of October (34.20 psu). The water column during much of the winter retained some slight stratification, with less saline water near the surface. In contrast to this observation the temperature profiles suggested that the water was well mixed. The occurrence of more saline water just under the ice on occasions between October and December may have been due to flow of hypersaline brine out of channels

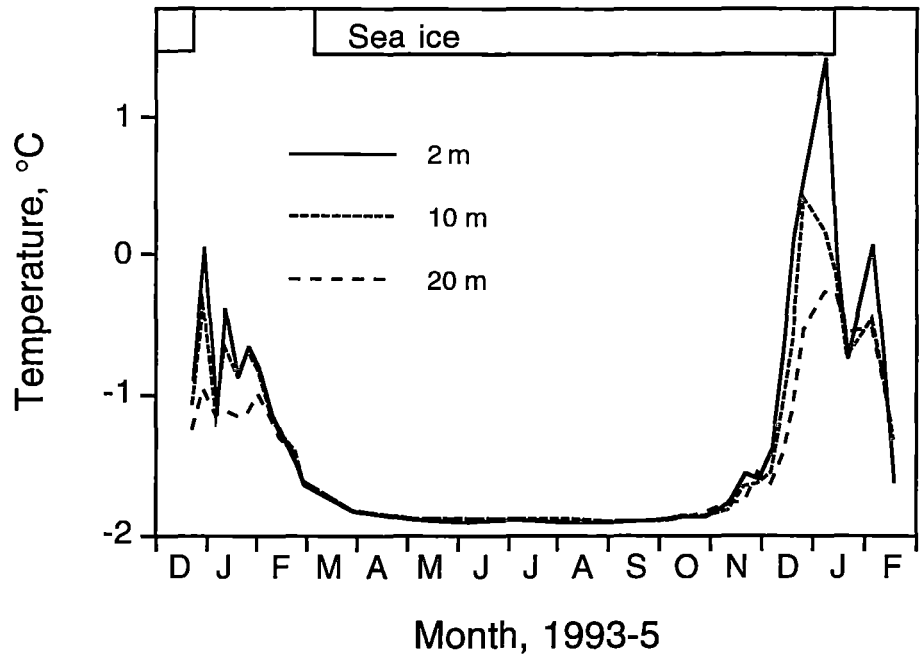


Figure 5.3. Water temperature (°C) at three depths at the O'Gorman Rocks site, December 1993 to February 1995.

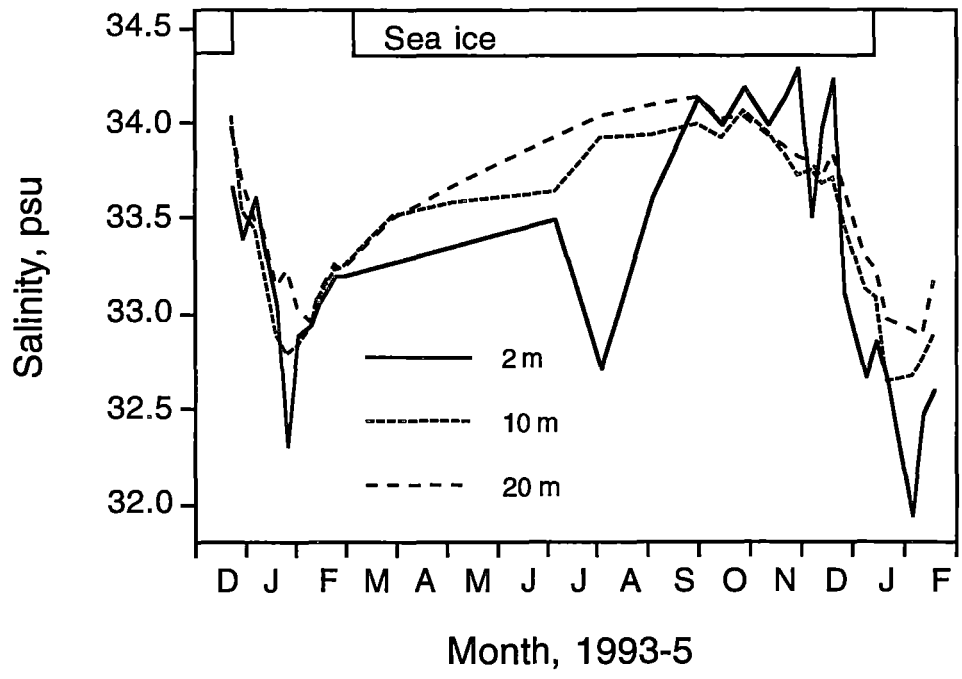


Figure 5.4. Water salinity (psu) at three depths at the O'Gorman Rocks site, December 1993 to February 1995.

in the ice as it decayed (Gallagher and Burton 1988), possibly exacerbated by the drilling of the ice hole through which the samples were collected (J. Gibson, personal communication, 1997).

5.3.1.2 Phytoplankton and ice algae

The seasonal cycle of chl *a*, integrated for the water column and the sea ice, is shown in Figure 5.5. A single major peak in chl *a* occurred in late January 1994 (maximum concentration: 350 mg m^{-2}), after which the concentration dropped rapidly to low winter background levels (less than 5 mg m^{-2}). Following a gradual rise in chl *a* that began in late October, three peaks of similar magnitude were observed during the 1994-5 summer (maxima: 210 mg m^{-2} on 7 December 1994; 220 mg m^{-2} on 4 January 1995; 230 mg m^{-2} on 13 February 1995), interspersed with periods of relatively low chl *a* (less then 20 mg m^{-2}). The 1994-5 peaks were less intense than the single 1993-4 maximum.

In the sea ice there were measurable quantities of chl *a* present throughout the winter (Figure 5.5). There was a peak in concentration in early May (13.6 mg m^{-2}), consistent with the autumn bloom described in Chapter 3. The concentration declined until July (8.5 mg m^{-2}), before gradually increasing to a maximum of 26.7 mg m^{-2} on 4 November. From the area plot in Figure 5.5 it can be clearly seen that the first strong pulse of primary production in the spring of 1994 occurred in the sea ice, approximately one month before there was a peak in the water column. The sharp drop in chl *a* concentration in the sea ice on 19 November was consistent with the observation that the brown colouration in the bottom few centimetres of the ice had all but disappeared at that time. The second smaller peak on 28 November (11.5 mg m^{-2}) was possibly related to an increase in biomass of the surface and internal ice communities.

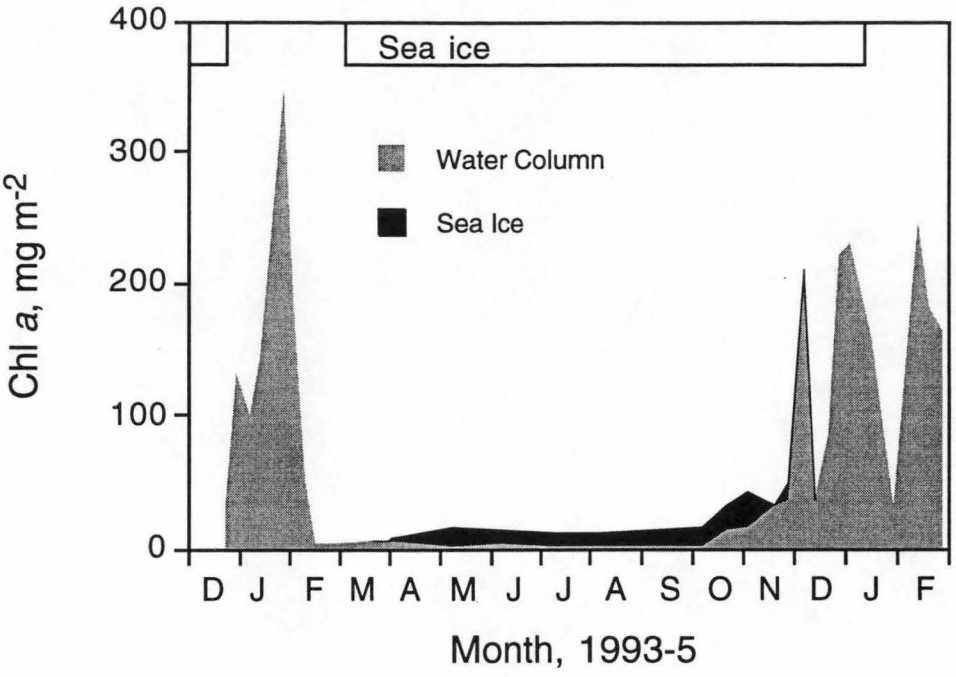


Figure 5.5. Concentration of chl *a* (mg m^{-2}) integrated for the entire water column (23 m) and the sea ice at the O'Gorman Rocks site, December 1993 to February 1995.

An examination of the seasonal cycle of phytoplankton at O'Gorman Rocks was undertaken by Gibson (1997) during the same period as this study. He found that the phytoplankton was dominated by five major species, or groups of species: (i) an undescribed cryptomonad ("cryptomonad A"); (ii) a wide range of diatoms including *Fragilariopsis* spp., *Nitzschia* spp., *Thalassiosira dichotomica* and *Entomoneis kjellmanii*; (iii) *Phaeocystis* cf. *antarctica*; (iv) *Pyramimonas gelidicola* and (v) dinoflagellates of several genera including *Gymnodinium*, *Gyrodinium*, *Peridinium*, *Protoperidinium*, *Dinophysis* and *Amphidinium*.

The sea ice was dominated by diatoms, particularly in the bottom few centimetres of ice. Major species present included *Navicula glacei*, *Nitzschia stellata*, *Fragilariopsis* spp., *Nitzschia* spp. and *Entomoneis kjellmanii*. There were also some flagellates, *Cryptomonas* spp., present, however these did not appear in large numbers.

5.3.1.3 Lipids in particulate matter

The concentration of lipids extracted from particulate matter at 2 m and 10 m in the water column exhibited a similar cycle to that shown by chl *a*, in that maximum concentrations occurred in summer with comparatively low concentrations from autumn to early spring (Figure 5.6). In contrast, particulate lipid concentrations in the sea ice were higher during the winter months, with minima in March and November, and a maximum in July (Figure 5.7). The major lipid classes recorded from both the sea ice and the water column were triacylglycerols, polar lipids including phospholipid and glycolipid, and free fatty acids. Data on all classes of particulate lipids present in the water column and sea ice at O'Gorman Rocks are presented in Appendices B.1 and B.2 respectively.

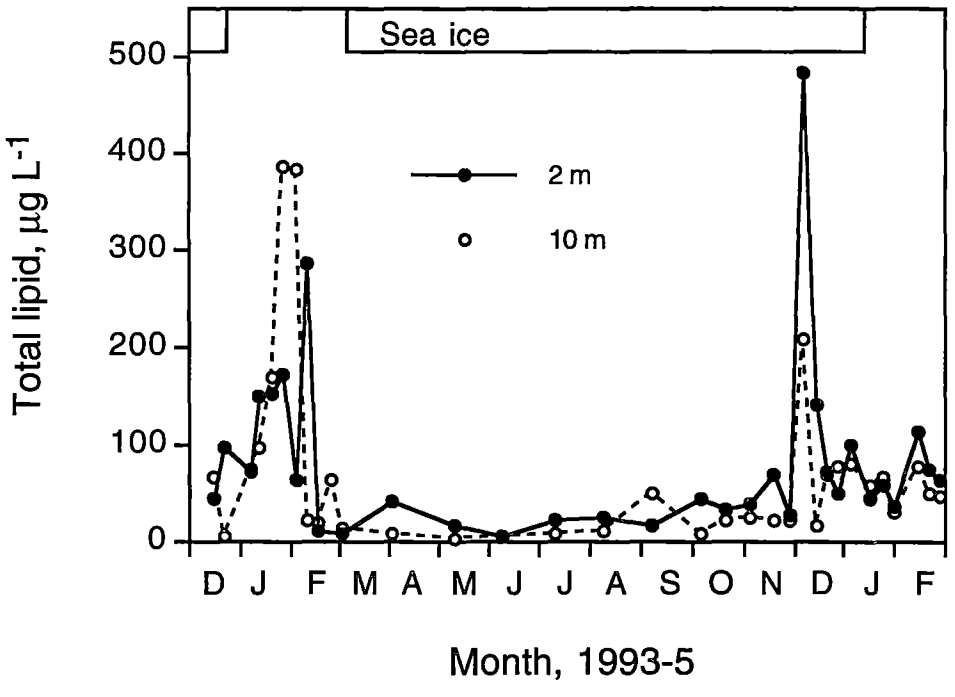


Figure 5.6. Concentration of particulate lipids (µg L^{-1}) in the water column at the O'Gorman Rocks site, December 1993 to February 1995.

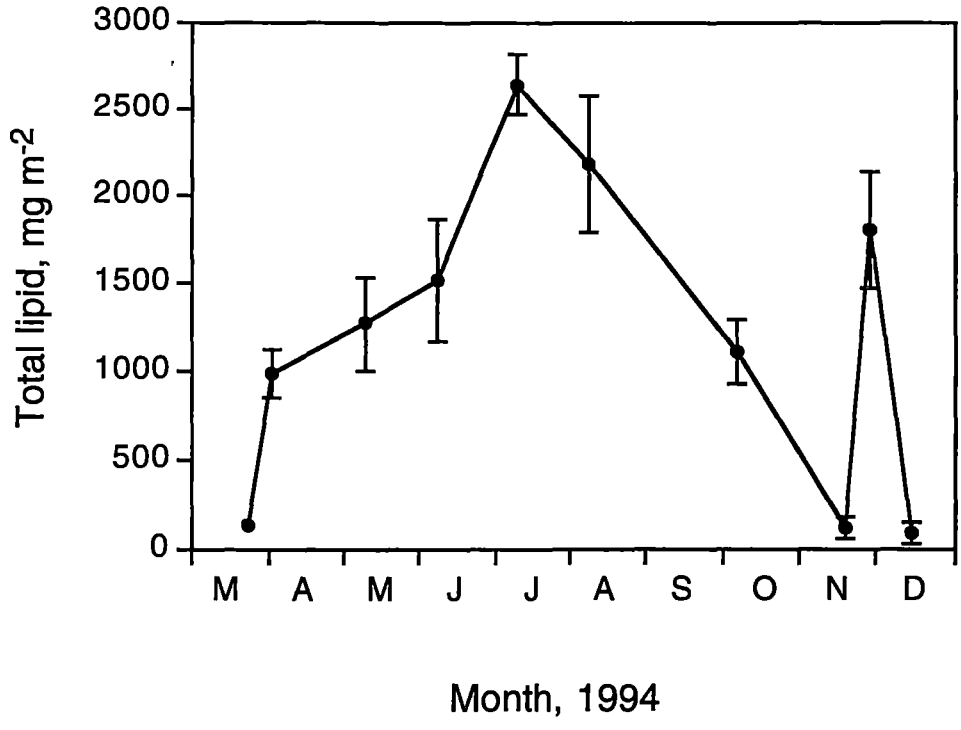


Figure 5.7. Concentration of particulate lipids (mg m^{-2}) in the sea ice at the O'Gorman Rocks site, March to December, 1994. Points represent mean (± s.e.) of three samples. Note that one error bar is too small to be shown.

5.3.2 Zooplankton and sympagic macrofauna

5.3.2.1 Seasonal cycle of abundance

The cycle of zooplankton abundance in the water column at O'Gorman Rocks is shown in Figure 5.8. At the beginning of the study, in December 1993, the density of zooplankton was the lowest that was recorded all year. Abundance increased after the break-out of sea ice, reaching a mean maximum of 16,240 m^{-3} on 15 February 1994. Density decreased to 5,160 m^{-3} in March, before reaching a second peak of 12,240 m^{-3} in April. From May until the end of October the density remained relatively stable at ≈ 3,000 m^{-3}. It was low throughout November (1,330 m^{-3}), before increasing to 5,500 m^{-3} in mid December. The maximum abundance reached during the 1994-5 summer (9,410 m^{-3}) was considerably less than that recorded in the previous summer.

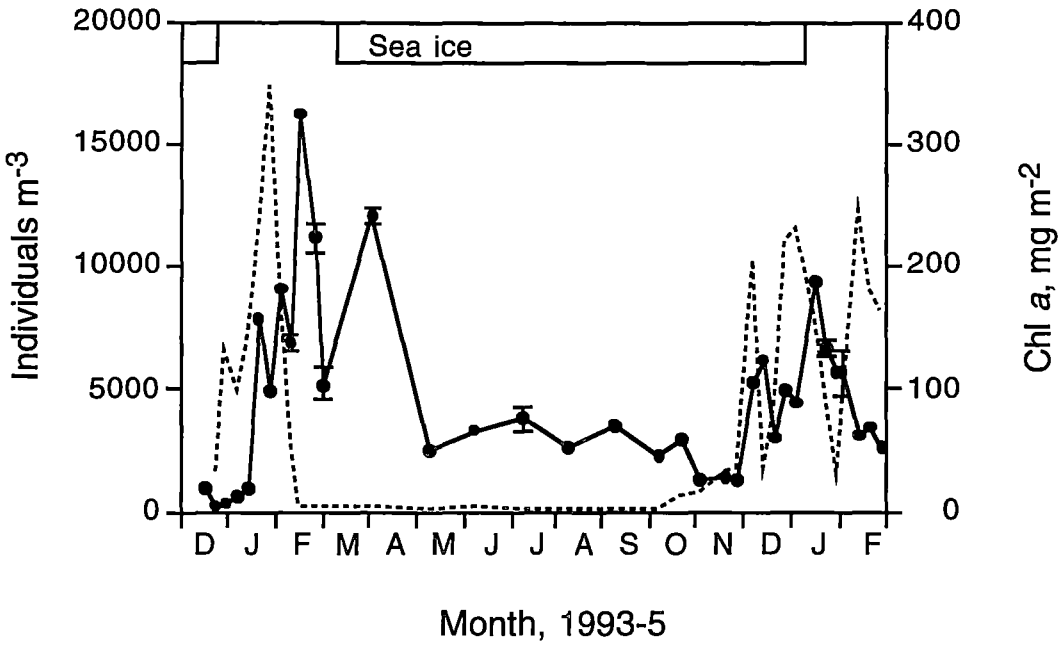


Figure 5.8. Total zooplankton density (individuals m^{-3}) at the O'Gorman Rocks site, December 1993 to February 1995. Points represent mean (± s.e.) of four samples. Note that some error bars are too small to be shown. Integrated chl *a* (mg m^{-2}) concentration is shown by the dashed line.

In the sea ice the density of sympagic macrofauna was very high, reaching a maximum of 277,210 m^{-2} in May (Figure 5.9). Density increased steadily during autumn as the ice formed and grew. Abundance declined in June and remained between 50,000 and 100,000 m^{-2} throughout the winter. There was an increase in late spring (202,870 m^{-2}) before total abundance declined sharply on 19 November.

5.3.2.2 Taxonomic composition

Thirty-four taxa or categories were identified from zooplankton samples collected from the water column at O'Gorman Rocks (Table 5.1). Copepods constituted at least 80 % of the total abundance, and from March to mid-November comprised at least 98 % of the collections (Figure 5.10). The three most frequently occurring species were *Oncaea*

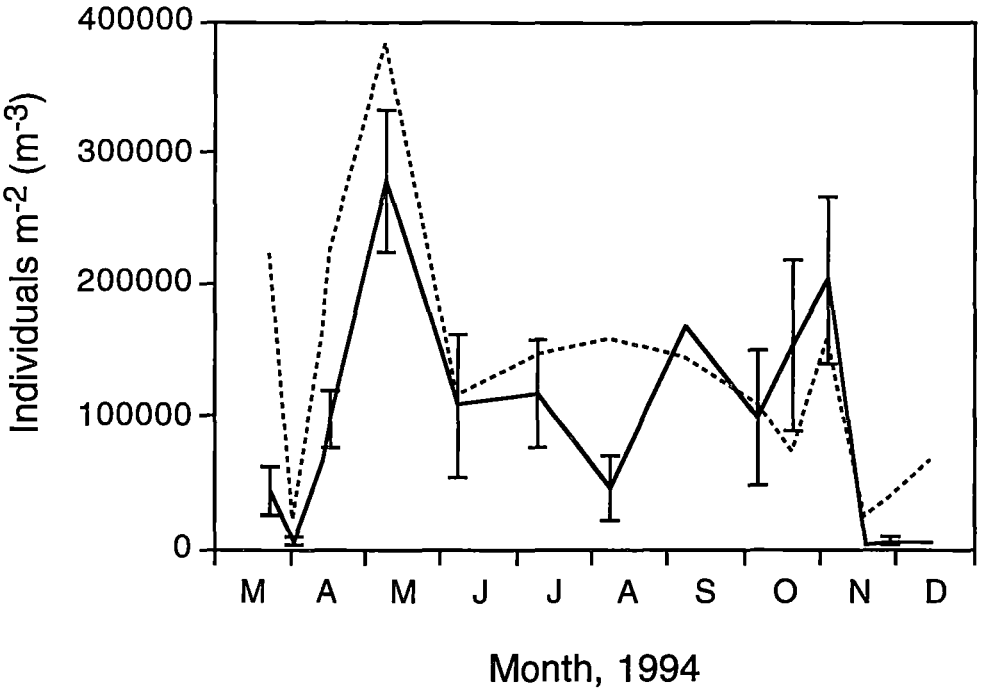


Figure 5.9. Density (individuals m^{-2}) of sympagic metazoans in the sea ice at O'Gorman Rocks from March to December 1994. Points represent mean (± s.e.) of four ice cores. Dashed line shows density as individuals m^{-3} for comparison with the water column.

curvata, *Oithona similis* and *Paralabidocera antarctica*. Furthermore, small nauplii, most probably belonging to *O. curvata* and *O. similis*, contributed substantially to the total (Figure 5.11). Other species, which contributed no more than 15 % to total copepod abundance, included *Stephos longipes*, *Calanoides acutus*, *Ctenocalanus citer*, unidentified harpacticoids, *Drescheriella glacialis*, *Oithona frigida*, and an unidentified calanoid copepod.

The seasonal cycles of abundance of each species of copepod, and several other taxa collected in the samples, are shown in Figure 5.12. *Oncaea curvata* reached densities of approximately 5,000 m^{-3} in both summers, and was the most common species recorded. *Oithona similis* was also abundant for much of the year, reaching a maximum density of 1,920 m^{-3} on 16 January 1995. Small cyclopoid-type nauplii were collected throughout the sampling period, particularly in summer and autumn. There

Table 5.1. Frequency of occurrence of each taxon or category collected at the O'Gorman Rocks site, December 1993 to February 1995 (n = 132 water samples, 47 sea ice samples)

Taxon	% Occurrence		Taxon	% Occurrence	
	Water	Ice		Water	Ice
Oncaea curvata	100	11	Turbellaria	19	
Oithona similis	100	17	*Paramoera walkeri*	14	
Cyclopoida nauplii	100	4	*Oithona frigida*	9	
Paralabidocera antarctica	95	96	Echinodermata auricularia	7	
Harpacticoida spp.	86	15	Echinodermata bipinnaria	6	
Stephos longipes	69	4	Egg sacs	6	
Calanoides acutus	62		Calanoida sp. 1	4	
Pelagobia longicirrata	56		*Chromatonema rubrum*	4	
Polychaete trochophores	55		*Drescheriella glacialis*	4	55
Ctenocalanus citer	52	17	Gastropoda	4	
Euphausia crystallorophias	48		Ostracoda	4	
Echinodermata pluteus	44		Bivalvia	3	
Callianira cristata	42		*Tomopteris* sp.	2	
Unidentified eggs	33	17	Ascidiacea larvae	2	
Fritillaria antarctica	32		Entoprocta larvae	2	
Rathkea lizzioides	23		Nematoda	1	
Ascidiacea eggs	21		Pisces larvae	<1	

were two distinct peaks in abundance of *Paralabidocera antarctica*; 2,320 m^{-3} on 15 February 1994 and 1,650 m^{-3} on 7 October 1994. *Stephos longipes* and *Calanoides acutus* were collected from the water column during both summers, and reached maximum densities of 1,100 and 150 m^{-3} respectively. *Ctenocalanus citer* reached a maximum density of 180 m^{-3} on 2 April 1994, and was quite common at several times during the year. Harpacticoid copepods, comprising at least three species, were

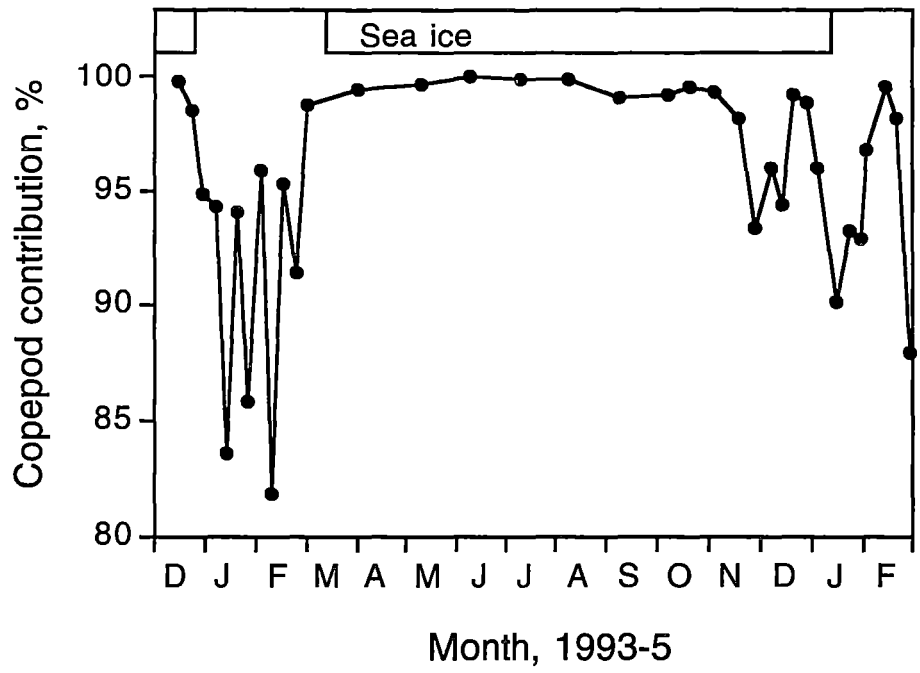


Figure 5.10. Contribution of copepods (%) to total zooplankton abundance collected from the water column at the O'Gorman Rocks site, December 1993 to February 1995.

collected on most sampling dates. *Oithona frigida* and Calanoid sp. 1 were observed in very low numbers and will not be considered further.

Several other taxa were seasonally abundant (Figure 5.12). The euphausiid *Euphausia crystallorophias* and the amphipod *Paramoera walkeri* occurred in 48 and 14 % of the samples, and reached mean densities of 106 m^{-3} and 7 m^{-3}, respectively. The polychaete *Pelagobia longicirrata* was abundant in both summers, reaching a maximum density of 180 m^{-2} on 16 January 1995. Numerous trochophore larvae of polychaetes (maximum density: 910 m^{-3}) were also collected in summer, and it is likely that many of those specimens belonged to *P. longicirrata.* Other polychaetes, such as *Tomopteris* sp., were collected only rarely. The meroplanktonic larvae of benthic species could only be identified to class. They were common during January in both summers (maximum abundance: 150 m^{-3}), and consisted mainly of pluteus larvae of echinoids, with lesser numbers of bipinnaria and auricularia larvae of asteroids. Gelatinous zooplankton, particularly the ctenophore *Callianira cristata* and the hydromedusa

Rathkea lizzioides, were collected in large numbers on several occasions. The appendicularian *Fritillaria antarctica* was abundant during the first summer (peak of 520 m^{-3}), but was virtually absent from the water column in the 1994-5 summer. Unidentified turbellarians were collected on seven occasions.

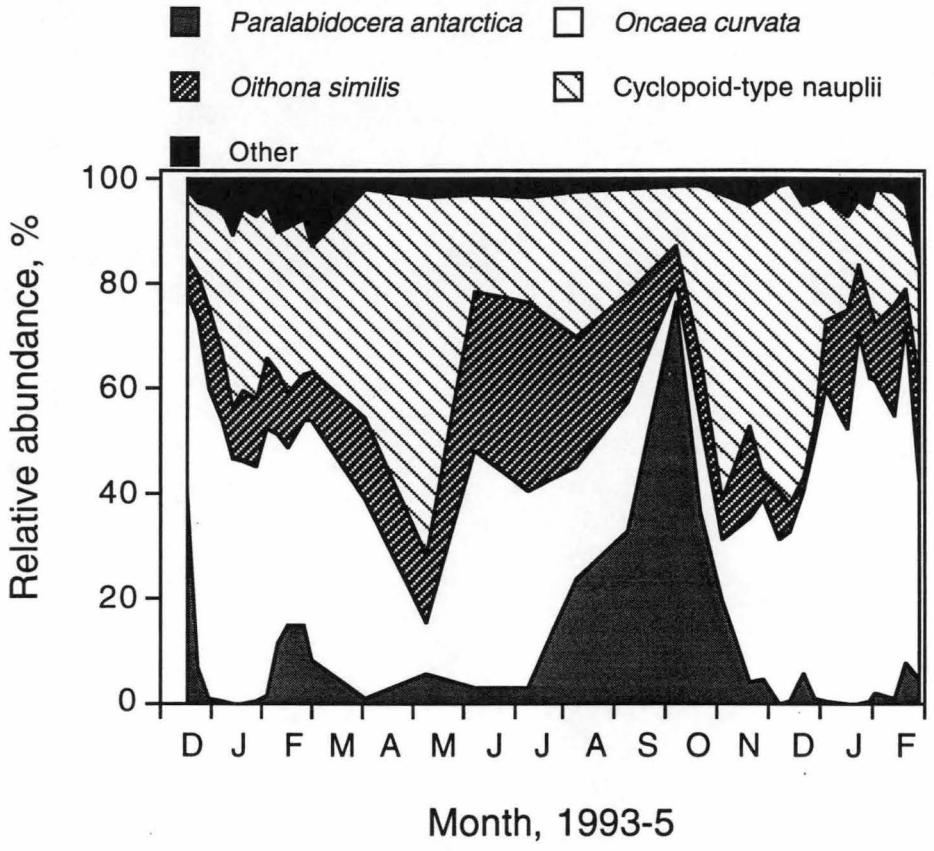


Figure 5.11. Relative abundance (%) of the copepod taxa collected from the water column at the O'Gorman Rocks site, December 1993 to February 1995.

Six species of copepods, along with unidentified harpacticoids, nauplii and eggs, were obtained from the sea ice cores (Table 5.1, Figure 5.13). *Paralabidocera antarctica* was numerically dominant, reaching a maximum density of 270,800 m^{-2} on 10 May 1994. *Drescheriella glacialis* was observed infrequently from March to August, but thereafter became abundant until early November (maximum density: 17,900 m^{-2}). *Stephos longipes*, *Ctenocalanus citer*, *Oithona similis*, *Oncaea curvata* and the unidentified specimens were all recorded in much lower densities.

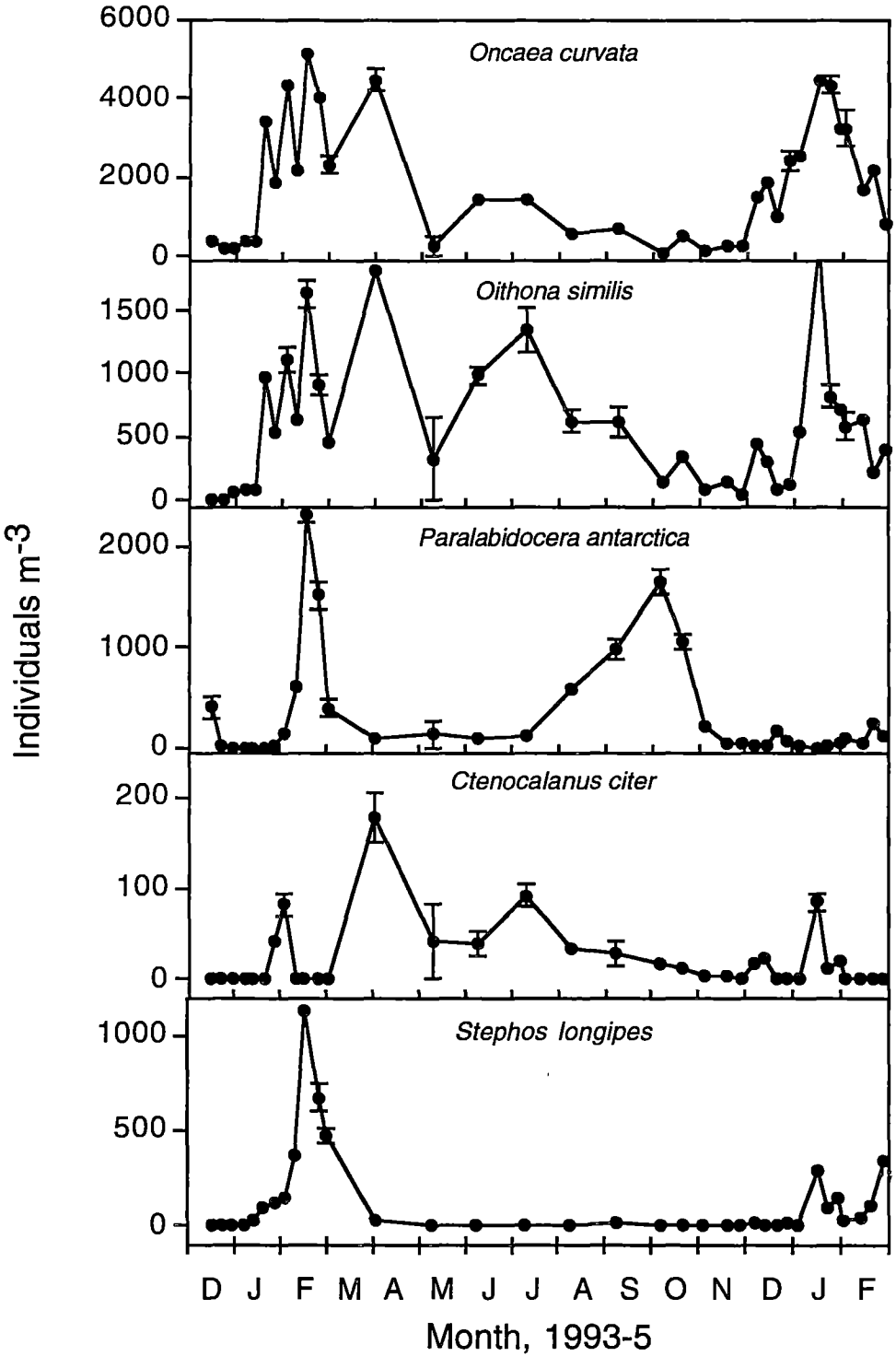
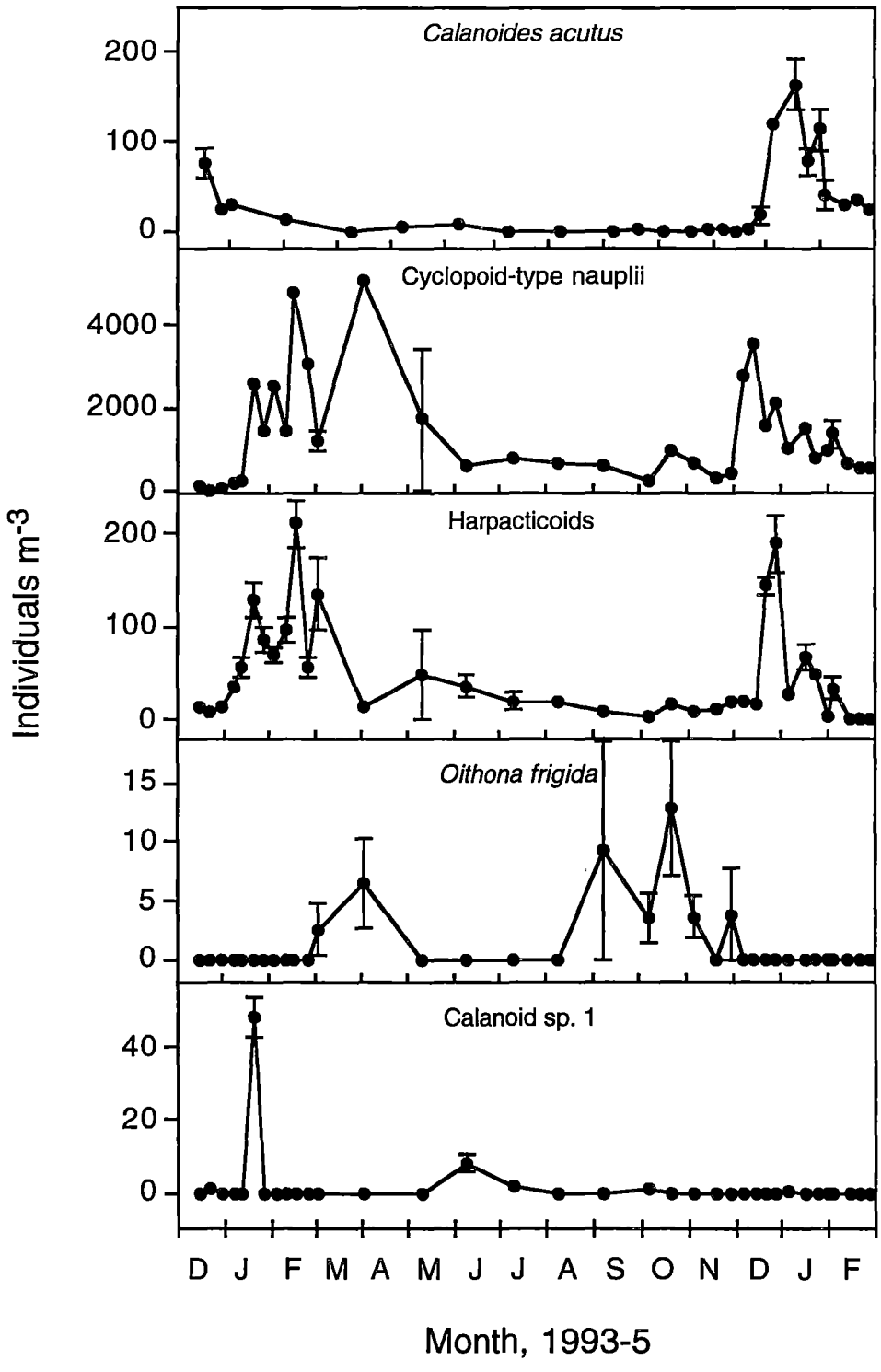


Figure 5.12. Density of zooplankton (individuals m^{-3}) collected from the water column at the O'Gorman Rocks site, December 1993 to February 1995. Points represent mean (± s.e.) of four samples. Note that some error bars are too small to be shown.



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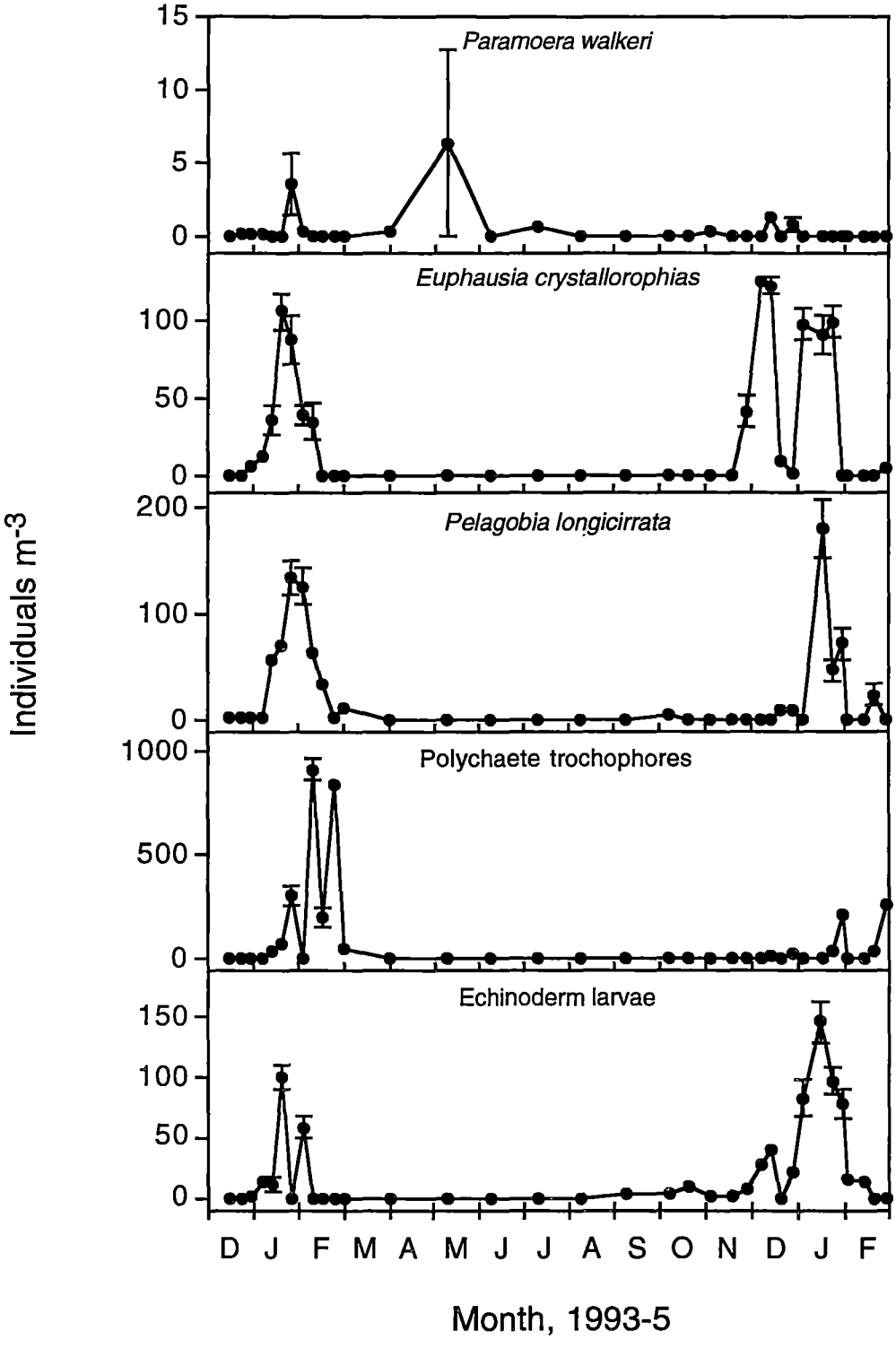

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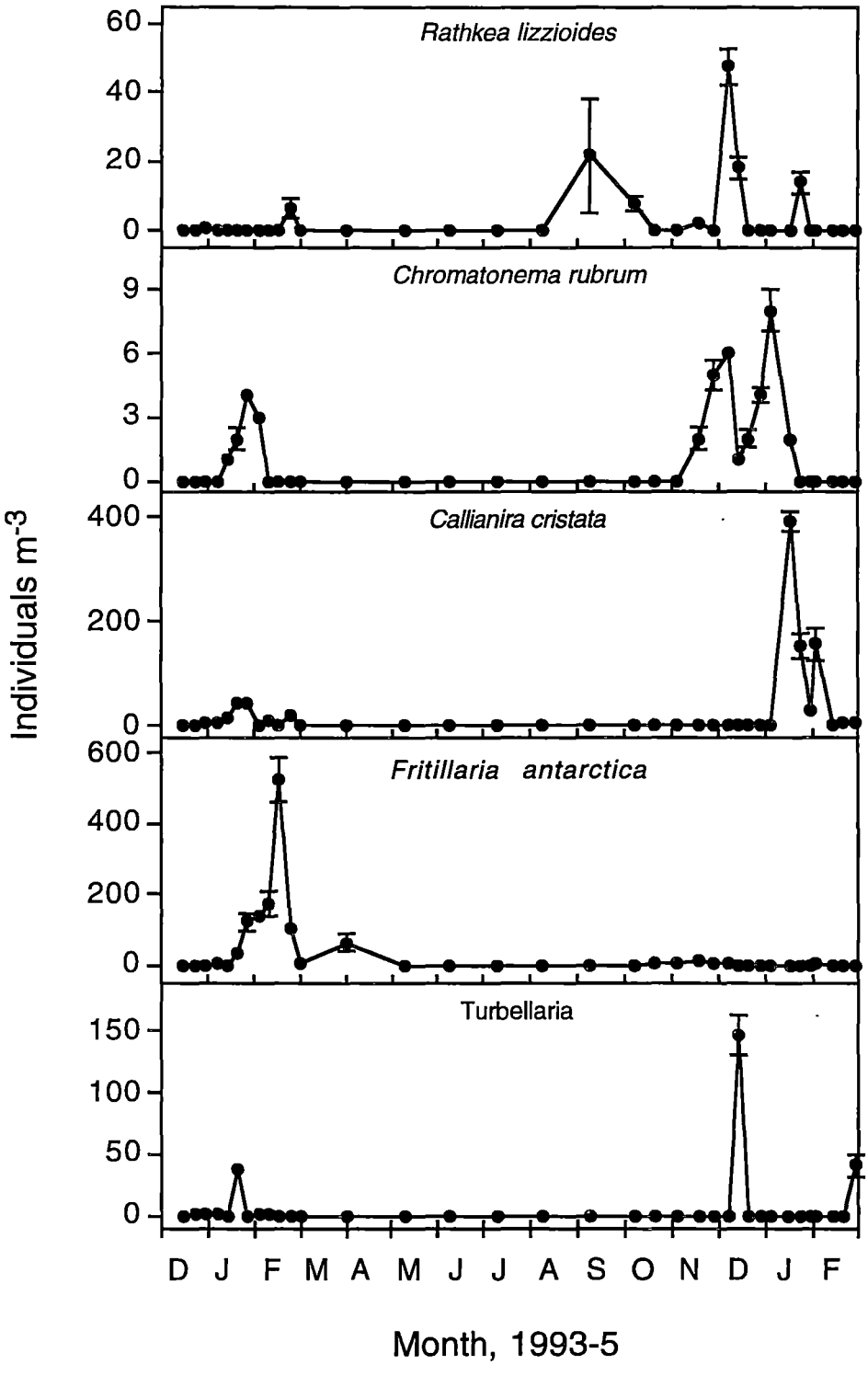

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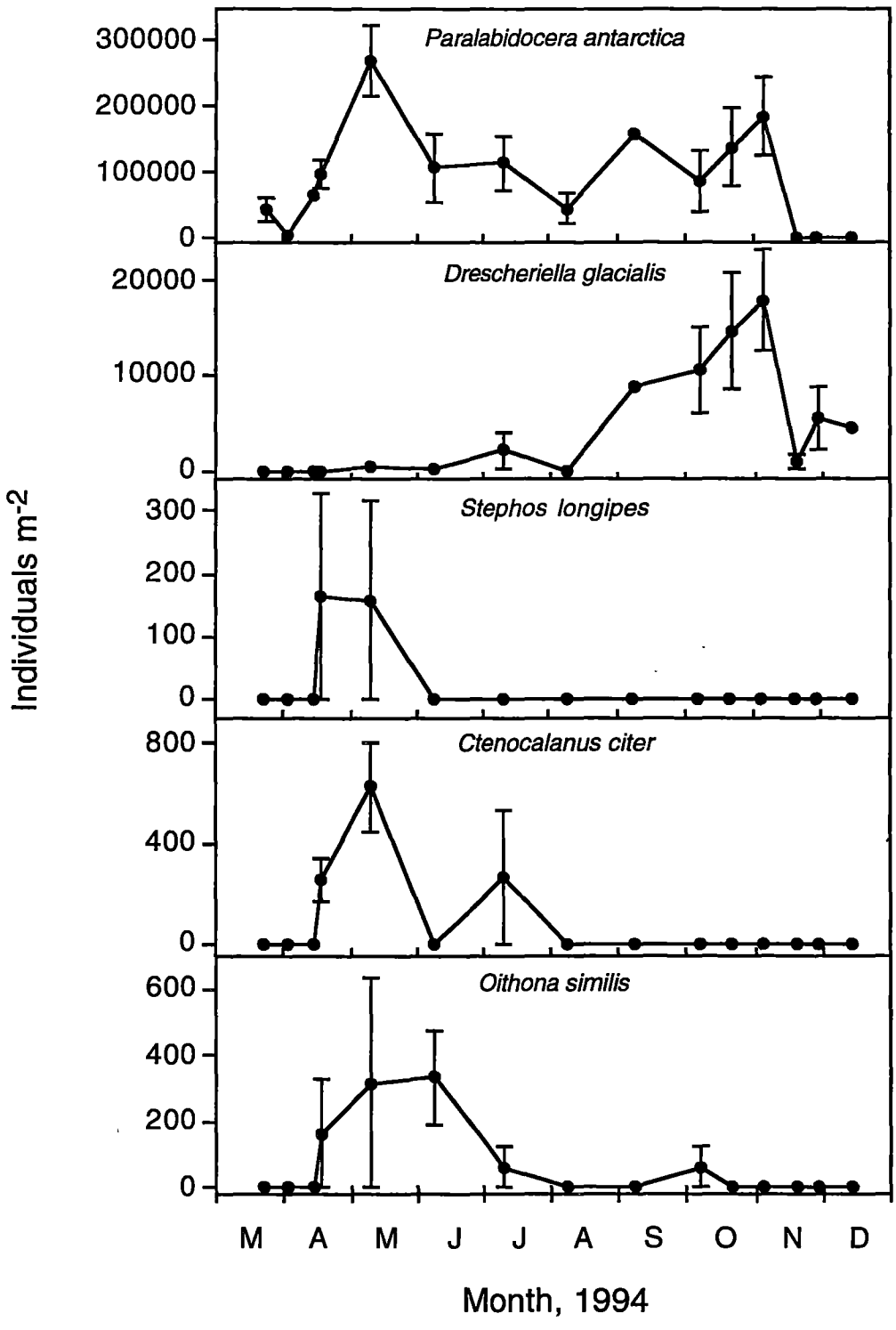

Figure 5.13. Densities of sympagic macrofauna (individuals m^{-2}) collected from the sea ice at the O'Gorman Rocks site, March to December 1994. Points represent mean (± s.e.) of four samples. Note that some error bars are too small to be shown.

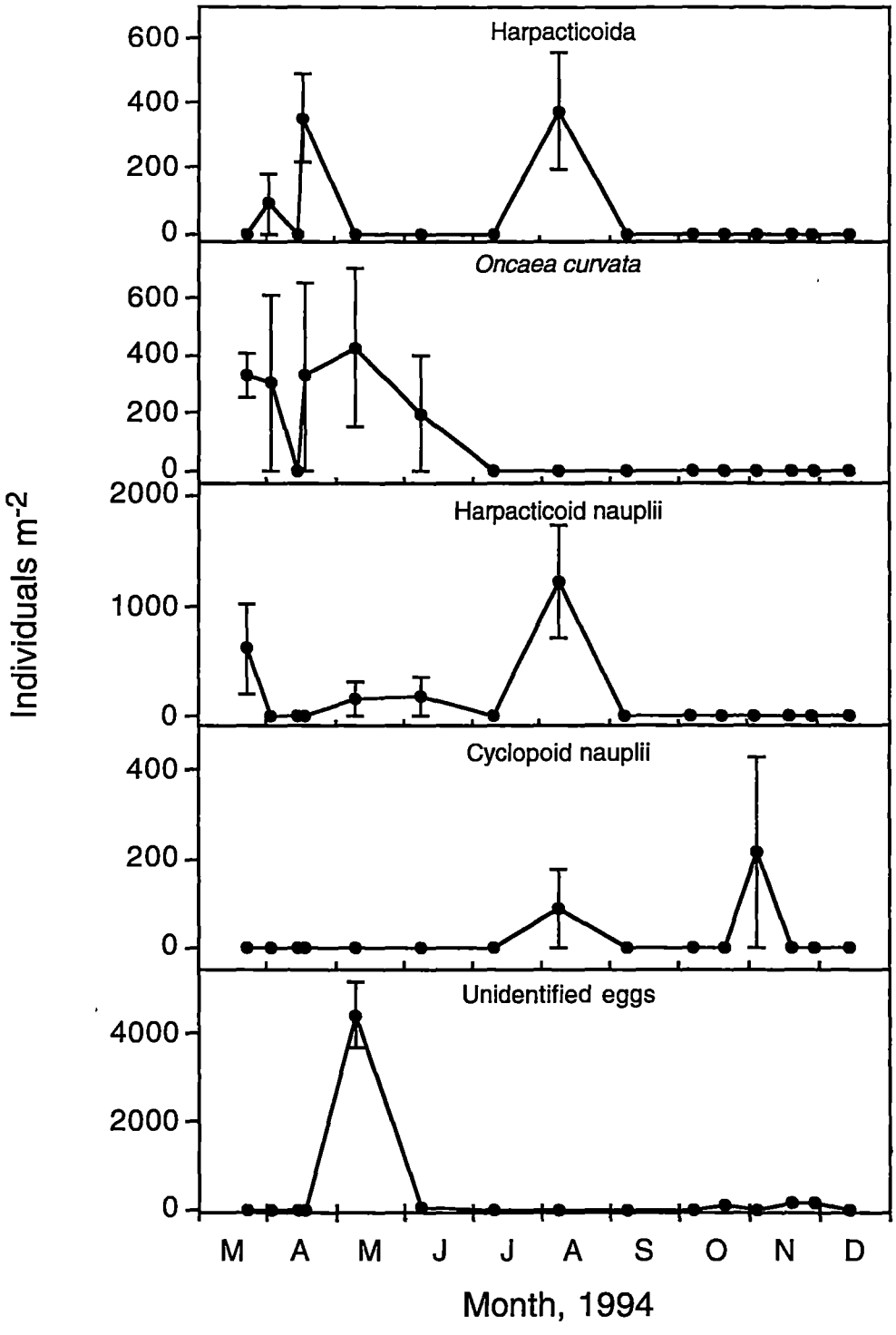

Figure 5.13. continued

5.3.2.3 Stage composition of frequently occurring copepods

5.3.2.3.1 *Oncaea curvata*

Adult and juvenile stages of *Oncaea curvata* were collected throughout the year (Figure 5.14). Copepodite stages I to V represented at least 50 % of the total abundance of *O. curvata* in February and March, and from July to October in 1994. Adults were common during January 1993-4, April, May, June, and from late December to mid-February of the second summer. Small numbers of females carrying paired egg sacs were observed during those times. The sex ratio was generally close to 1:1, although males were six times more abundant in October. *Oncaea curvata* was recorded from the sea ice, especially from March to June, in very low densities.

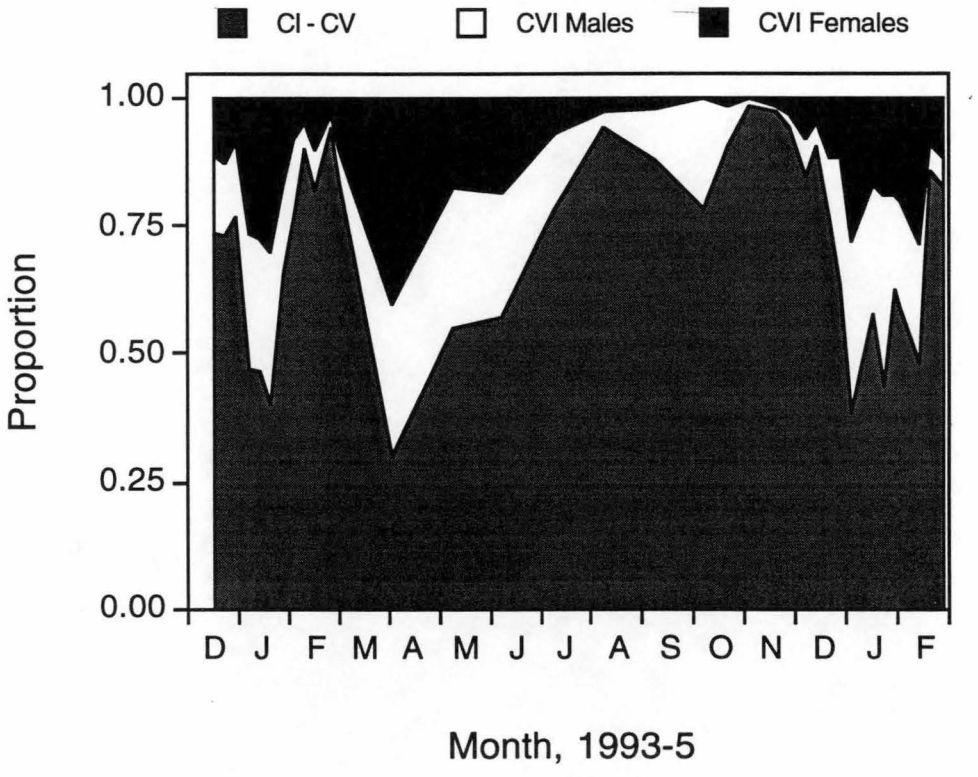

Figure 5.14. Stage distribution of *Oncaea curvata* sampled from the water column at the O'Gorman Rocks site, December 1993 to February 1995. Nauplii were not identified.

5.3.2.3.2 *Oithona similis*

Copepodite stages I to V of *Oithona similis* were collected from the water column throughout the study period (Figure 5.15). They represented from 50 to 100 % of the total abundance of this species. Females occurred quite frequently, with the highest proportion (49 %) recorded on 14 December 1994. Attached egg sacs were observed on very few occasions. Males were rarely encountered in the samples and never comprised more than 6 % of the abundance of *O. similis*. April to July and December to February were the months when male *O. similis* were captured by the umbrella net. During the times that males were present in the samples, the ratio of females to males ranged from a low of 3 : 1 to a high of 60 : 1.

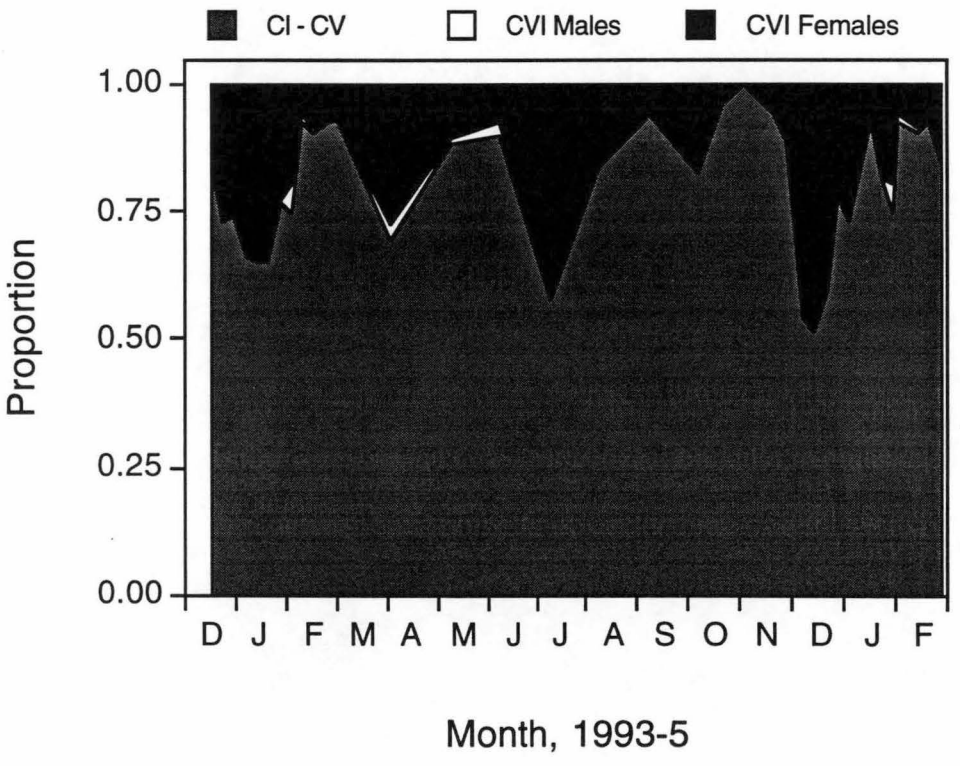

Figure 5.15. Stage distribution of *Oithona similis* sampled from the water column at the O'Gorman Rocks site, December 1993 to February 1995. Nauplii were not identified.

5.3.2.3.3 *Ctenocalanus citer*

Ctenocalanus citer was present in many of the samples collected throughout the year, although it was most abundant from April to July, and in January of both years (Figure 5.16). Juvenile stages were collected from March to November. Copepodite stages I to III were common during this time, accounting for 50 to 100 % of the total abundance of *C. citer*. Stages CIV and CV appeared in August and were collected in moderate densities until November. Adults constituted the majority of the population from December to February. The ratio of males : females was usually slightly < 1. *Ctenocalanus citer* was also recorded from the sea ice in April, May and June, coinciding with peaks in abundance in the water column. The animals in the ice were all copepodite stages I to III.

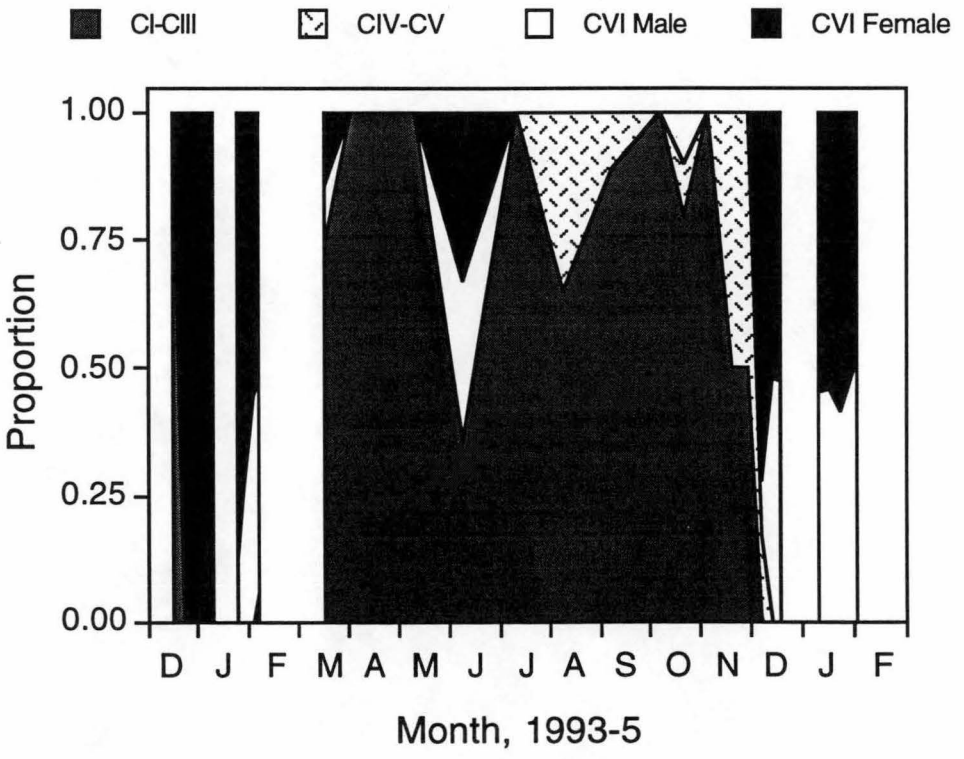

Figure 5.16. Stage distribution of *Ctenocalanus citer* sampled from the water column at the O'Gorman Rocks site, December 1993 to February 1995.

5.3.4.3.4 *Stephos longipes*

Stephos longipes was collected from both the sea ice and the water column at the O'Gorman Rocks site. All stages appeared at irregular times throughout the study period, with the proportions of the different stages changing frequently (Figure 5.17). The ratio of males : females was approximately 4 : 1 during February 1994, and less than or equal to one for the remainder of the year. This species was recorded in the sea ice in April and May; the specimens in the ice were all stage CII.

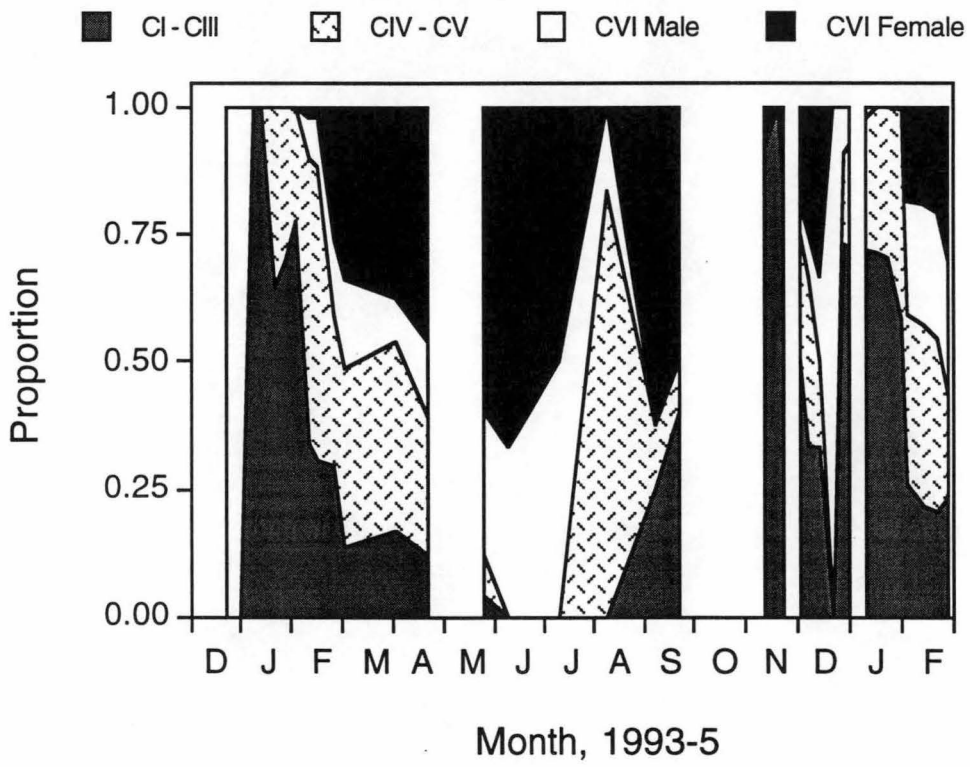

Figure 5.17. Stage distribution of *Stephos longipes* sampled from the water column at the O'Gorman Rocks site, December 1993 to February 1995.

5.3.2.3.5 *Calanoides acutus*

Copepodite stages I to IV of *Calanoides acutus* were recorded from the water column at the O'Gorman Rocks site (Figure 5.18). No CV or adult stages were collected. Copepodites CI and CII were the most abundant stages collected, often accounting for 100 % of the population. This species was never recorded in the sea ice samples.

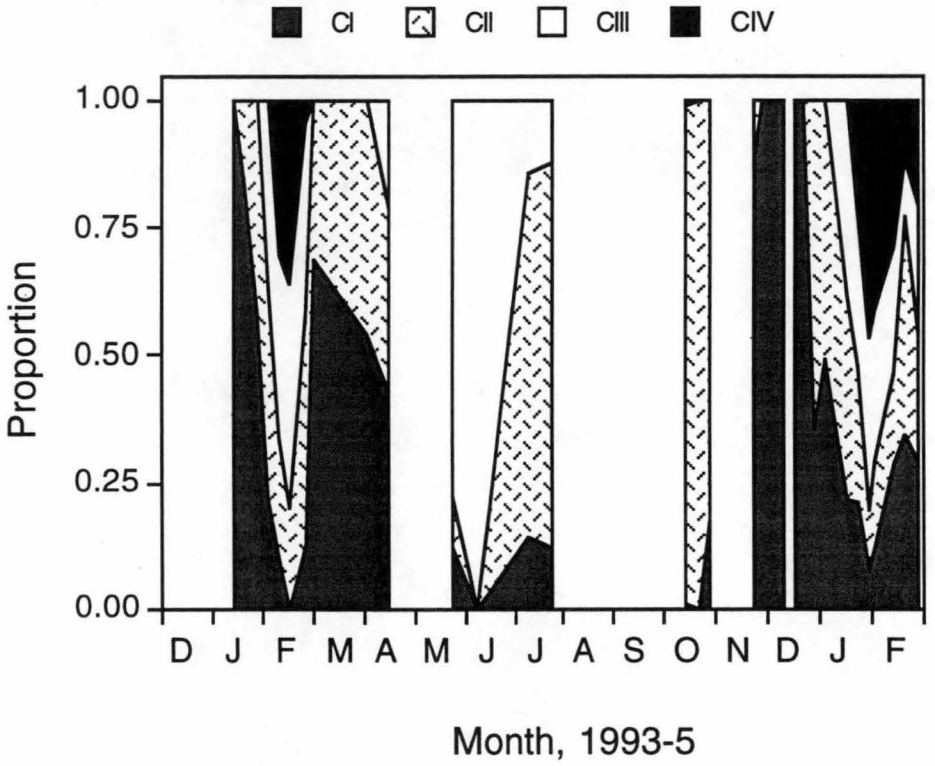

Figure 5.18. Stage distribution of *Calanoides acutus* sampled from the water column at the O'Gorman Rocks site, December 1993 to February 1995.

5.3.2.3.6 *Drescheriella glacialis*

All stages of *Drescheriella glacialis,* including nauplii, juveniles and adults, were present in the sea ice samples (Figure 5.19). Naupliar stages comprised at least 70 % of the population from May until November. Copepodite stages I to V dominated in

late November, however, at this time the total density of *D. glacialis* in the ice was very low (Figure 5.13). This species was collected in very small numbers in the water column and it is possible that they were dislodged from the ice during the drilling of the sampling holes.

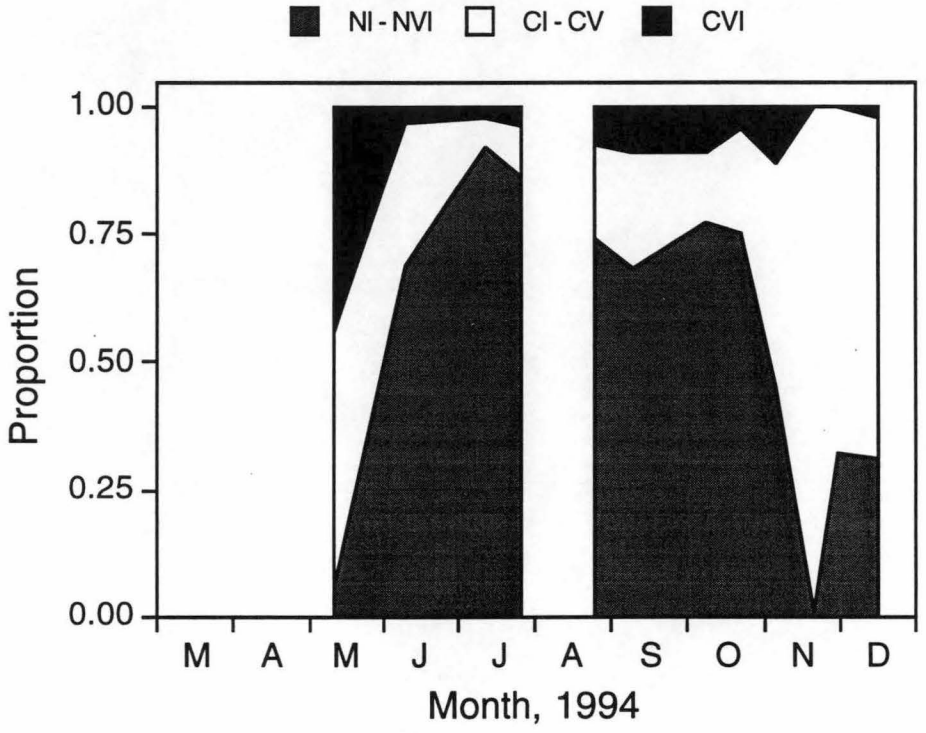

Figure 5.19. Stage distribution of *Drescheriella glacialis* sampled from the sea ice at the O'Gorman Rocks site, March to December 1994.

5.3.2.3.7 *Paralabidocera antarctica*

Paralabidocera antarctica was collected from the sea ice and the water column throughout the study period. Densities in the ice were generally much higher than those in the water column. The developmental stages of *P. antarctica* were studied in detail throughout the year, and a comparative study was made with a population isolated in a saline lake of the Vestfold Hills. A detailed comparison of the distribution of *P. antarctica* in both habitats is provided in Chapter 7.

5.3.4.4 Lipids in copepods

Lipids were extracted from three copepod species: *Oncaea curvata*, *Oithona similis* and *Paralabidocera antarctica*. Microscopic observations revealed that *O. curvata* and *O. similis* both stored lipids in a large sac that was located dorsally in the prosome, and which filled up to 30 % of the body cavity. The size of the lipid sac varied with season. In contrast, *P. antarctica* stored lipids in many small sacs distributed throughout the body. The number and size of the sacs were highly variable between individuals. The lipids of developmental stages of *P. antarctica* are discussed in detail in Chapter 7.

As noted in the Methods (A.12) copepodites of *Oncaea curvata* and *Oithona similis* were pooled for lipid analysis without regard to stage. Thus, while the following figures provide information on seasonal changes in lipid classes for the entire population, no information is available on ontogenetic changes in lipid storage.

The total lipid content of *Oncaea curvata* ranged from 5 to 18 % of dry weight (Figure 5.20). Lipids consisted primarily of wax esters and polar lipids, with minor contributions from triacylglycerols, sterols and hydrocarbons. Polar lipids accounted for no more than 5 % of total lipid. The amount of wax esters varied more widely, with maximum contributions from January to May, and minimum from October to December.

The dry weight of *Oithona similis* comprised up to 16 % lipid (Figure 5.21). This species also primarily stored wax esters, but also, at times, contained substantial amounts of triacylglycerols, sterols and ketones. Polar lipids comprised up to 6 % of the total lipids. The proportion of wax esters changed during the year. Maximum concentrations occurred from January to August. Minimum concentrations were recorded in November and December.

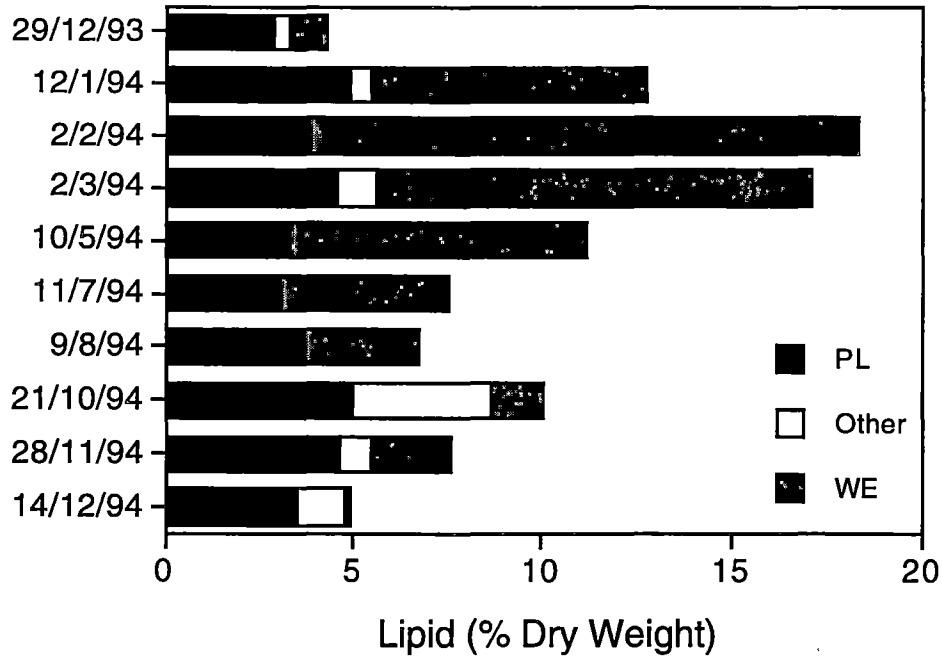

Figure 5.20. Seasonal changes in lipids of *Oncaea curvata* collected from the O'Gorman Rocks site. Abbreviations are: PL = Polar lipids; WE = wax esters.

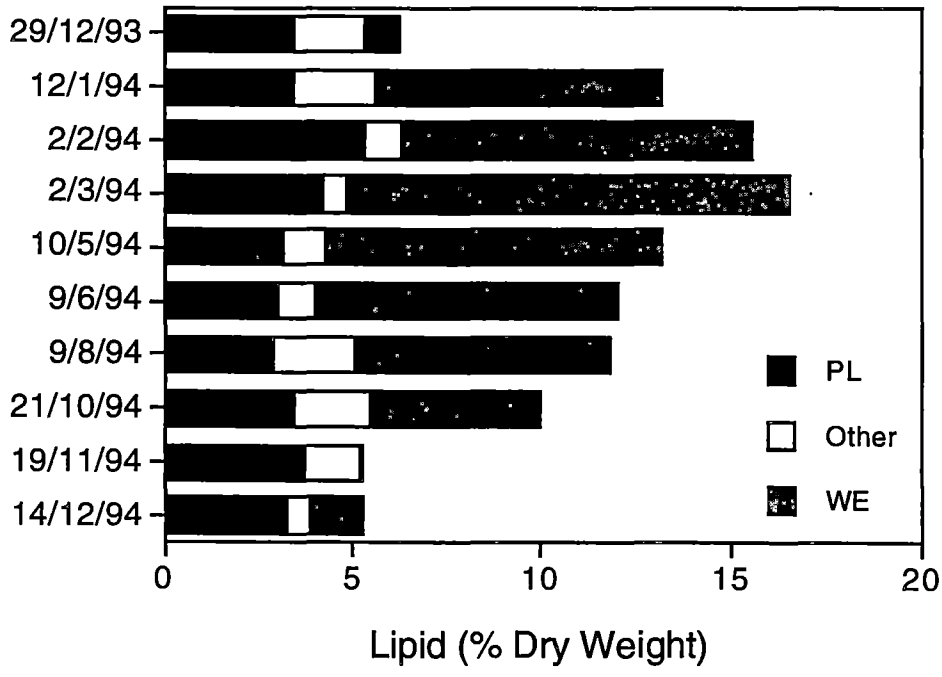

Figure 5.21. Seasonal changes in lipids of *Oithona similis* collected from the O'Gorman Rocks site. Abbreviations are: PL = Polar lipids; WE = wax esters.

5.4 Discussion

5.4.1 Abundance and diversity of coastal Antarctic zooplankton

The planktonic fauna at the O'Gorman Rocks site underwent a cycle of abundance whereby maximum densities were recorded between December and April, and minimum densities occurred between May and November. Exceptions to this pattern were the very low abundances recorded at the beginning of this study from 15 December 1993 to mid January 1994. The fauna was numerically dominated by copepods, especially *Oncaea curvata*, *Oithona similis*, *Paralabidocera antarctica*, and small cyclopoid-type nauplii. Other taxa, including *Stephos longipes*, *Ctenocalanus citer*, *Calanoides acutus*, echinoderm larvae, Harpacticoida, *Fritillaria antarctica*, *Callianira cristata*, *Rathkea lizzioides*, *Pelagobia longicirrata*, polychaete trochophores and *Euphausia crystallorophias*, were seasonally abundant.

A total of 31 taxa was recorded from the water column. Taxonomic diversity was slightly lower during the winter months, when copepods represented at least 98 % of the total abundance. Peaks in diversity occurred in both summers during periods of no sea ice cover. In contrast, only 8 species were recorded from the sea ice throughout the study: *Paralabidocera antarctica*, *Stephos longipes*, *Ctenocalanus citer*, *Oncaea curvata*, Oithona *similis*, *Drescheriella glacialis*, and two unidentified species of harpacticoid copepods. Non-copepod taxa that were common at times in the water column, such as polychaetes and echinoderm larvae, were not observed in the sea ice samples. The sympagic macrofauna was recorded in high densities from mid-April to early November, with a maximum abundance of 280,000 m^{-2} recorded on 10 May.

Two previous year-round studies have examined the zooplankton assemblage of inshore waters near Davis. Zooplankton collected at three sites on a transect from Davis Station to Gardner Island were described by Tucker (1983) and Tucker and

Burton (1988, 1990). Kirkwood (1993) sampled seven sites in nearby Ellis Fjord (Figure 2.4) throughout 1985 and the summer of 1987-8. In Tucker's (1983) study total abundance peaked (2,000 m^{-3}) in May 1982, and was at a minimum in November and December (< 20 m^{-3}). The fauna was dominated numerically by small copepods, predominantly *Oncaea curvata* and *Oithona similis*. Other species, including *Calanoides acutus*, *Calanus propinquus*, *Ctenocalanus vanus* (now believed to be *C. citer*) and *Paralabidocera antarctica*, were recorded from the water column at various times throughout the year, usually in low numbers (< 50 m^{-3}). That low numbers of *P. antarctica* were recorded in that study (Tucker 1983, Tucker and Burton 1988) probably reflects the low sampling frequency of the water column (i.e. monthly) during the period when the species was abundant. Furthermore, sea ice cores were not collected during Tucker's (1983) study.

Both Tucker (1983) and the present study reported a drop in total abundance from May to December. However, Kirkwood (1993) found that density (range: 90 to 16,029 m^{-3}) and biomass (range: 0.7 to 130 mg m^{-3}) exhibited high degrees of temporal and spatial variability, and he concluded that no single representative picture emerged to describe the seasonal dynamics of individual species. Many of the densities recorded by Kirkwood (1993) and in the present study were much higher than those reported by Tucker (1983), and were most likely the result of differences in sampling equipment, although they might truly reflect interannual variation. Tucker (1983) used a 1 m long 'umbrella' net with mesh size of 210 µm, whereas both Kirkwood (1993) and the present study used a 2 m long 'umbrella' net with mesh size of 100 µm. The coarser net would have substantially undersampled small organisms such as naupliar and early copepodite stages of *Oncaea curvata* and *Oithona similis*. Furthermore, Kirkwood (1993; appendix 1) described a comparison whereby it was clear that a 1 m net used to sample his sites collected substantially less plankton than did the 2 m net used at the same time.

Tucker (1983) and Kirkwood (1993) collected animals from the ice/water interface, either by scraping the bottom of the ice (Tucker 1983, Tucker and Burton 1988, 1990) or by a specially designed epontic net (Kirkwood and Burton 1987, Kirkwood 1993). Species notable for their association with the under-ice environment were *Paralabidocera antarctica*, amphipods, especially *Paramoera walkeri*, the euphausiid *Euphausia crystallorophias* and the ice fish *Pagothenia borchgrevinkii*. Unsurprisingly, both studies recorded species that were not found in the ice cores examined during the present study. The methods of Tucker (1983) and Kirkwood (1993) were efficacious for sampling the larger species that live in the loose ice crystals found directly at the ice water interface, whereas the SIPRE corer only sampled those smaller organisms that live within the ice. Nevertheless, *P. walkeri* and *E. crystallorophias* were both captured by the sampling net in the present study.

The suite of common planktonic species recorded from waters around the Vestfold Hills was not markedly different from other coastal sites around the Antarctic continent. Bunt (1960) listed 11 copepod species from inshore waters near Australia's Mawson Station, the most common of which were *Oncaea curvata*, *Oithona similis*, *Calanoides acutus*, *Paralabidocera antarctica* and *Scolecithricella glacialis*. Zvereva (1972) found *O. similis*, *O. curvata*, *Stephos longipes* and *Ctenocalanus citer* to be common in coastal waters off the Russian Stations Molodezhnaya and Mirny (see Figure 2.1 for locations).

In collections made near the Japanese Station Syowa, Fukuchi et al. (1985) recorded that calanoid copepods, particularly *Euchaeta antarctica*, were the dominant planktonic species. In contrast, Tanimura et al. (1986), from a site also offshore from Syowa, described samples that were dominated by *Oncaea curvata* and *Oithona similis*. The large mesh size of the net used in the former study (1000 μm) most likely accounted for this difference. The sea ice near Syowa Station was sampled regularly during 1970, 1975 and 1982 (Hoshiai and Tanimura 1986). The sympagic macrofauna

reached a maximum density of 526,000 m^{-2} in March 1970, of which > 99 % consisted of unidentified eggs. Other common taxa included *Paralabidocera antarctica*, *Ctenocalanus vanus* (probably *C. citer*), *O. similis* and three species of harpacticoids. Specimens of *O. curvata*, polychaete larvae and benthic larvae were also noted occasionally (Hoshiai and Tanimura 1986).

The planktonic fauna of McMurdo Sound was numerically dominated by *Oithona similis*, *Oncaea curvata*, *Metridia gerlachei*, *Ctenocalanus citer*, *Calanoides acutus*, and the mollusc *Limacina helicina* (Foster 1987, 1989, Hopkins 1987, Knox et al. 1996). Tide cracks in the region were important habitat for *Paralabidocera grandispina*, *Tisbe prolata* and *Pseudocyclopina belgica* (Waghorn and Knox 1988). Finally, in the coastal regions of the eastern Weddell Sea the planktonic fauna consisted predominantly of *O. similis*, *O. curvata* and *C. citer* (Fransz 1988), while the sea ice was inhabited by *Stephos longipes*, turbellarians, *Drescheriella glacialis* and several unidentified species of harpacticoids (Dahms et al. 1990, Kurbjeweit et al. 1993)

The picture that emerges from the preceding discussion is that the composition of the planktonic fauna of nearshore regions around the Antarctic continent is fairly consistent. The numerical dominance of small copepods, including *Oncaea curvata*, *Oithona similis* and *Ctenocalanus citer* is clear. There are, however, regional differences in the relative importance of these species. Copepods usually numerically dominate a zooplankton assemblage, yet other species often contribute substantially to the biomass. In particular, during summer, amphipods, euphausiids, polychaetes, larvaceans and gelatinous zooplankton are commonly recorded from inshore regions. In general, the diversity of the neritic community is lower than that found in oceanic waters (e.g. Hosie and Stolp 1989, Siegel et al. 1992), with fewer species adapted to living in shallower waters with extended periods of ice cover. In summary, the Antarctic neritic fauna can be defined broadly as including: (i) a subset of oceanic species which are adapted to the nearshore habitat; (ii) meroplanktonic larvae of benthic

species; and (iii) those species which are strongly associated with the seasonal ice cover.

5.4.2 Life history strategies of common inshore copepods

The zooplankton common in the inshore waters near the Vestfold Hills adopted at least one of the following strategies for living in the neritic zone: (1) strong association with the sea ice; (2) the timing of reproduction to coincide with the phytoplankton bloom; (3) accumulation of energy stores to survive long periods of starvation; and (4) ontogenetic migration to deep waters.

The two species found in highest abundance in the sea ice cores were *Paralabidocera antarctica* and *Drescheriella glacialis*. *Paralabidocera antarctica* overwintered in the sea ice, developing through several stages before shifting to the under-ice habitat in mid-November. It took approximately one year to complete its life cycle, and development within the population was synchronous (see Chapter 7 for details). *Drescheriella glacialis* was found in high abundance from September to November. Most developmental stages of *D. glacialis* occurred together in the cores collected at the O'Gorman Rocks site (also see Chapter 4). While clasping pairs of *D. glacialis* were never recorded from the samples, it is presumed that they mated within the interstitial brine channels. As discussed in Chapter 4, the life history traits of *D. glacialis* enable it to colonise available patches in the sea ice habitat.

A third species of copepod which is known to associate with sea ice is *Stephos longipes*. *Stephos longipes* is common in the Weddell Sea where it has been found in high densities in the sea ice and at the under-ice surface (Kurbjeweit et al. 1993, Schnack-Schiel et al. 1995). In the present study *S. longipes* was found in large numbers in summer only, especially during periods of open water. During January and early February copepodite stages CI to CIII were common. By late February and

March stages CIV to CV had become dominant. During winter adults were reported in low densities. The only stage found in association with the sea ice was CII, which occurred in low densities in April and May. The nauplii were never observed in the sea ice at the O'Gorman Rocks site or at other locations around the Vestfold Hills (Chapter 4).

The above observations concur with the life cycle constructed for *Stephos longipes* by Schnack-Schiel et al. (1995) from collections in the Weddell Sea. Briefly, rapid development from CI to CIII occurred during summer in the upper 50 m of the water column. In autumn CIV were found in mid-water, whereas nauplii inhabited the sea ice. Part of the Weddell Sea population overwintered as CIV and CV in deeper water, whereas a younger generation overwintered in the sea ice. Reproduction appeared to take place over an extended period from late winter to autumn (Schnack-Schiel et al. 1995). The species feeds on ice algae (Hopkins 1987), and the presence of triacylglycerols as energy stores suggest that it feeds year-round (Schnack-Schiel et al. 1995).

The absence of large numbers of *Stephos longipes* in the sea ice at the O'Gorman Rocks site suggests that it was not actively reproducing in the nearshore waters. Instead, it is possible that increased water circulation after the break-out of sea ice carried the animals in from further offshore. A relatively strong westerly current, part of the cyclonic Prydz Bay Gyre, flows along the coast offshore from Davis, and during periods of strong winds water from further offshore or deeper in the water column is introduced into the coastal waters (Gibson et al. 1997a). Therefore, if adults had appeared in surface waters offshore for mating it is likely that the new generation of CI would be carried in with the currents. While a few *S. longipes* did become incorporated into the sea ice in autumn the population might be prevented from establishing because of the lack of deep water necessary for the migration of CIV and CV stages. In the Weddell Sea incorporation of *S. longipes* into the sea ice may be

facilitated by sticky eggs that attach to frazil ice crystals as they rise to the surface (Kurbjeweit et al. 1993). In contrast, the formation of congelation ice around the Vestfold Hills is not conducive to concentrating organisms by this method. Therefore, the type of ice formation coupled with the shallow water depths of the neritic region of the Vestfold Hills might combine to prevent *S. longipes* from establishing the dense populations that are observed in the Weddell Sea.

The highest abundance of *Calanoides acutus* also occurred during the summer. CV and CVI stages of *C. acutus* were not recorded from the samples. *Calanoides acutus* is common in the deeper waters of Prydz Bay (Hosie and Stolp 1989, Hosie and Cochran 1994), and so this species is also likely to be an offshore migrant. The appearance of CI in the water column at O'Gorman Rocks is suggestive of this species being brought in from offshore after females had ascended to shallower waters for spawning (Atkinson et al. 1997). *Calanoides acutus* stores large concentrations of wax esters and overwinters at depth before mating in the spring. Maximum reproductive activity is timed to coincide with the phytoplankton bloom (Schnack-Schiel and Hagen 1994, 1995, Hagen and Schnack-Schiel 1996).

Ctenocalanus citer undergoes an ontogenetic migration to deeper waters and possibly overwinters as mid-stage copepodites. The species probably reproduces in springtime, before the onset of the phytoplankton bloom (Fransz 1988, Schnack-Schiel and Mizdalski 1994). Evidence from gut content analysis indicates that *C. citer* feeds on ice algae for at least part of its life cycle (Hopkins 1987). In the present study stages CI to CIII were most common from March to November and adults were common from December to February, suggesting that they were taking advantage of the phytoplankton bloom. Reproduction in the population at the O'Gorman Rocks site appeared to be somewhat later than that observed in the Weddell Sea. Low densities of *C. citer* were reported from sea ice cores in this study and at Syowa Station (Hoshiai and Tanimura 1986), however the extent of its association with the sea ice is not clear.

Oncaea curvata and *Oithona similis* are very important components of the inshore Antarctic ecosystem. Both have a circum-Antarctic distribution and *O. similis* is common throughout the world's oceans (Conover and Huntley 1991). It has been suggested that a mesh size of 100 µm may be too large for quantitative sampling of *O. similis* as the width of *Oithona* nauplii is 60 to 100 µm, whereas that of copepodites is 100 to 300 µm. *Oncaea curvata* are even narrower (Fransz 1988, Tanimura et al. 1997). Therefore, the abundances reported in the present study might be somewhat underestimated, especially those of the nauplii.

There are several similarities in the life history strategies of the two species, including prolonged periods of reproduction, low rates of egg production throughout the year, short development times for nauplii, the lack of clear cohorts over a year, and copepodite development times of 14 to 28 days per stage (Metz 1996). In the present study most developmental stages of *Oncaea curvata* were present throughout the year, supporting the contention of Metz (1996) that reproduction occurred over an extended period. The presence of several developmental stages of *O. curvata* at any one time is a common occurrence (Fransz 1988, Metz 1995, Tanimura et al. 1997). Therefore, it raises the question of how the species obtains sufficient nourishment to reproduce all year, notwithstanding their generally low metabolic expenditure (Paffenhöfer 1993). Various food sources, including detritus, colonies of *Phaeocystis* and diatoms (Hopkins 1987, Metz 1995) have been ingested, whereas motile food, such as copepods and flagellates, were not consumed by female *O. curvata* (Metz 1996). The storage of wax esters suggests that *O. curvata* can survive extended periods of starvation. Kirkwood (1993) did not observe lipid sacs in *O. curvata* collected from Ellis Fjord. This might relate to the length of storage time before the samples were examined or it could be a real difference in that the Ellis Fjord population were consuming an alternative food source.

Oithona similis also stored wax esters, enabling it to survive extended periods of starvation. This species consumes a variety of food, including faecal pellets (González and Smetacek 1994), motile taxa (Atkinson 1995) and diatoms (Hopkins 1987). While in deeper waters, such as those of the Weddell Sea, *O. similis* underwent slight ontogenetic migrations (Metz 1995), in shallower waters it was distributed evenly throughout the water column (Tanimura et al. 1997). The association of *O. similis* with sea ice is unclear. It has been observed feeding on planktonic algae under the ice prior to a phytoplankton bloom (Atkinson 1995), and it is preyed on heavily by the ice fish *Pagothenia borchgrevinkii* (Hoshiai and Tanimura 1981, Hoshiai et al. 1989). Furthermore, the species might have an indirect link with sea ice production via the consumption of faecal pellets that are produced by species feeding on ice algae (González and Smetacek 1994). Thus, while *O. similis* probably cannot be defined as a truly sympagic species, local populations might be utilising the sea ice for foraging.

5.5 Conclusions

The planktonic fauna of the inshore waters near the Vestfold Hills was typical of that found in coastal regions around Antarctica. There was a temporal cycle in abundance whereby maximum densities were recorded from December to May, and minima from June to November. The fauna was characterised by high abundance and low diversity, and was dominated numerically by the small copepods *Oncaea curvata* and *Oithona similis*. Other taxa were seasonally abundant. The sympagic fauna was also characterised by low diversity and high abundance of one or two species of copepods.

The large variation in sea ice cover and food supply experienced over an annual cycle was reflected in the range of life history strategies adopted by the copepods. At least two species were strongly associated with the sea ice, using it as a source of nourishment, as well as a probable refuge from predation. Several other species were

loosely associated with the under-ice surface, possibly grazing on diatoms present on the surface of the ice crystals. At least three species were seasonal migrants to the region, circulating in with water from offshore when the sea ice broke out.

The storage of wax esters by *Oncaea curvata* and *Oithona similis* suggests that these species were able to survive periods of starvation. Many species time their peak reproductive activity to coincide with the phytoplankton bloom when it is expected that grazing will be at a maximum. The impact of grazing by the copepod assemblage on phytoplankton before and after sea ice break-out is addressed in the following chapter.

Chapter 6
Grazing of Phytoplankton by Copepods at O'Gorman Rocks[1]

6.1 Introduction

Zooplankton play an essential role in carbon cycling in the Antarctic marine ecosystem, forming a link between primary production and higher consumers such as fish, seabirds and whales. Presently little is known about the grazing activities of the smaller copepods that dominate the inshore zooplankton assemblage (Chapter 5). The impact of copepod grazing on phytoplankton in Antarctic coastal waters is of interest because (1) in the absence of krill (*Euphausia superba*) they represent the major trophic link to higher consumers and thus could play an important role in the transport of carbon through the food web, and (2) phytoplankton not grazed by copepods might be an important food source for benthic species in the coastal region, which, in turn, play a role in the remineralisation of carbon to the water column.

Several methods have been employed to study grazing by Antarctic and Southern Ocean zooplankton. These include SEM and light microscopic analysis of gut contents of herbivorous and carnivorous species (Hoshiai et al. 1987, Øresland and Ward 1993), the gut pigment method to study herbivory (Atkinson et al. 1992a, 1992b) and bottle incubations to examine ingestion of both phytoplankton and microzooplankton (Schnack 1985, Atkinson 1994). A radiotracer technique designed specifically for studying *in situ* grazing by zooplankton communities has been refined by White and Roman (1991, 1992). The method involves the use of incubation chambers (Haney 1971, Roman and Rublee 1981) to which radiolabelled methylamine hydrochloride

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($CH_3NH_2.HCl$) is added. Methylamine (MeA) is an ammonia analogue (Balch 1985, 1986) and the mechanisms of its uptake by phytoplankton and bacteria are similar. Unlike ^{14}C labelled bicarbonate, methylamine is taken up under both light and dark conditions (Balch 1985, White and Roman 1991). Given the low light intensities experienced by phytoplankton living under sea ice, and the need to keep *in situ* grazing experiments as short as possible, it was believed that the use of radiolabelled MeA would provide an effective method for measuring grazing rates of copepods.

This chapter describes a study that applied the method of White and Roman (1991, 1992) to measure ingestion and grazing rates of the copepods which commonly occur in surface waters near O'Gorman Rocks. The data were used to evaluate the impact of copepod grazing on phytoplankton standing stock and primary production. Experiments were performed both before and after the break-out of sea ice to determine if there were differences in grazing rates.

6.2 Methods

6.2.1 Sampling dates and phytoplankton sampling methods

Grazing experiments were conducted on five occasions during the summer of 1994-5: two before (21 and 28 December 1994) and three after sea ice break-out (2, 11 and 20 February 1995). During December the sun did not set, but by the last experiment the period of darkness had increased to 4 hr 45 min (Chapter 2, Figure 2.3).

Four water samples were collected from 2m water depth for the determination of total chl *a* (Appendix A.8). On each sampling date (except 21 December) an additional four water samples were collected and fractionated into the following size classes - > 100 µm, 53 - 100 µm, 20 - 53 µm, 8 - 20 µm, 5 - 8 µm, 3 - 5 µm and 0.7 - 3 µm. The >

20 µm fractions were collected on mesh sieves then backwashed onto Whatman GF/F filters, and the smaller fractions were filtered onto Activon polycarbonate filters. The contribution of each of these fractions to total chl *a* was quantified.

Primary productivity at 2 m water depth was measured on each sampling date using standard methods employing $NaH^{14}CO_3$ (Parsons et al. 1984). Clear plastic 'Whirlpak" bags (35 mL) were inoculated with 37 x 10^3 Bq mL^{-1} (1 µCi mL^{-1}) $NaH^{14}CO_3$ and incubated *in situ* for up to 4 hr. Calculations of hourly photosynthetic rates were as given in Parsons et al. (1984). Equipment failure on 21 December meant that primary productivity could not be measured accurately, so the results were discarded. During the December experiments a tent was erected over the holes drilled in the sea ice to minimise light shocking of organisms.

Uptake of radioisotopes by phytoplankton and bacteria can be influenced by the size of the particles (White and Roman 1991). Therefore, to assess any variation in uptake rates, uptake of MeA into the above size fractions was measured on three sampling dates. Seawater samples were inoculated with 1.85 x 10^6 Bq l^{-1} (50 µCi l^{-1}) MeA and then incubated at 2 m water depth for 1 hr. Seawater particulate matter was then collected and fractionated as outlined above. Filters were returned to the laboratory and processed for analysis of radioactivity. Uptake of MeA was expressed on a per µg chl *a* basis for each size fraction.

6.2.2 Zooplankton grazing rates

Zooplankton were collected from the upper 2 m of the water column. Dry weights were determined by the methods given in Appendix A.5. Carbon concentration was assumed to be 50 % of corrected dry weight for the smaller species (Båmstedt 1986) and 45 % of corrected dry weight for *Calanoides acutus* (Schnack 1985).

Experiments were carried out *in situ* using clear plastic 2 L chambers (Haney 1971, Roman and Rublee 1981). Copepods were collected from 2 m water depth, diluted if necessary into filtered seawater, then transferred gently into the chambers which were filled with water also collected from 2 m (final concentration of animals was 50 to 100 individuals L^{-1}). Each chamber was then inoculated immediately with 3.7 x 10^6 Bq (100 µCi) of ^{14}C-MeA.HCl and the animals were left to graze for approximately one hour (mean experiment duration = 1 hr, 9 min; range = 59 min to 1 hr, 15 min). The short incubation was necessary as laboratory experiments showed that animals produced faecal pellets at an average rate of one per hour. Experiments were conducted in triplicate near solar noon. Before sea ice break-out each incubation chamber was deployed beneath the ice through a separate hole. Effects on feeding behaviour of increased light coming through the hole were minimised by using a hinged harness to situate the chambers away from the hole (Figure 6.1). The chambers were agitated periodically to ensure that particulate matter remained in suspension.

At the end of each experiment, the animals were filtered rapidly (< 15 s) from the seawater onto a 100 µm mesh sieve, rinsed with GF/F filtered seawater, anaesthetised with a carbonated water / seawater mixture (Kleppel et al. 1988), and returned to the laboratory. They were then sorted by taxa onto preweighed 8 µm polycarbonate filters, rinsed with distilled water and dried at 60 °C to constant weight. Intact specimens were picked randomly from the filters. No effort was made to sort animals on the basis of developmental stage.

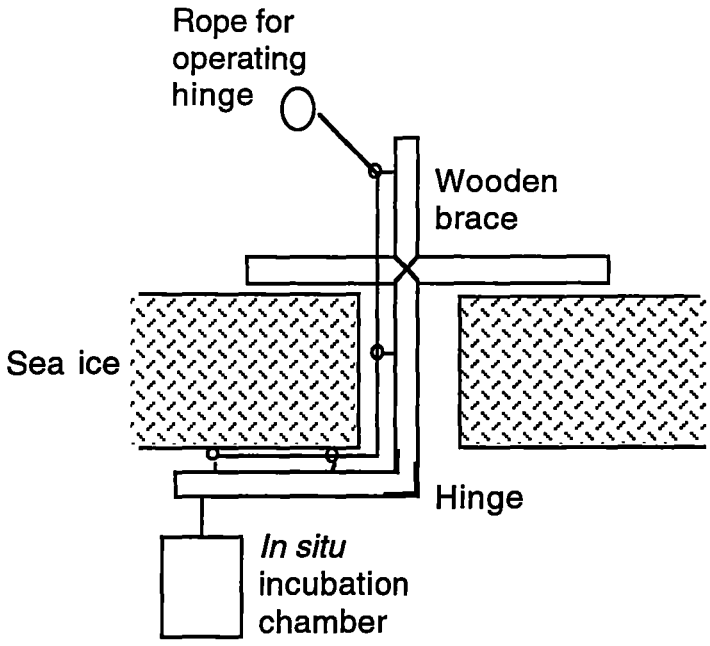


Figure 6.1. Diagram of incubation chamber showing hinged harness used to situate chamber away from direct influence of stray light from the sampling hole.

Radioactivity of the samples was determined, within one week of collection, using a Beckman Scintillation Counter (LS 6500) employing 10 mL Optiphase HiSafe III as the scintillation cocktail. Particulate matter from the incubation chambers was collected onto 3 μm polycarbonate filters which were placed into scintillation vials and acidified with 35 μL glacial acetic acid (White and Roman 1992) before radioactivity analysis. Ethyl acetate (1 mL) was added to the scintillation vials to dissolve the polycarbonate filters. The choice of 3 μm as the cutoff for 'available' food was based on previous observations that capture efficiency by copepods of particles
< 3 μm was considerably reduced (Nival and Nival 1976, Berggreen et al. 1988).

6.2.3 Calculation of grazing rates

Clearance rates (mL individual^{-1} hr^{-1}) for six copepod taxa and unidentified copepod nauplii were determined using the equations of Daro (1978).

$$\text{Clearance} = \frac{2 \times dpm_z}{dpm_p \times t} \qquad (6.1)$$

where dpm_z = activity per individual, dpm_p = activity per mL of water filtered, and t = duration of experiment in hours.

The weight specific ingestion rate [μgC (μg bodyC)$^{-1}$ d^{-1}] was determined by multiplying the calculated clearance rate by phytoplankton carbon (μgC L^{-1}) and dividing the result by copepod carbon (White and Roman 1992). A carbon to chl *a* ratio of 75 was determined in another study undertaken at the same site (Gibson 1997). Finally, grazing rate (μgC m^{-3} h^{-1}) for the copepod assemblage was determined by multiplying the above ingestion rate by biomass. The daily grazing rate of copepods was assessed by multiplying the hourly rate by 24. Some Antarctic copepods are thought to exhibit diel periodicity in feeding, whereby they feed at higher rates at night (e.g. Tanimura et al. 1984a), so these values might be underestimates and should serve as a guide for comparison only.

6.3 Results

6.3.1 Phytoplankton

Chl *a* was highest on 21 December (Figure 6.2), when there was a bloom of an identified cryptomonad, cryptomonad A (see Chapter 5), just under the ice (8 x 10^6 cells L^{-1}) (Gibson et al. 1997a). Chl *a* had decreased by late December, by which time numbers of cryptomonad A had dropped by an order of magnitude (3 x 10^5 cells L^{-1}). Following the break-out of the sea ice in January, a mixed bloom of diatoms occurred, including *Nitzschia* spp. and *Fragilariopsis* spp. This bloom disappeared, and chl *a* levels were again low on 2 February, after low-chlorophyll water had circulated into

the bay (Gibson et al. 1997a). By 11 February, an intense bloom of the diatom *Thalassiosira dichotomica* had developed which lasted until after the final experiment (20 February).

The majority of chl *a* usually occurred in the 8-20 μm fraction. This was especially evident on February 11 and 20 (Figure 6.3), when the phytoplankton was dominated by *Thalassiosira dichotomica*. The typical size range for this species is 15 to 22 μm (Medlin & Priddle 1990). In general the > 53 μm fraction accounted for only a small percentage of the total chl *a*, consistent with the observed lack of large species or cellular aggregations, particularly colonies of *Phaeocystis antarctica* and chain forming diatoms, which had been common the previous summer (Gibson et al. 1997a). Uptake of MeA by particulate matter varied both between size fractions and between sampling dates (Figure 6.4). The highest overall chl *a* specific uptake occurred on 11 February, with the chl *a* -rich 8 to 20 μm fraction generally showing the greatest uptake.

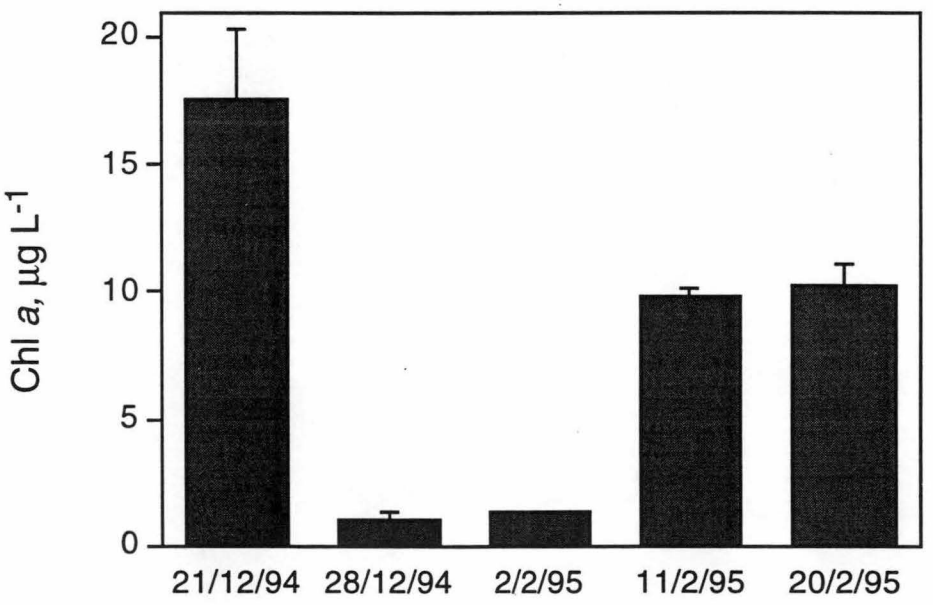


Figure 6.2. Total chl *a* concentrations (μg L^{-1}) at the O'Gorman Rocks site on five dates. Bars represent mean (± s.e.) of four samples. Note that one error bar is too small to be shown.

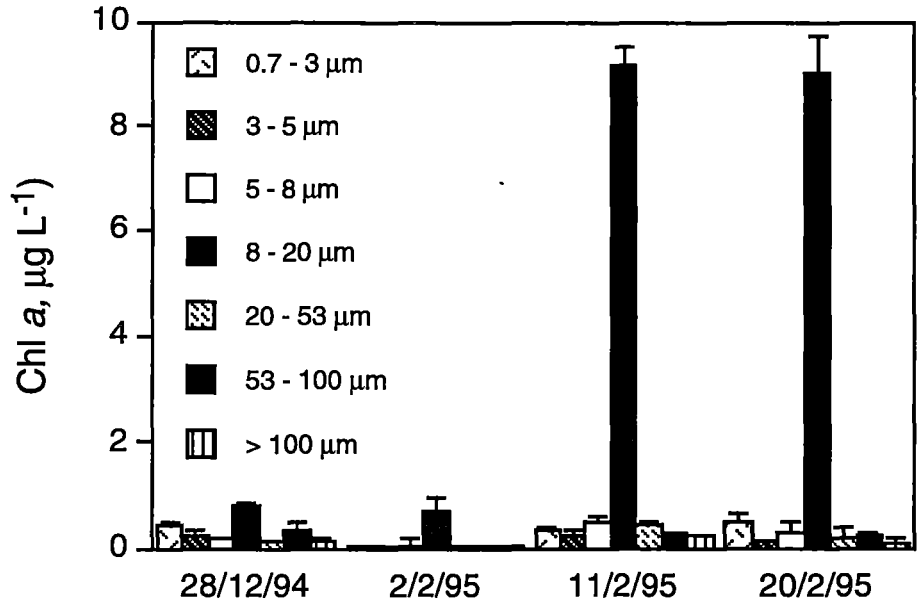


Figure 6.3. Size-fractionated chl *a* (µg L^{-1}) at the O'Gorman Rocks site on four dates. Bars represent mean (± s.e.) of four samples. Note that some error bars are too small to be shown.

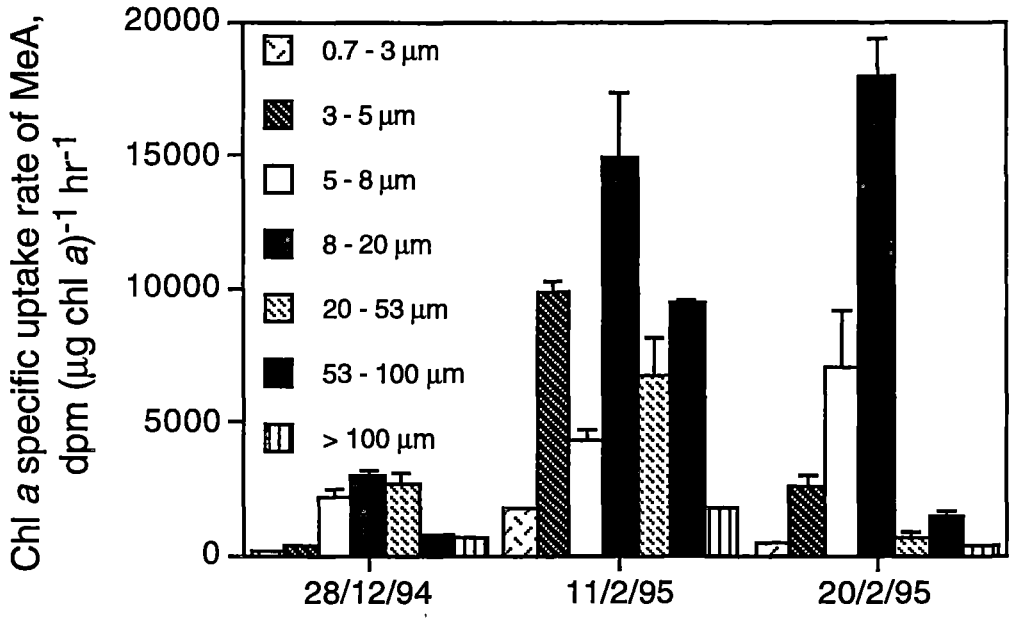


Figure 6.4. Chl *a*-specific uptake of methylamine (dpm (µg chl *a*)$^{-1}$ hr^{-1}) at the O'Gorman Rocks site on three dates. Bars represent mean (± s.e.) of four samples. Note that some error bars are too small to be shown.

6.3.2 Zooplankton composition and biomass

Mean zooplankton abundance ranged from 3,770 individuals m^{-3} on 21 December to 6,150 individuals m^{-3} on 28 December. Biomass ranged from 7.1 mgC m^{-3} on 21 December to 43.2 mgC m^{-3} on 11 February (Figure 6.5). Before sea ice break-out, copepods, in particular *Paralabidocera antarctica*, harpacticoids and small numbers of *Calanoides acutus*, accounted for at least 65 % of the total biomass (Figure 6.6); larval polychaetes accounted for most of the remainder. However, the poecilostomatoid copepod *Oncaea curvata* and small nauplii (most probably *O. curvata*) were numerically dominant (> 85 %) on both sampling dates prior to ice break-out.

Total zooplankton biomass increased after the break-out of sea ice (Figure 6.5). Copepod species largely associated with sea ice, such as *Paralabidocera antarctica* and the harpacticoids, were not present after break out. *Stephos longipes* also has a life cycle associated with sea ice (Kurbjeweit et al. 1993), but appeared in the water column after ice break out (Chapter 5). During February, the most numerically abundant taxa collected were *Oncaea curvata* (> 55 %), unidentified copepod nauplii (≥ 10 %), *Oithona similis*, polychaetes and early copepodite stages of *Calanoides acutus*. On 2 February large numbers of small ctenophores accounted for two-thirds of the biomass, while on 11 February larval polychaetes (probably *Pelagobia longicirrata*) dominated (> 65 %). By 20 February copepods again dominated the biomass, mainly due to the presence of *C. acutus*.

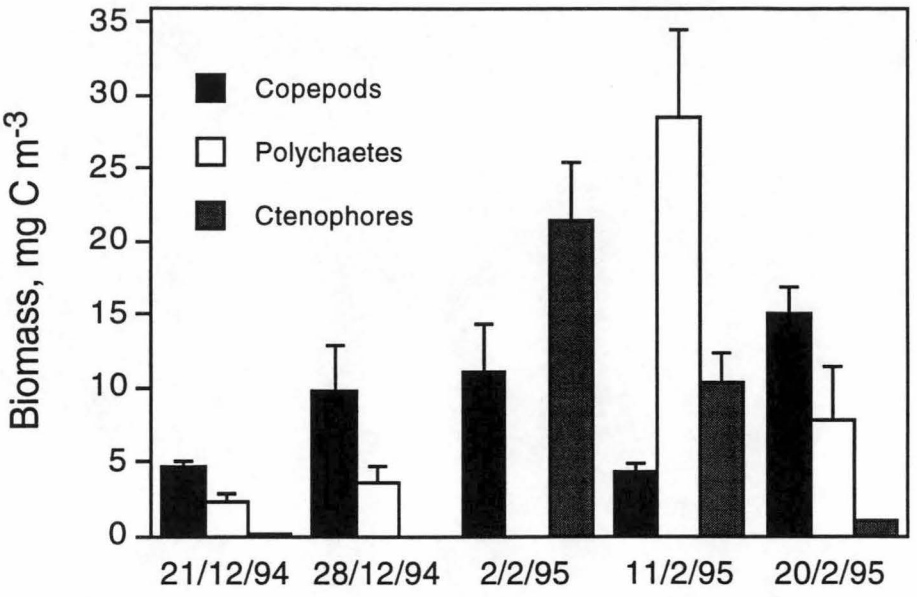


Figure 6.5. Biomass (mg C m^{-3}) of major zooplankton groups collected at the O'Gorman Rocks site on five dates. Bars represent mean (± s.e.) of four samples. Note that some error bars are too small to be shown.

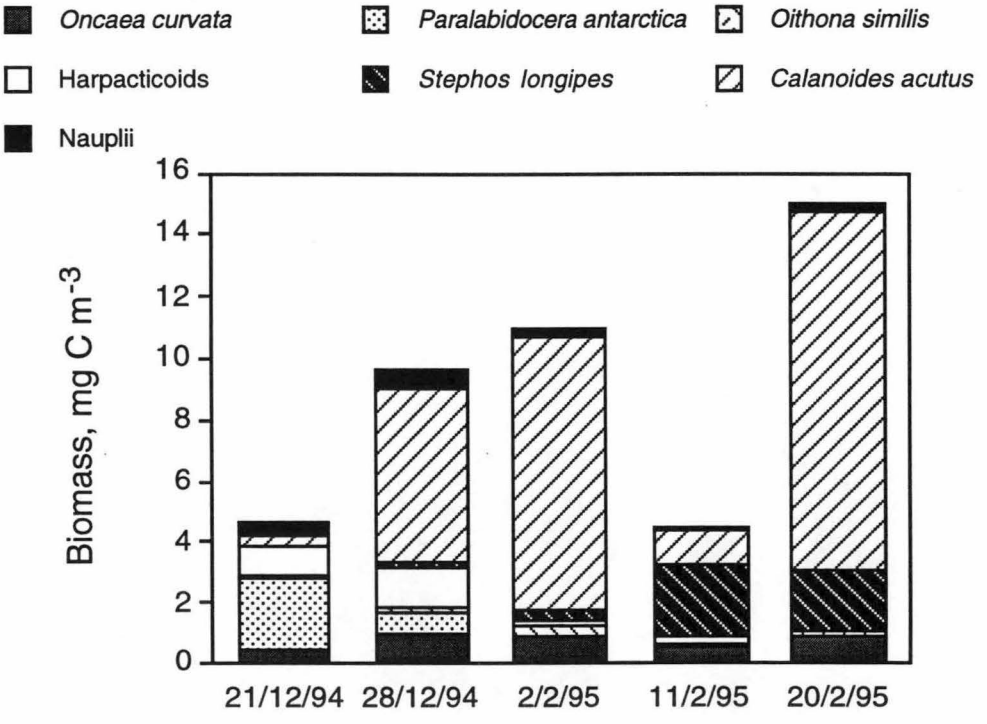


Figure 6.6. Biomass of individual copepod taxa collected at the O'Gorman Rocks site on five dates.

6.3.3 Clearance, ingestion and grazing rates.

Mass-specific ingestion rates of small copepods were much higher than those of larger animals (Table 6.1). Ingestion rates tended to follow the trend of chl *a*, so that when chl *a* was high in the water column overall ingestion rates were also high, and ingestion was low when chl *a* was low (Figures 6.2 and 6.7). The smaller copepods (*Oncaea curvata* and *Oithona similis*) ingested around 120 % of body carbon per day, whereas the daily rations of the larger calanoid species ranged from 5 % (*Calanoides acutus*) to 29 % (*Paralabidocera antarctica*).

Table 6.1. Mean (± S.D.) daily clearance and ingestion by copepods over entire study. Conversion from clearance rates to carbon ingestion assumes a C : chl *a* ratio of 75. N is the number of measurements.

Species (and Stage)	Clearance (mL ind^{-1} d^{-1})	Ingestion (µg C $ind^{-1}d^{-1}$)	Weight (µg C ind^{-1})	Rations (% body C d^{-1})	N
Paralabidocera antarctica (CV to CVI)	8.58 (0.14)	5.93 (7.40)	20.54	29	9
Oncaea curvata (CI to CIV)	2.89 (0.96)	0.84 (1.74)	0.59	142	15
Oithona similis (CI to CIV)	4.54 (0.68)	0.87 (1.62)	0.78	111	12
Stephos longipes (CII to CVI)	8.83 (8.99)	2.39 (1.68)	15.42	15	12
Calanoides acutus (CI to CIV)	14.87 (11.02)	5.25 (2.28)	113.17	5	9
Harpacticoids (CIII to CV)	4.13 (1.20)	3.41 (4.43)	5.56	61	6
Nauplii	1.38 (1.75)	0.37 (0.17)	0.26	142	15

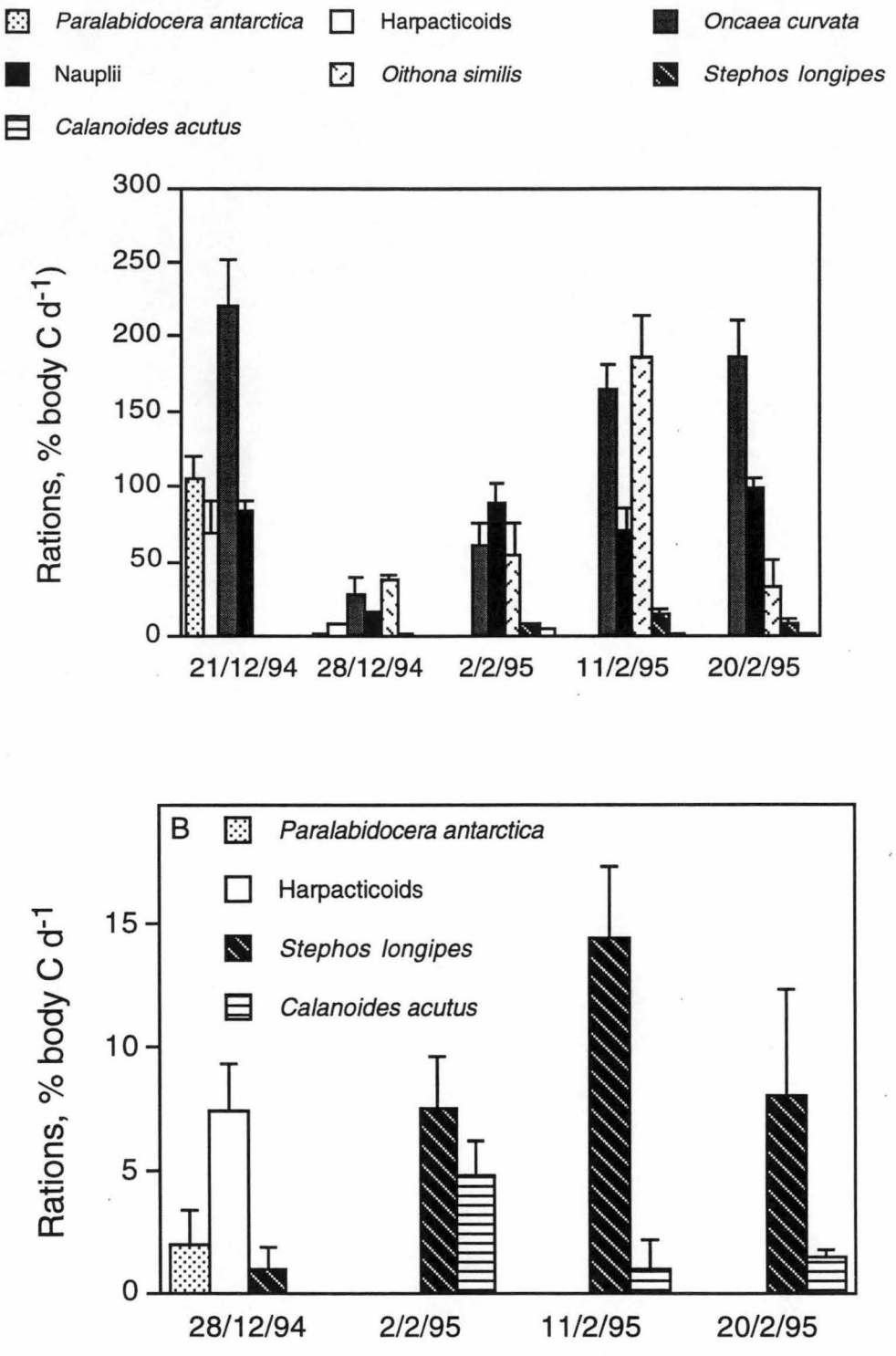


Figure 6.7. A. Daily rations for copepods collected at the O'Gorman Rocks site on five dates. B. same data as in A. but with y-axis expanded. Note that some error bars are too small to be shown.

Maximum grazing by copepods was recorded on 21 December, when chl *a* values were also at their highest (Figure 6.8). High biomass and moderate ingestion rates for

Paralabidocera antarctica and the harpacticoid copepods, combined with high ingestion and high numbers of *Oncaea curvata* and *Oithona similis*, resulted in this maximum. Grazing rates were significantly lower both one week later and again on 2 February. Although copepod biomass on these dates was approximately double that of 21 December, phytoplankton biomass was much lower, leading to low ingestion rates and a considerable reduction in overall grazing rates. By the middle of February copepod biomass had decreased but, coupled with high ingestion rates, the grazing pressure was again high. This trend continued until 20 February, when biomass reached a maximum and ingestion was still high. For the 4 experiments where primary production was measured, grazing impact by the copepod assemblage on primary productivity was consistently low, ranging between 1 and 5 % (Table 6.2).

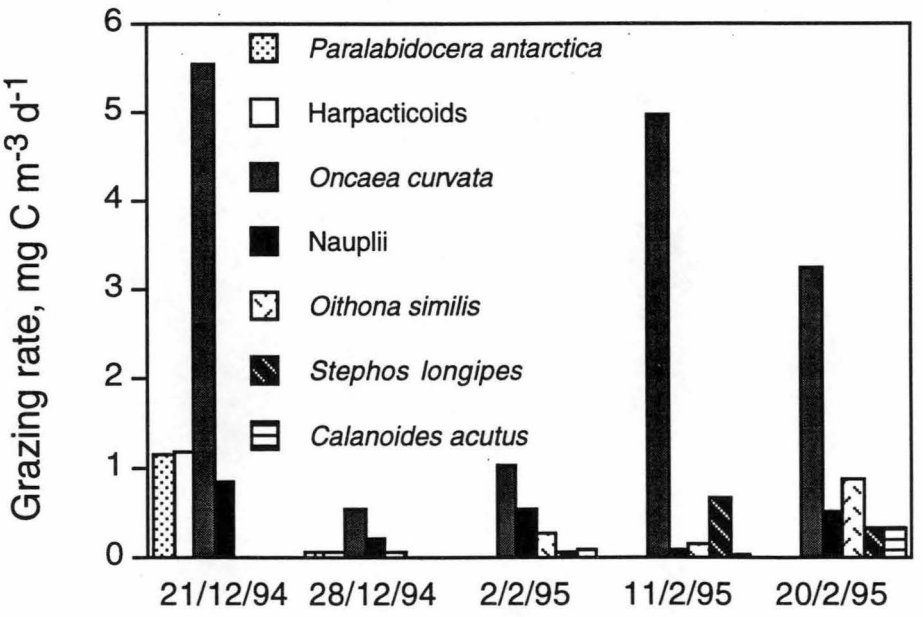


Figure 6.8. Daily grazing rates of total copepod assemblage collected at the O'Gorman Rocks site on five dates.

Table 6.2. Summary of phytoplankton standing stock (assumed C : chl *a* = 75) and primary productivity, and total grazing by copepods collected from the O'Gorman Rocks site. Percentage of primary productivity grazed by copepods is shown. Primary productivity was not measured on 21 December 1994 due to equipment failure.

	Under ice		Open water		
	21/12/94	28/12/94	2/2/95	11/2/95	20/2/95
Phytoplankton standing stock ($\mu g\ C\ L^{-1}$)	1316	83	102	741	769
Primary productivity ($mg\ C\ m^{-3}\ d^{-1}$)		112.8	187.2	218.4	120.0
Total copepod biomass ($mg\ C\ m^{-3}$)	5.2	10.7	12.1	4.8	16.5
Total grazing ($mg\ C\ m^{-3} d^{-1}$)	8.7	0.9	2.0	5.9	5.3
Grazing : primary productivity (%)		0.9	1.1	2.7	4.4

As a result of both large numbers and high ingestion rates, the grazing pressure exerted by *Oncaea curvata* was generally higher than for the other species, reaching a maximum of 6 $mgC\ m^{-3}\ h^{-1}$ (Figure 6.8). *Oncaea curvata* accounted for at least 50 % of the grazing pressure, reaching a maximum of 80 % (Figure 6.9). Nauplii, by virtue of their large numbers and therefore high biomass, were significant grazers of phytoplankton, particularly on February 11 and 20.

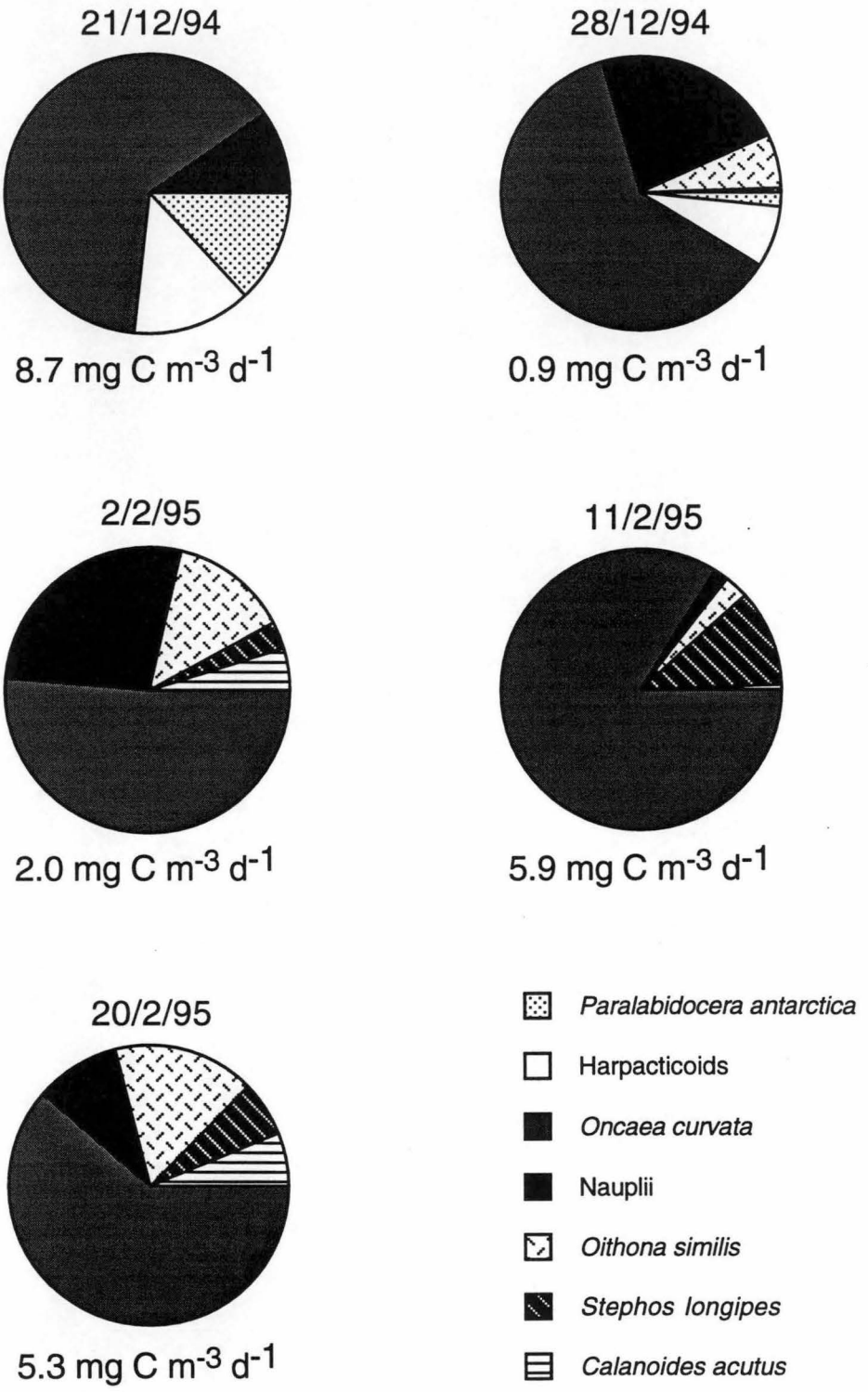


Figure 6.9. Partitioning of grazing by copepods collected from the O'Gorman Rocks site on five dates. Percentage of grazing by each taxa is represented by pie areas; total daily grazing is shown below each pie chart.

6.4 Discussion

6.4.1 Evaluation of ^{14}C-Methylamine

^{14}C-MeA.HCl proved to be a useful tracer for estimating *in situ* grazing rates of copepods, although it is necessary to interpret the results in light of the limitations of the method. The present study differed from that of White and Roman (1991, 1992) who used ^{3}H-MeA.HCl in their grazing experiments. While it is not anticipated that there would be major differences between the two methods, it would be useful in future to run parallel experiments comparing the two forms of MeA. The use of ^{3}H-MeA.HCl has one advantage in that it can be used in conjunction with ^{14}C-labelled bicarbonate to run parallel grazing experiments in the light and dark, thereby distinguishing between heterotrophic and autotrophic production. Unfortunately, at the time of the present study, attempts to purchase the tritiated compound were unsuccessful, and so the ^{14}C-labelled MeA was substituted.

MeA was rapidly taken up by phytoplankton, including those organisms living under the sea ice where light intensities were low, thus allowing experimental times to be kept short. The method minimised experimental manipulation of the animals and enabled grazing by small species to be assessed. Overall uptake of MeA in this study was lower than that recorded for Chesapeake Bay (White and Roman 1991), but as uptake rates have been shown to increase with temperature, the low temperatures commonly recorded in Antarctic waters (around -1°C) may account for this difference. Nevertheless, uptake was rapid enough to give confidence in the dpm measured (i.e at least 50,000 times higher than background). MeA uptake decreases with increasing ammonium concentration (Wheeler 1980, White and Roman 1991). Ammonium concentrations measured at O'Gorman Rocks during the period of study were always very low (< 1 µM; J. Gibson, unpublished data), and thus were unlikely to have suppressed MeA uptake.

Caveats applying to the use of MeA for studying grazing rates have been discussed in detail in White and Roman (1991). Briefly, Daro's (1978) equation assumes that no recycling of isotope occurs between the different storage pools, that uptake of MeA is linear over time, and that different sized phytoplankton have the same rate of uptake.

In this study, the potential for recycling of MeA between storage pools was minimised by keeping the experimental times to approximately one hour. Uptake of MeA by particulate matter is linear over the first hour of incubation (Balch 1985, White and Roman 1991). Uptake of MeA in this study was not uniform between size classes of particulate matter or between sampling dates. Uptake was highest in the fractions > 3 μm and < 20 μm. The fact that uptake was not uniform between size classes of phytoplankton can lead to underestimates in grazing rates (White and Roman 1991). For example, it was possible that larger copepods such as *Calanoides acutus* were preferentially ingesting those cells > 20 μm; i.e. those with a low uptake-rate. Thus, if the dpm_p term used in equation 6.1 to calculate clearance rates included many small cells with high activity that were not ingested by *C. acutus*, the clearance rate for this species would be underestimated. At the other end of the scale, if small copepods such as *Oncaea curvata* were ingesting matter that was < 3 μm, then grazing would be overestimated, because the 3 μm filter cutoff meant that this fraction was not included in the equation. While it is important to view the results with these constraints in mind, they nevertheless provide a useful basis for comparison of community grazing rates and a comparison between large and small grazers.

6.4.2 Dominant grazers

Small copepods, notably *Oncaea curvata*, but also *Oithona similis* and small nauplii, always accounted for the highest proportion of grazing in each experiment. This observation agrees with that of Morales et al. (1991), who concluded that, while large

species can dominate the biomass, numerically dominant small species may contribute the most to grazing pressure, and hence carbon turnover. It is now becoming clear that small copepods, including *Oncaea* spp. and *Oithona* spp., are very common throughout the world's oceans and more work is needed to clarify their position in the marine trophic web.

Little is known about the trophic role of *Oncaea* species, although the genus is assumed to be omnivorous (reviewed in Paffenhöfer 1993). On average, *Oncaea curvata* ingested approximately 140 % of body carbon per day and had a mean daily clearance of 2.9 mL individual^{-1} d^{-1}. Given that water temperature at the time of the experiments was around -1 °C, these results are high compared to values recorded for other small copepods, including *Oncaea* spp., at warmer temperatures (e.g. Paffenhöfer 1993, Uitto 1996). However, Metz (1996) measured grazing rates of *O. curvata* collected from the Weddell Sea, and estimated rations up to 300 % of body carbon per day, when the copepods were feeding on *Phaeocystis* sp. at higher than ambient concentrations. This result, obtained using a traditional bottle clearance method, gives confidence that the high rations obtained in the present study are not unrealistic. As discussed in section 6.4.1, these rates could be somewhat overestimated due to the lack of data for particles < 3 µm in the denominator of Daro's equation. Paffenhöfer (1993) postulated that it is likely that *Oncaea* spp. require surfaces on which to feed. Before the break-out of sea ice, small patches of under-ice algae might have been incorporated into the incubation bottles and provided a surface on which *O. curvata* could feed. However, after the break-out of sea ice, it is not known to what extent particles in the water column might have formed aggregates in the bottles.

In this study, *Oithona similis* ingested approximately 110 % of body carbon per day and had a mean daily clearance of 4.5 mL individual^{-1} d^{-1}, which is similar to the results of Atkinson (1994) and Atkinson and Shreeve (1995) who, using bottle

incubation methods, recorded maximum values of 120 % and 5 to 7 mL individual^{-1} d^{-1} respectively. Studies of the feeding ecology of *Oithona* species have often been contradictory, and the relative importance of herbivory and carnivory in their diets is yet to be determined, although Atkinson (1994, 1995) reported that *Oithona* spp. clears motile taxa more rapidly than it does diatoms. In addition, coprophagy provides *Oithona* species with a substantial amount of their daily carbon requirements (González and Smetacek 1994).

Daily ingestion rates for *Calanoides acutus* in this study were low (mean of 5 %) as were clearance rates (15 mL individual^{-1} d^{-1}). Schnack (1985) reported higher clearance rates (10 to 400 mL individual^{-1} d^{-1}) for *C. acutus*, yet calculated daily rations to be 3 to 28%, and Atkinson et al. (1992b) reported daily rations of 6 to 27 %. The much lower clearance rates calculated in the present study may reflect the high abundance of *Thalassiosira dichotomica* recorded during the experiments after the break-out of sea ice, when *C. acutus* was abundant. Schnack (1985) observed that *C. acutus* did not filter centric diatoms as efficiently as it filtered microflagellates. Further, Atkinson (1994, 1995) reported that when chlorophyll values were fairly high, *C. acutus* had higher clearance rates on diatoms > 20 μm than on those < 20 μm. Thus, as stated in section 6.4.1, grazing by this species might have been underestimated if it had a preference for larger cells which were not taking up MeA as rapidly as smaller cells. *Calanoides acutus* collected during this study were probably not from a resident, actively reproducing population but rather had come in with newly circulated water when the sea ice broke out (Chapter 5). As such it is difficult to know whether they were in a very active feeding state at the time.

6.4.3 Copepod grazing rates

Grazing pressure exerted by copepods on phytoplankton was consistently low throughout this study. Only 1 to 5 % of primary production was grazed by the copepod assemblage. The impact of grazing on phytoplankton by mesozooplankton, including copepods, has been reported for other marine environments and is shown to be highly variable. Values reported for Antarctic and Southern Ocean waters have ranged from as low as approximately 1 % for McMurdo Sound (Hopkins 1987) and 8.4 % in the Bellingshausen Sea (Atkinson and Shreeve 1995) to as high as 81 % near the Prince Edward Archipelago (Perissinotto 1992); thus the range calculated for this study is close to the low values reported for zooplankton at the higher latitudes.

Where might primary production not grazed by copepods go? Three likely sinks for ungrazed phytoplankton are: (1) other mesozooplankton; (2) grazing by microzooplankton; (3) sedimentation and subsequent utilisation by the benthic fauna.

In addition to copepods, larval polychaetes, probably *Pelagobia longicirrata* (see Chapter 5), were the only other potential herbivores recorded in large numbers in this study. These animals were not included in the analysis of grazing rates as they were observed to become easily stressed and to possibly regurgitate their gut contents during handling. For polychaetes of a similar size to those in this study, White and Roman (1992) calculated a clearance rate of 5.6 mL animal^{-1} d^{-1} in Chesapeake Bay. Applying this rate gives a rough estimate of grazing pressure by polychaetes of approximately 30 % of primary production; thus, it will be useful in future to quantify accurately the contribution to total zooplankton grazing made by polychaetes during their residence in the water column. Other taxa which are probably significant grazers of phytoplankton, including *Ctenocalanus citer*, *Euphausia crystallorophias* and echinoderm larvae, were also abundant in the plankton samples at several times during the summer (see Chapter 5), but, unfortunately, not on the dates when grazing

experiments were performed. Ctenophores were abundant during the latter part of this study. The magnitude of their predation on herbivorous copepods, and subsequent transfer of phytoplankton carbon to these higher order consumers, also needs to be assessed.

Microzooplankton have been shown to graze a substantial amount of phytoplankton, especially in nearshore environments (e.g. Gifford 1988, Dagg 1995). In the Canadian Arctic, microzooplankton grazed from 37 to 114 % of primary production (Paranjape 1987), and along a transect in the Bellingshausen Sea microzooplankton were estimated to graze between 21 and 271 % of phytoplankton production (Burkill et al. 1995). Thus, microzooplankton grazers have a potentially significant impact on primary production in coastal polar waters. Studies on grazing by protozooplankton near O'Gorman Rocks during the 1993-94 summer (Archer et al. 1996b) showed that heterotrophic dinoflagellates ingested up to 25 % of daily primary production.

The fate of most of the primary production that is not grazed by zooplankton is to settle to the sediments where it becomes available to benthic grazers. Knox (1990) calculated that at least 80 % of primary production in McMurdo Sound sedimented to the benthos. However, at the O'Gorman Rocks site it was estimated that only 10 % of primary production sedimented to the benthos (Gibson 1997). The remainder was either consumed by grazers or carried away by water currents. An abundant and diverse benthic fauna has been described for the inshore waters around Davis (Everitt et al. 1980). It is characterised by deposit feeders and motile grazers such as polychaetes and amphipods. The region also supports a high abundance of benthic macroalgae, and the relative importance of phytoplankton and benthic algae to the diets of benthic animals is yet to be determined.

6.4.4 Effects of photoperiod

The experiments in this study were all performed during daylight hours. Zooplankton often exhibit diel periodicity in grazing (Head et al. 1985, Peterson et al. 1990), where there is a peak in ingestion during the hours of darkness. If the copepods were not feeding at their maximum during experiments in this study, then grazing rates for the assemblage have been underestimated. However, the pattern of diel feeding behaviour described above is by no means universal, and several studies have described the lack of a distinct peak in nighttime feeding, especially at high latitudes when the hours of darkness were reduced (e.g. Huntley and Escritor 1991). The first two experiments in this study were conducted during a period when the sun did not set, the latter three in periods of darkness ranging from two hours (11 February) to 4 hours 45 minutes (20 February). If the feeding behaviours of the copepods were unaffected by photoperiod, then there is less possibility that multiplying hourly rates by 24 underestimated daily grazing rates. Nonetheless, it is important that future studies take into account the possible existence of diel feeding cycles and at least some experiments should be carried out over a full 24 hour period.

6.5 Conclusions

Grazing impact by the copepod assemblage on primary productivity was consistently low, ranging between 1 and 5%. These values were consistent with measurements made from other high latitude localities. Daily grazing impact was dominated by small copepods, in particular *Oncaea curvata* which was the numerically dominant species present throughout the study, and which accounted for at least 50% of total grazing on each sampling date. Unfortunately, to date there have been few attempts to quantify the grazing impact of smaller copepods in Antarctic and Southern Ocean waters. Therefore, as species such as *O. curvata* and *Oithona similis* occur in high densities in

many areas, it is probable that estimates of total copepod consumption of primary production in the Southern Ocean may be substantially underestimated.

Chapter 7
Comparative Life Histories of Neritic and Lacustrine Populations of *Paralabidocera antarctica* (I.C. Thompson)

7.1 Introduction

In the Southern Ocean the life cycles of large, oceanic copepods, particularly *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas* and *Metridia gerlachei* have received considerable attention (Atkinson 1991, Bathmann et al. 1993, Schnack-Schiel and Hagen 1994, 1995, Atkinson et al. 1997, Ward et al. 1997). One difficulty with studying life cycles of Antarctic copepods is that they are generally long in comparison with many tropical and temperate species, taking at least one year to complete. Therefore, by necessity, most of the life cycles described thus far have been reconstructed from data gathered from different localities in different years. The present study provided an opportunity to investigate the life cycle of a small Antarctic copepod over a full annual cycle. This study aimed to compare the life history strategies of a neritic population of *Paralabidocera antarctica* with one isolated in a saline lake for several thousand years.

From the limited information available about the lacustrine population (Bayly and Burton 1987), it appeared that the organisms did not have the same association with the lake ice cover, when sampled in early January 1982, as had been recognised for the coastal population by Tanimura and co-workers (Tanimura et al. 1984a,b, Hoshiai and Tanimura 1986, Hoshiai et al. 1987, Tanimura et al. 1996). Furthermore, biochemical analysis of specimens collected in February 1984 from Ace Lake revealed that the animals stored large concentrations of triacylglycerols (Volkman et al. 1988). Thus several questions arose about this species, including:

a) did the lacustrine population associate with the lake ice at any time in its life cycle?;
b) did the neritic population also store triacylglycerols as the primary energy reserve?;
c) were there seasonal and ontogenetic variations in the lipid stores?; and
d) how did isolation from predators and competitors affect the life cycle of the lacustrine population?

This chapter describes the developmental cycles, including ontogenetic and seasonal changes in lipid content, of two populations sampled from Ace Lake and O'Gorman Rocks. Ace Lake formed some time within the last 5,000 years as a result of isostatic uplift of the Vestfold Hills when the polar ice cap retreated (Zwartz et al. 1998). The biota of the lake is derived from organisms that were trapped as the lake was isolated from the sea. At present, *Paralabidocera antarctica* is the only planktonic metazoan existing in the lake. A small, harpacticoid, *Idomene scotti*, has been observed in the algal mats that fringe the lake. Specimens of this species were observed on only two or three occasions in planktonic samples in the present study, and then in very small numbers (1 to 3 specimens per sample). *Paralabidocera antarctica* is found in two other marine derived lakes (Lake Abraxas, Pendant Lake) and three partially enclosed lagoons (Burton Lake, Lake Fletcher and Deprez Basin) in the Vestfold Hills.

7.2 Methods

Ace Lake was sampled 15 times from 20 April 1994 to 13 March 1995, and the O'Gorman Rocks site 35 times from 15 December 1993 to 27 February 1995. The sea and lake ice was sampled with a SIPRE corer, and the water column with a 2 m long, 100 μm mesh 'umbrella' net fitted with a plastic cod-end. The specimens were enumerated and identified to developmental stage. Females were examined for the presence of spermatophores. Naupliar stages I to VI were pooled for the lipid analysis and dry weight determinations, as large numbers were required and sorting the nauplii

was very time consuming. In all other cases individual stages were treated separately. Salinity and temperature of the water column in Ace Lake was measured with a Platypus Submersible Data Logger. Concentration of chl *a* was measured in the lake ice and at three depths in the water column. Concentration of particulate lipids was measured in the water column only. Details of methods are provided in Appendix A.

Female *Paralabidocera antarctica* collected from the O'Gorman Rocks site during December 1993 were used in an egg production experiment. Twenty animals collected on either 15 or 29 December 1993 (10 per date) were transferred to individual 100 mL crystallising dishes, and fed a natural diet of phytoplankton collected on 29 December from the same site. Half of each group were fed particles that passed through a 200 µm mesh sieve. The other half were fed particles that were retained by the sieve, largely colonies of *Phaeocystis antarctica* and diatom chains. No estimate of the concentration of food was made. The animals were kept at 0 °C in constant low light. Each day the number of eggs and faecal pellets produced were counted and the pellets and eggs removed from the crystallising dishes. The experiment was run for six days. A mean daily egg production rate was estimated from these experiments. While not performed under rigorous experimental conditions, the results nevertheless provide useful information that can be added to the knowledge of the life history of *Paralabidocera antarctica*. Unfortunately, experiments designed to measure *in situ* egg production rates of female *P. antarctica* in Ace Lake were unsuccessful, as the animals died in the incubation apparatus.

7.3 Results

A physical description of the habitat at the O'Gorman Rocks site was provided in Chapter 5. Relevant information will be reiterated when necessary.

7.3.1 Habitat description of Ace Lake

7.3.1.1 Physical limnology

When this study commenced in April 1994 the ice cover on Ace Lake was 0.85 m thick (Figure 7.1). It reached a maximum thickness of 1.80 m in late October. The ice began to break up in late January 1995, and had disintegrated completely by 14 February 1995. There was a short period of open water before re-freezing began. Consolidation of the ice cover was rapid and it was again traversable by 10 March 1995. Snow cover was variable, ranging from 0 to 340 mm (Figure 7.1).

Bulk salinity of the ice cores was low, reaching no more than 3 psu (Figure 7.2). There was a gradual decrease in salinity from May to September as air temperatures dropped and brine was excluded from the ice matrix. Salinity increased again during October as air temperatures gradually increased, causing melting and enlargement of brine channels, and enhanced flushing of lake water through the ice.

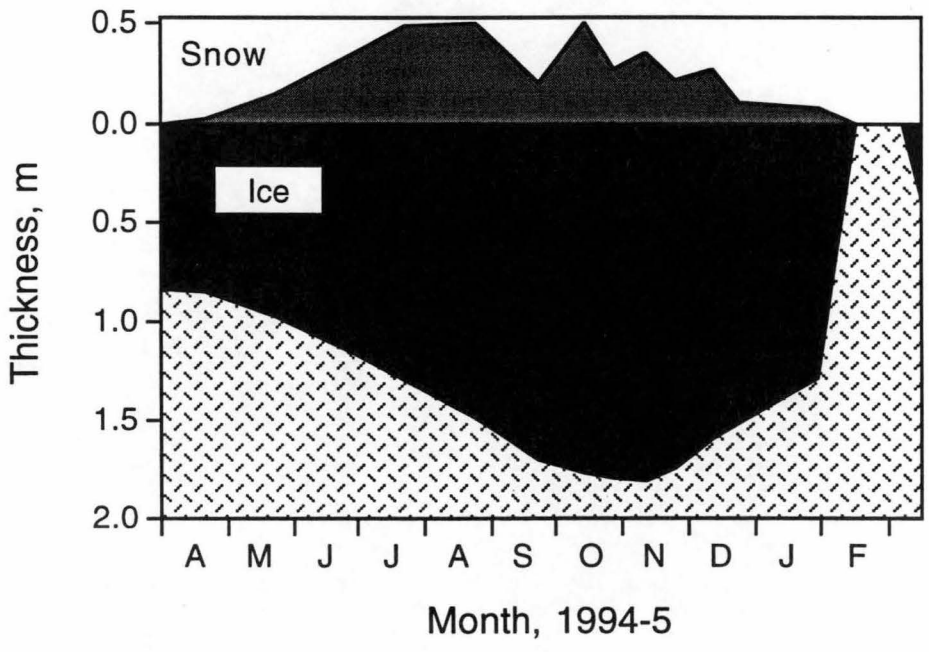


Figure 7.1. Ice and snow thickness (metres) at the Ace Lake site, April 1994 to March 1995.

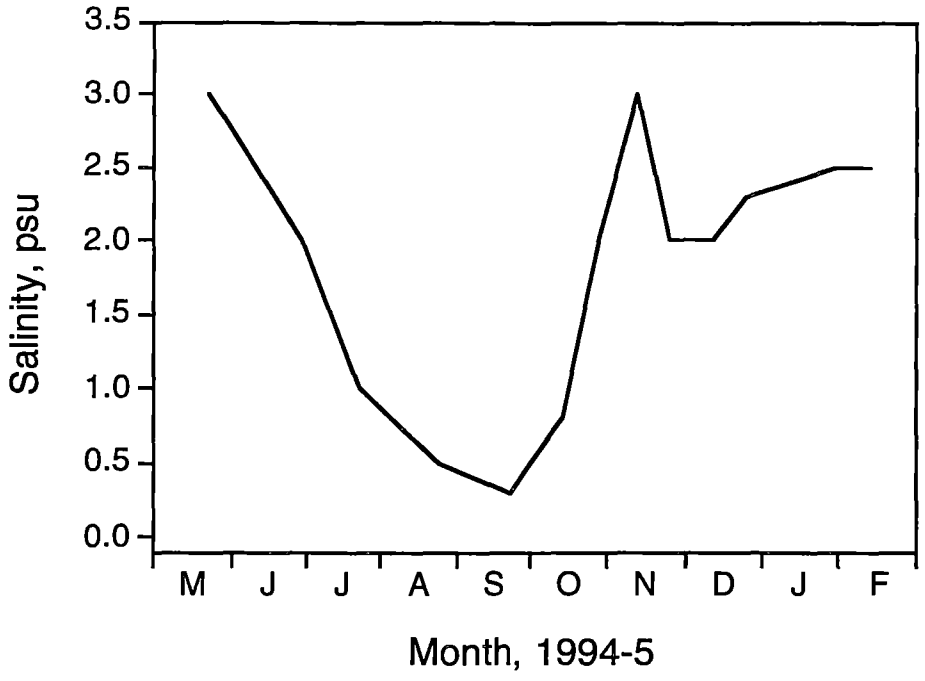


Figure 7.2. Bulk salinity (psu) of the ice cores sampled from the Ace Lake site, May 1994 to February 1995.

As expected for a meromictic lake, there was considerable stratification of both the salinity and temperature of the water column. During 1994 an oxycline existed at approximately 11 m. Salinity varied substantially in the top 2 m of the water column (Figure 7.3). The water just under the ice increased from a minimum of 7 psu in May to a maximum of 16 psu during winter and spring. This was due to the exclusion of brine from the forming ice as air temperatures decreased. Salinity at 2 m decreased in mid-January as a result of dilution due to melting of the ice cover. Some surface wind mixing would have occurred during the brief window when the lake was ice free. Salinity then increased again in late February and early March as brine was excluded from the newly forming ice. At 5 m and below, salinity was essentially constant throughout the year, but increased with depth from 17 psu at 5 m to 32 psu at 15 m. The salinity of water below 18 m was greater than that of seawater.

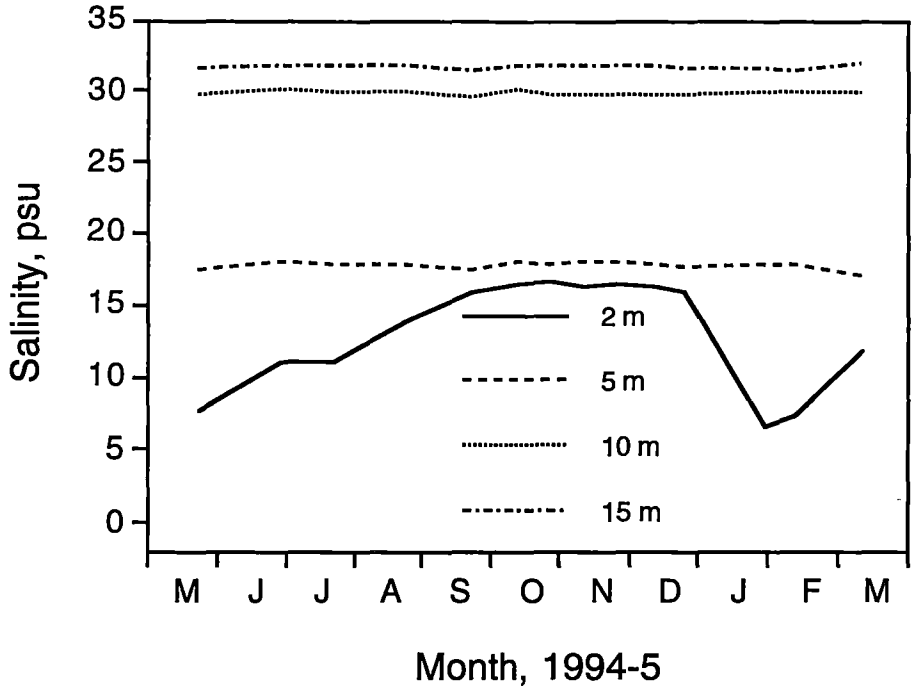


Figure 7.3. Salinity (psu) of the water column at four depths in Ace Lake, May 1994 to March 1995.

Temperature at four depths in the water column is shown in Figure 7.4. At 2 m there was an increase in temperature from 0 °C in the winter to 4 °C during summer when air temperatures were high and surface irradiation was at its maximum. Water temperature at 5 m decreased from 4.5 to 3 °C in winter, then increased to 8 °C in late summer. At 10 m the change in temperature was not as great, but it also reached a maximum, of 10 °C, in late summer. Waters in the anoxylimnion remained thermally stable, as indicated by the constant temperature (6 °C) recorded at 15 m.

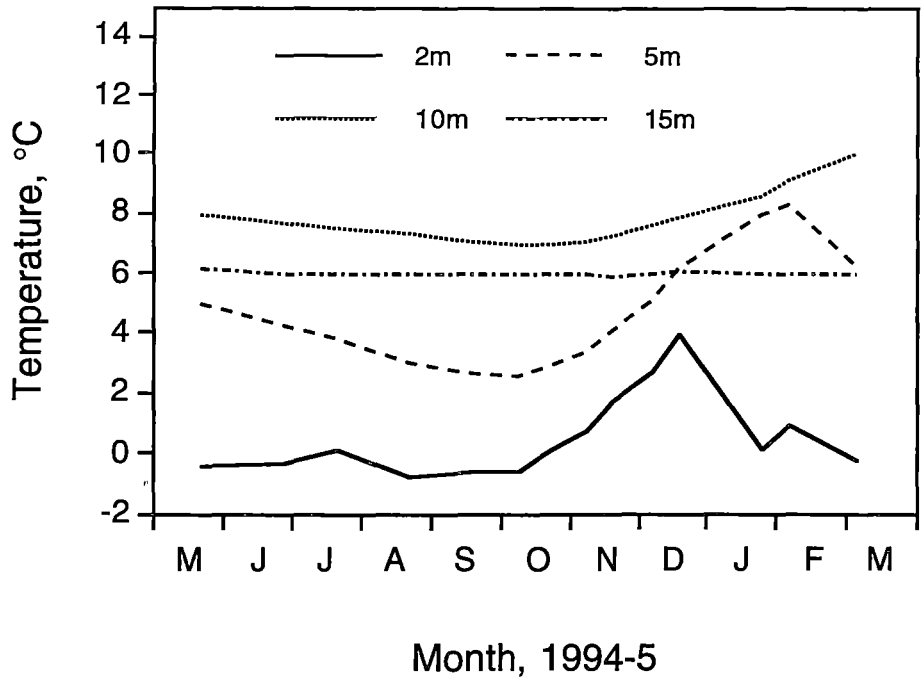


Figure 7.4. Water temperature (°C) at four depths in Ace Lake, May 1994 to March 1995.

7.3.1.2 Chlorophyll *a*

Chl *a* was measured at 2, 5, and 10 m in the water column (Figure 7.5). Concentrations of chl *a* fluctuated over the year, ranging between 0.5 and 3.3 μg L^{-1}. The maximum (3.3 μg L^{-1}) was recorded at 2 m in July. The concentration of chl *a* in the lake ice was generally low, never reaching more than 1.5 mg m^{-2} (1 μg L^{-1}) (Figure 7.6). Maximum concentrations were recorded in August and September.

As observed in previous studies of the lake (Burch 1988, Volkman et al. 1988), there was some vertical zonation of the protistan assemblage. The dominant species present were the ciliate *Mesodinium rubrum*, the flagellate *Pyramimonas gelidicola* and an unidentified cryptomonad (Gibson et al. 1997b). Lesser number of diatoms, and dinoflagellates, including a species of *Gymnodinium*, were also recorded.

Pyramimonas gelidicola was most abundant at 10 m, with a peak in density occurring in April. *Mesodinium rubrum* was recorded from all three depths, however it was usually most abundant at 2 m. The highest densities were recorded in December, with the peak abundance at 5 m (3.5 x 10^5 cells L^{-1}). The highest density of *Cryptomonas* was recorded at 2 m in late November (3 x 10^5 cells L^{-1}). At that time it also increased in abundance at 5 m. It was generally found in low numbers at 10 m (Gibson et al. 1997b).

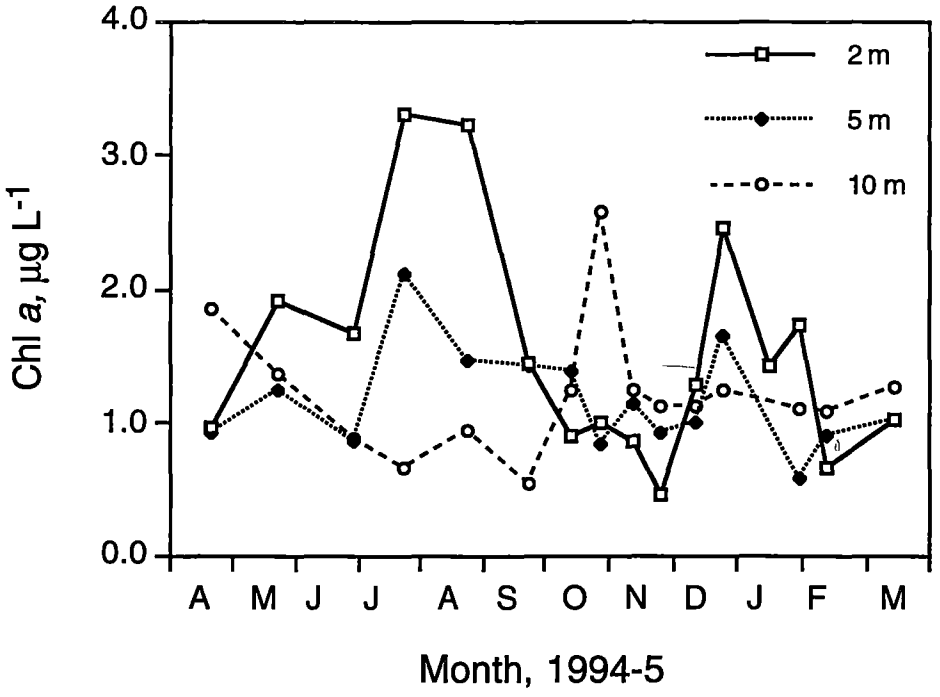


Figure 7.5. Concentration of chl *a* (µg L^{-1}) at three depths in Ace Lake, April 1994 to March 1995.

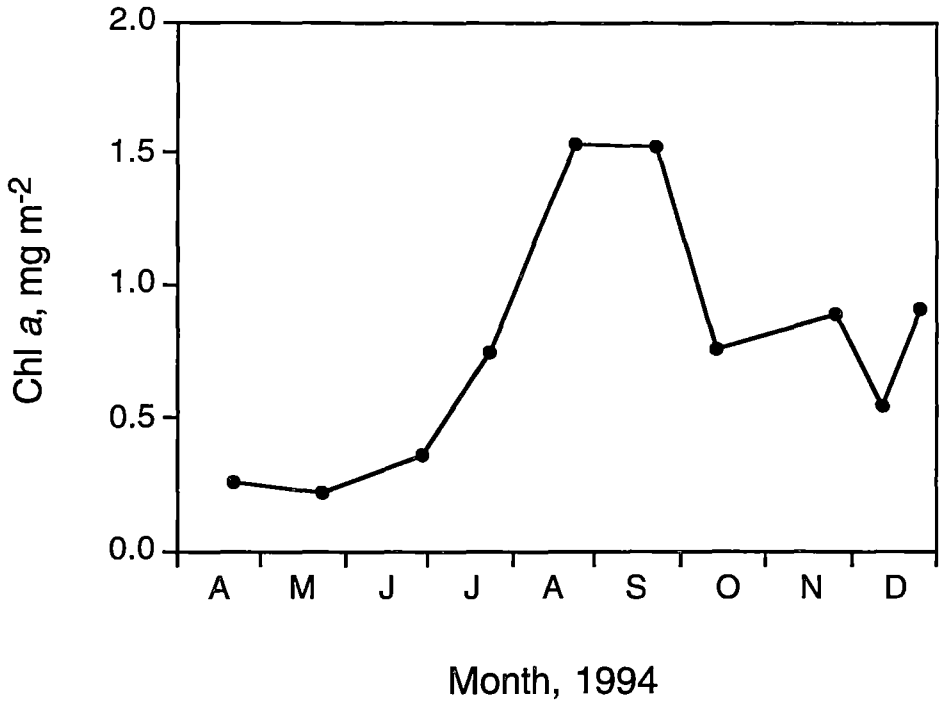


Figure 7.6. Concentration of chl *a* (mg m^{-2}) in the ice at Ace Lake, April to December 1994.

7.3.1.3 Particulate lipids

Full details on the particulate lipids extracted from the water column are provided in Appendix B.3. There was no analysis of lipids in the lake ice.

The concentration of particulate lipids fluctuated at all three sampling depths throughout the study period (Figure 7.7). In general, the concentration decreased with depth. Exceptions to this trend occurred in April when the concentration at 5 m was higher than that at 2 m, and from early December to late January when the concentration at 10 m exceeded that at 5 m. The concentration of particulate lipids ranged from 50 to 225 μg L^{-1}, from 10 to 240 μg L^{-1} and from 20 to 160 μg L^{-1} at 2, 5 and 10 m respectively. The main lipid classes recorded were triacylglycerols and polar lipids, with lesser amounts of hydrocarbons, wax esters and free fatty acids.

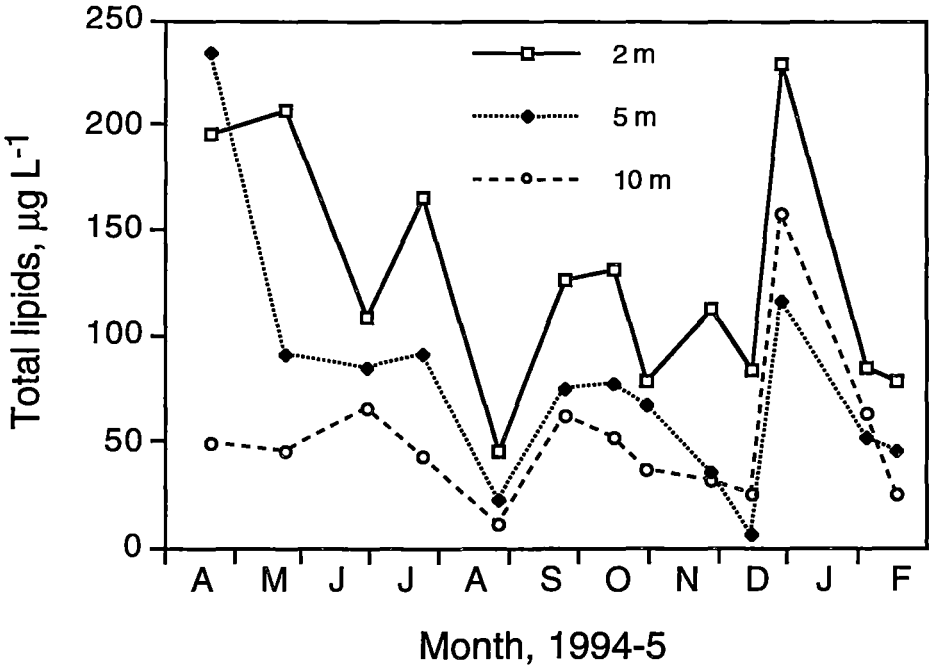


Figure 7.7. Concentration of particulate lipids (µg L^{-1}) at three depths in Ace Lake, April 1994 to February 1995.

7.3.2 *Paralabidocera antarctica*

7.3.2.1 Total abundance

The abundance of *Paralabidocera antarctica* in the water column at O'Gorman Rocks was highest in late February 1994, reaching a maximum of 2,300 m^{-3}. Low densities (< 300 m^{-3}) were recorded from April to July, followed by an increase in August and September. A second peak of 1,700 m^{-3} was reached in early October (Figure 7.8). At the same time, the density of *P. antarctica* in the sea ice was at least two orders of magnitude higher than in the water column (Figure 7.9). Maximum abundance (270,800 m^{-2}) was reached in March, and a minimum of 45,200 m^{-2} occurred in August. The density then increased again from September to 4 November, before dropping sharply on 19 November.

The density of *Paralabidocera antarctica* in the water column in Ace Lake was variable, ranging from approximately 6,000 m^{-3} on 28 June to a maximum of 34,000 m^{-3} on 26 October (Figure 7.10). There was a sharp decline in late December, before the density rose to 10,000 m^{-3} in February. Cores from the Ace Lake ice cover were examined regularly for the presence of *P. antarctica*. Two copepodites were observed in September, but in all other ice samples no individuals were present.

7.3.2.2 Abundance of life stages

In December 1993 the population of *Paralabidocera antarctica* recorded from the water column at O'Gorman Rocks consisted mainly of CV females and adults (CVI) (Figure 7.11 a,b). The number of adults dropped sharply in late December, and they were absent from the water column by the end of January. The peak in abundance in February comprised the NI stage only. During winter, low numbers of naupliar stages I to IV were observed. From August to October the population was dominated by late stage nauplii. Low densities of copepodite stages I to IV were also noted. Stage CV males and females were rarely observed, and CVI was again the dominant stage by late December. As in the previous summer, adults had disappeared by the end of January. The abundance of NI in February 1995 was much less than observed in February 1994.

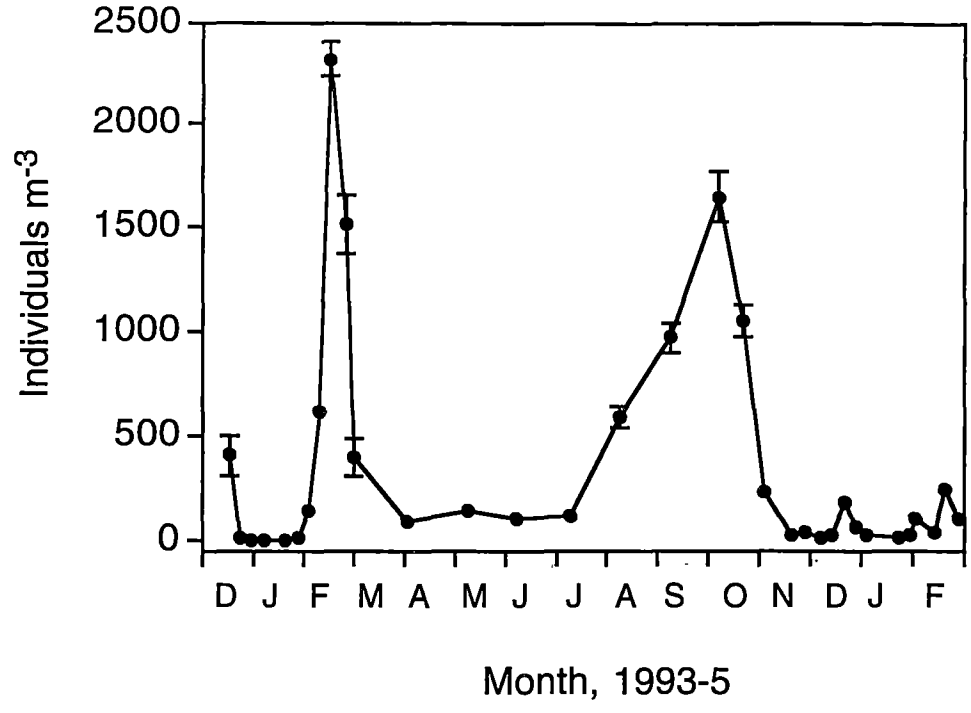


Figure 7.8. Density of *Paralabidocera antarctica* (individuals m^{-3}) in the water column at the O'Gorman Rocks site, December 1993 to February 1995. Density is mean ± s.e. (n = 4); some error bars are too small to be shown.

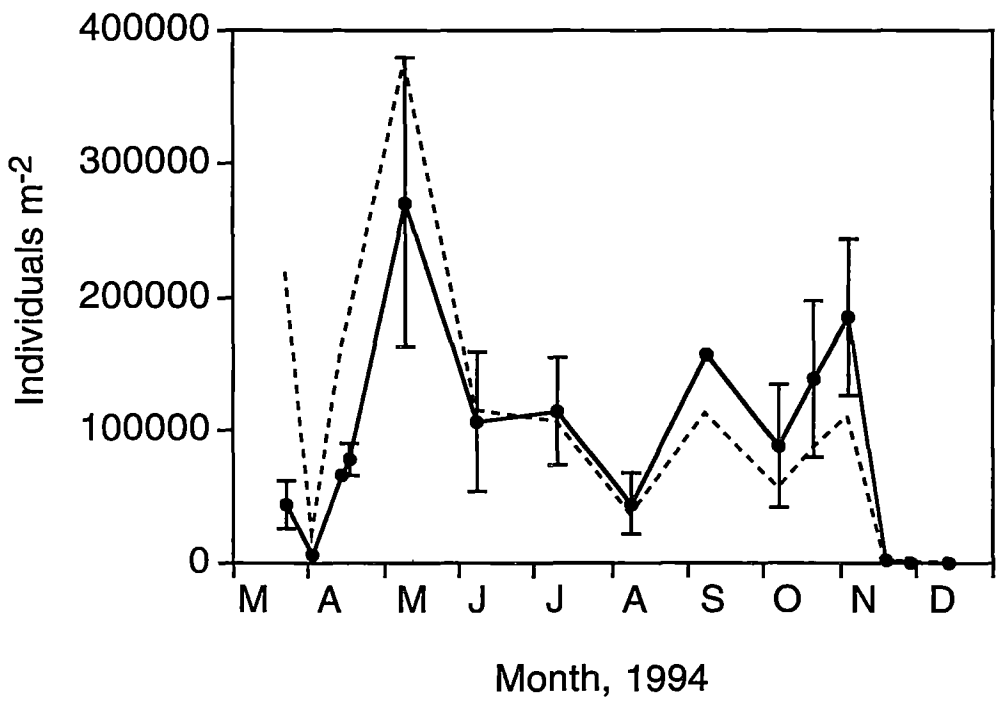


Figure 7.9. Density of *Paralabidocera antarctica* (individuals m^{-2}) in the sea ice at the O'Gorman Rocks site, December 1993 to February 1995. Dashed line represents individuals m^{-3} for comparison with the water column.

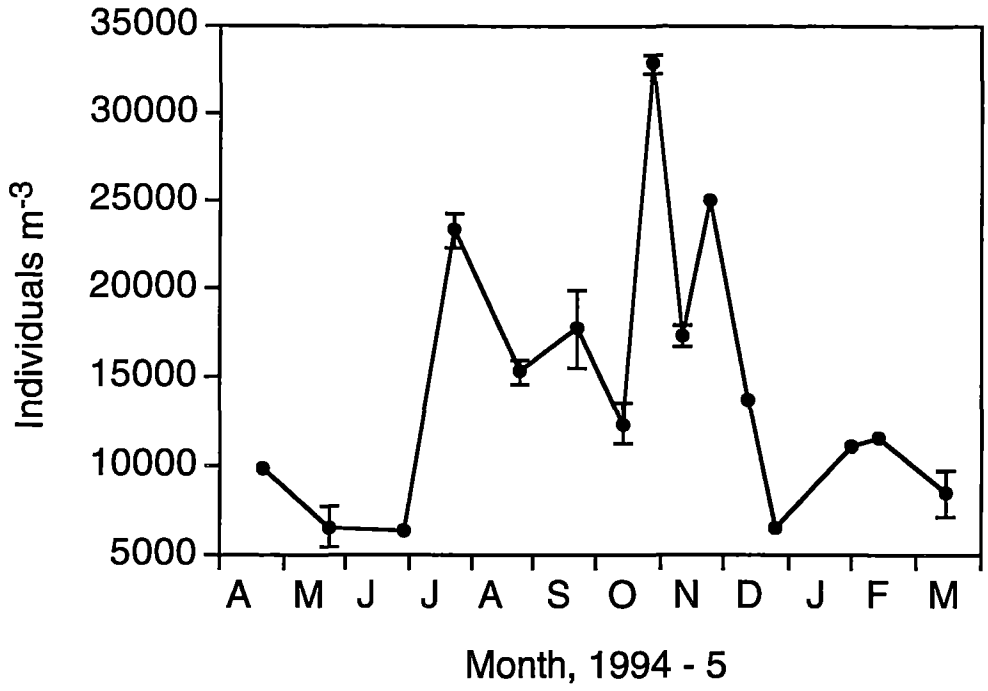


Figure 7.10. Density of *Paralabidocera antarctica* (individuals m^{-3}) in the water column at Ace Lake, April 1994 to March 1995. Density is mean ± s.e. (n = 4); some error bars are too small to be shown.

In the ice cores collected from O'Gorman Rocks, most naupliar stages were observed in high abundance (Figure 7.11 c,d), with the exception that very few NI were recorded. Copepodites were not observed in the ice until September, and the density of these stages reached a maximum of 167,900 m^{-2} on 4 November, before declining to 56 m^{-2} on 19 November. Very few CV and no CVI were recorded from the ice cores.

In Ace Lake, all naupliar stages were observed in the samples throughout the year (Figure 7.11 e,f). A maximum density of 21,400 nauplii m^{-3} was recorded in July. Copepodite stages were also found throughout the year, generally in lower abundance than the nauplii. The exception to this was the period from mid October to late November when copepodite density reached a peak of 20,000 m^{-3}. The peak abundance of CVI occurred on 10 November (4,920 m^{-3}).

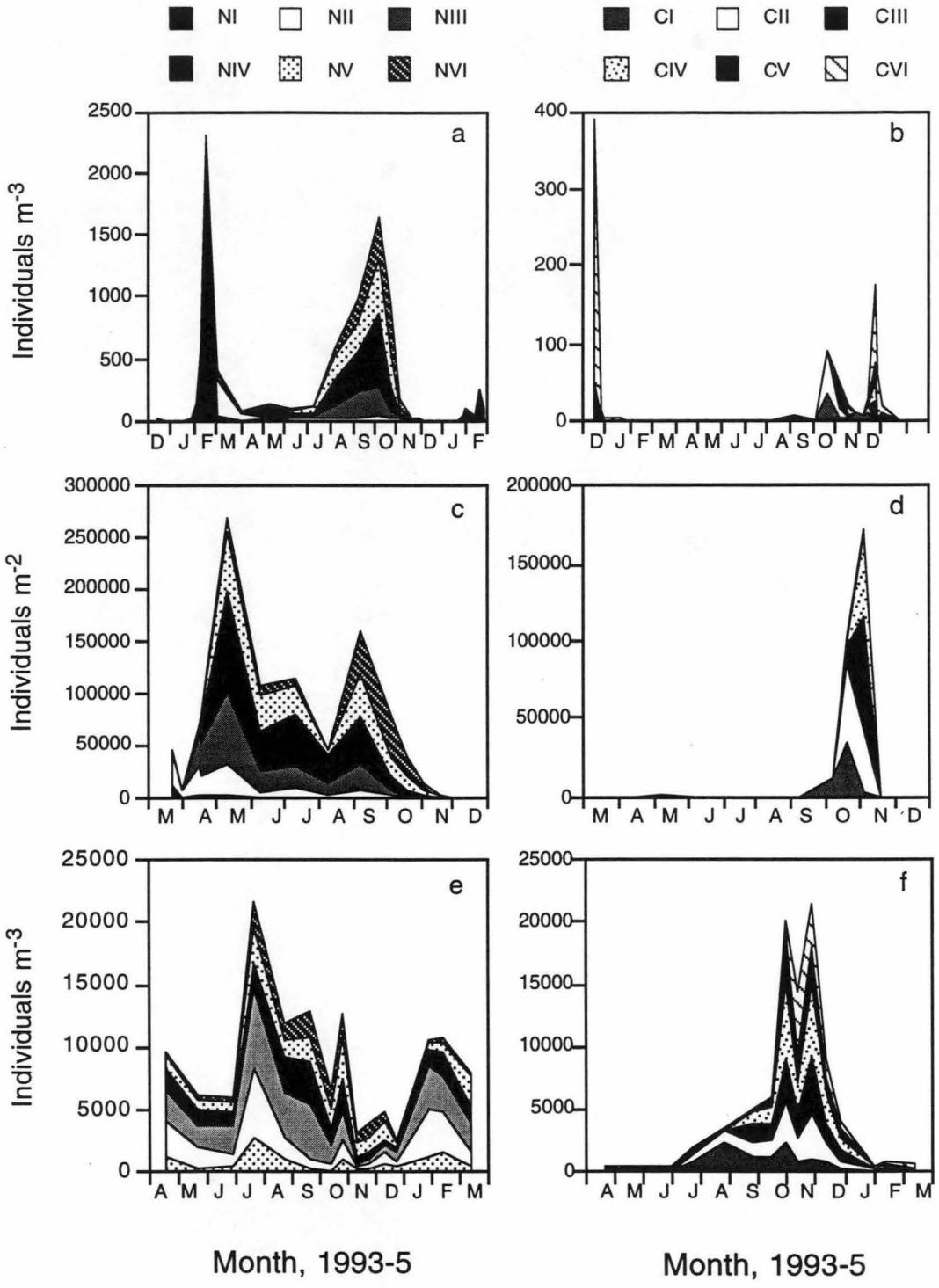


Figure 7.11. Mean abundances (water: individuals m^{-3}; ice: individuals m^{-2}) of the developmental stages of *Paralabidocera antarctica* in the water column (a,b) and sea ice (c,d) at O'Gorman Rocks and the water column in Ace Lake (e,f).

7.3.2.3 Population structure

The percentage composition of all the developmental stages present at O'Gorman Rocks and Ace Lake are shown in Figures 7.12 and 7.13 respectively. At O'Gorman Rocks on 15 December 1993, females were the dominant stage (Figure 7.12), all of which possessed spermatophores. The population consisted mainly of adults until 19 January, however from 22 December to 19 January the total density was very low (< 10 m^{-3}), suggesting that the peak reproductive period had passed and the animals were probably dying. From late January to the end of February 1994 the dominant stage collected was NI. These individuals developed into naupliar stage II by the beginning of March and this was the dominant stage in the ice and the water column when both habitats were sampled in April. There was a rapid development to NIV, which thereafter remained the modal stage until August. Most of the population had developed to late naupliar stages (NV, NVI) by early October, and a few CI had appeared. In the ice the population developed rapidly to the copepodite stage IV, with the modal stage on November 4 being CIII. In the water column over the same period the modal stage was only NVI. From 19 November onwards most of the development occurred in the water column. Those few specimens remaining in the ice were still in the naupliar stages. Once again the population appeared to develop rapidly through the CV stage and adult males were the dominant stage from late December to early January. From late January to the end of the study naupliar stage NI accounted for at least 70 % of the population.

The nauplii of *Paralabidocera antarctica* collected from Ace Lake followed a similar developmental cycle to that described for O'Gorman Rocks (Figure 7.13). Stage NII was the most common stage present in April and much of the population developed rapidly to NIV, which then remained the modal stage until September. By mid-October the composition of the population was spread quite evenly between stages NIII to CIV.

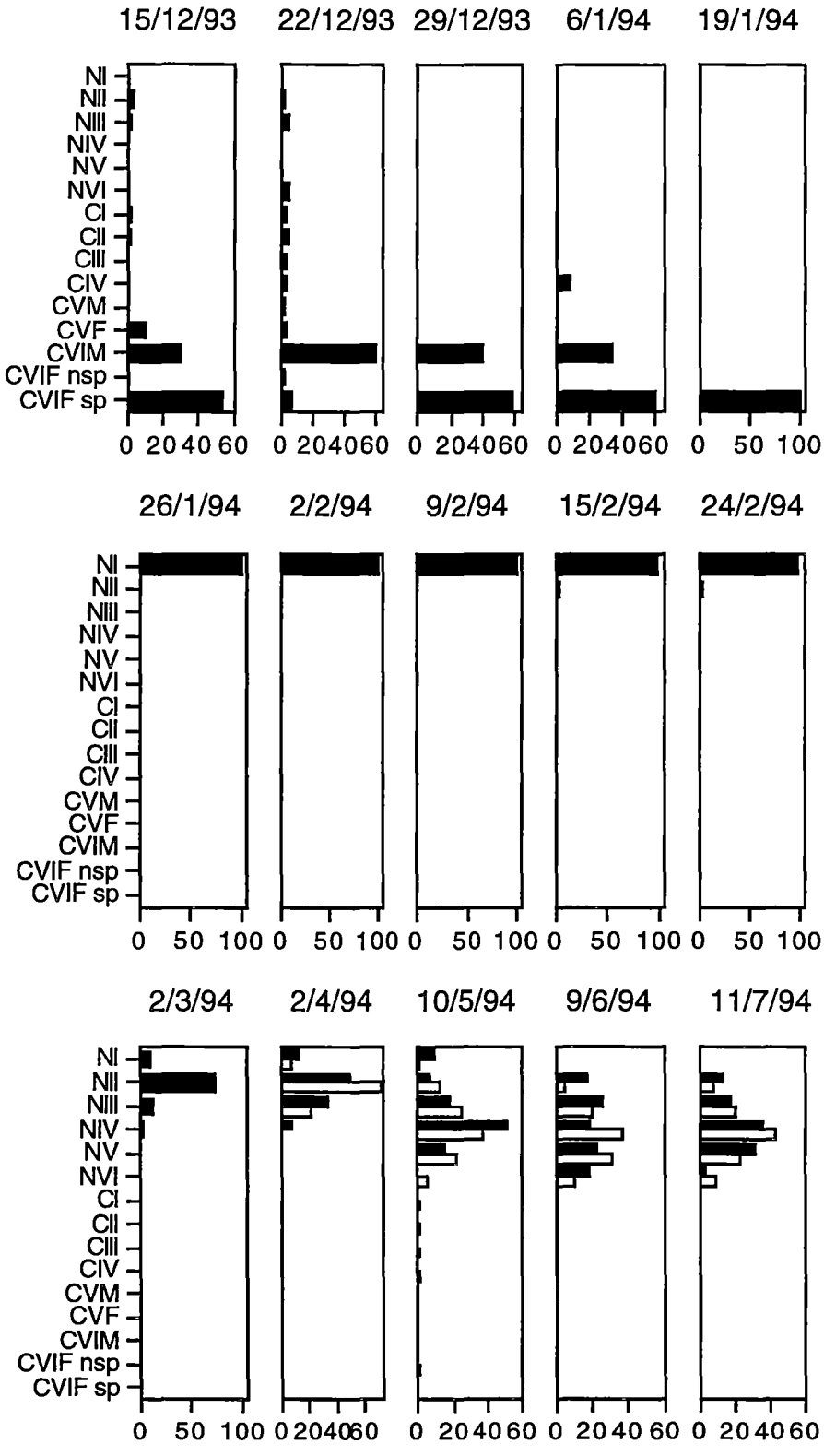


Figure 7.12. Percentage composition of developmental stages of *Paralabidocera antarctica* in the water (filled bars) and sea ice (open bars) at the O'Gorman Rocks site, December 1993 to Feb 1995. CVIF nsp are females without spermatophores; CVIF sp are females with spermatophores.

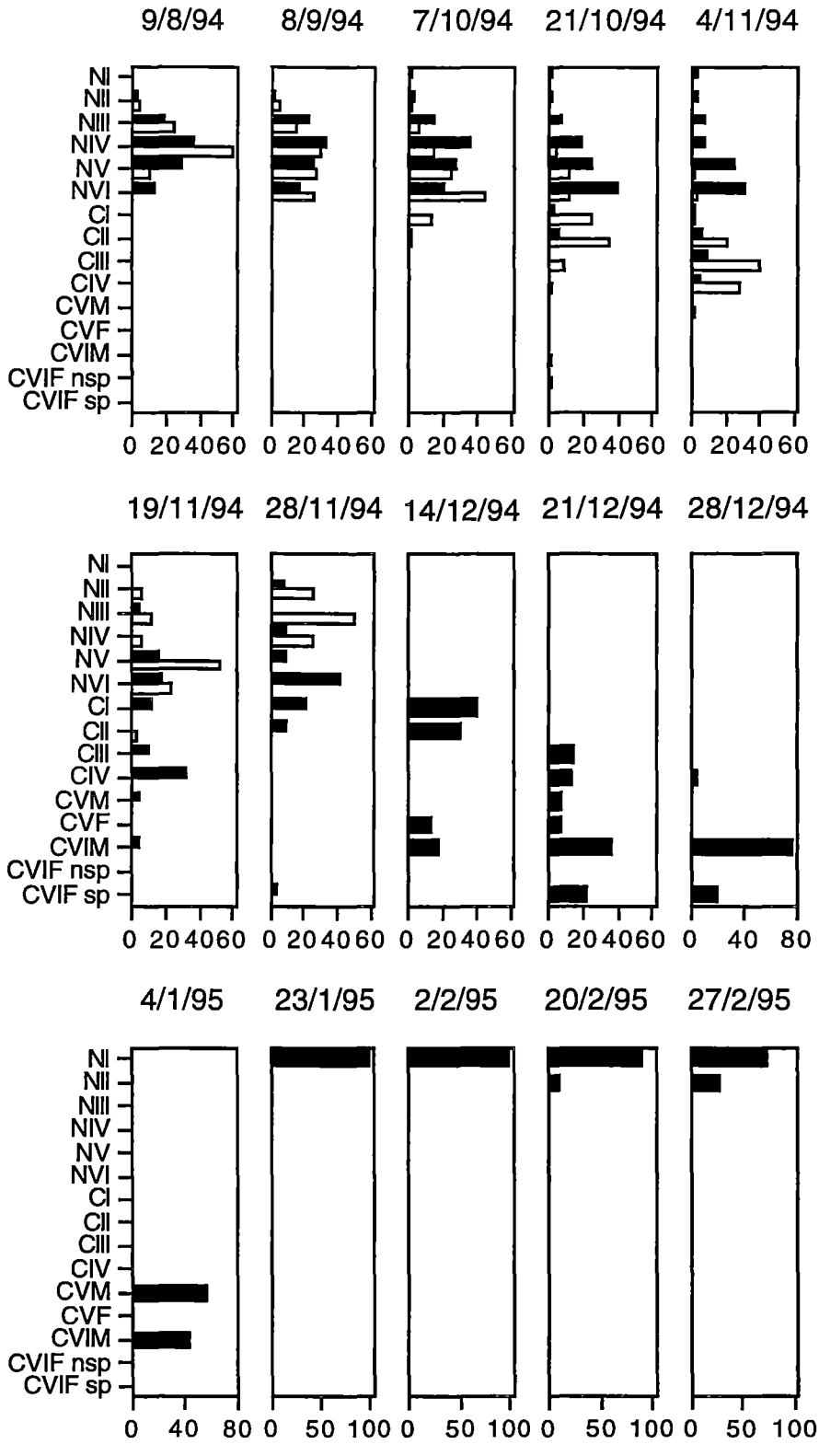


Figure 7.12. continued

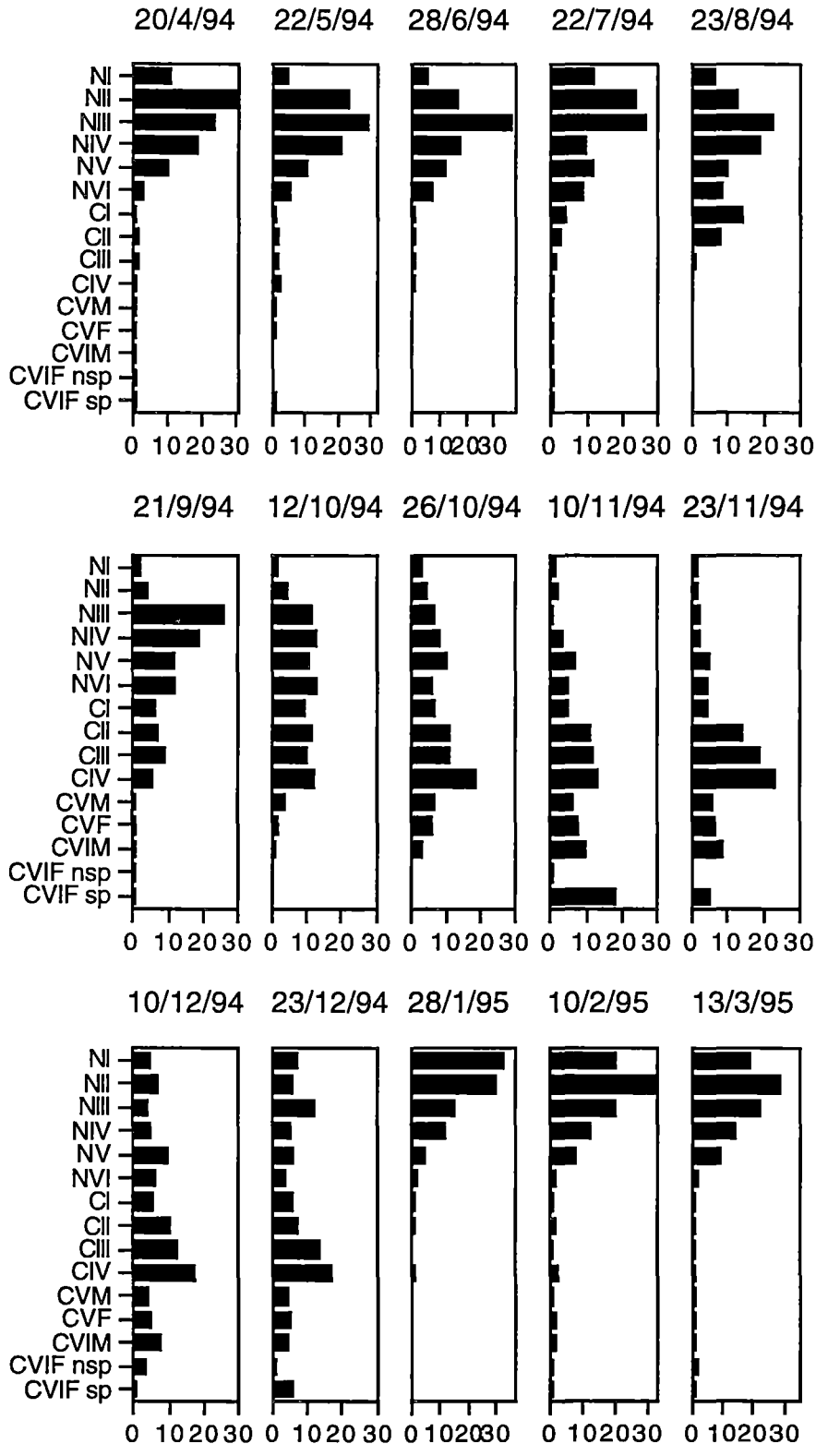


Figure 7.13. Percentage composition of developmental stages of *Paralabidocera antarctica* in Ace Lake, April 1994 to March 1995. CVIF nsp are females without spermatophores; CVIF sp are females with spermatophores.

Throughout late October and November there was a shift to copepodite stages CII to CIV. Furthermore, during that time, there was rapid development by many animals to the CVI stage. Females, most with spermatophores attached, were the dominant stage on 10 November. Copepodites remained the most common stage during December, however substantial numbers of nauplii had begun to appear. By late January early naupliar stages dominated the population, although small numbers of copepodites remained.

The structures of the two populations were further examined by calculating the mean population stage [S], as described by Huntley and Escritor (1991).

$$[S] = \frac{N_{NI} + 2N_{NII} + ... + 12N_{CVI}}{\sum N} \qquad (7.1)$$

where N_{NI}, N_{NII}.....N_{CVI} are the number of each naupliar and copepodite stage NI, NII....CVI; and $\sum N$ is the sum of all individuals. The results of these calculations are plotted in Figure 7.14. From March to September the plots followed similar patterns and the mean age of both populations was NIV. From September until early November *Paralabidocera antarctica* found in the water column at O'Gorman Rocks were considerably younger than those found in the sea ice and those in Ace Lake. The sea ice population was very sparse from mid-November onwards and consisted of a few nauplii that possibly failed to develop further. At that time the Ace Lake population was approximately one stage older than the O'Gorman Rocks population that had descended into the water column. Females were the dominant stage in Ace Lake in mid-November, however the peak value of [S] = 9 (stage CIII) reflects the high proportion of nauplii and early copepodite stages that were also quite common. The short breeding period at O'Gorman Rocks in mid to late December, followed by the appearance of NI of the next generation, is shown clearly for both summers.

During the times that adults were present the sex ratio was usually different from 1 : 1 (Figure 7.15). Males were up to six and seven times more abundant than females at Ace Lake and O'Gorman Rocks respectively. Females were more abundant than males in Ace Lake during winter, and in early November and late December.

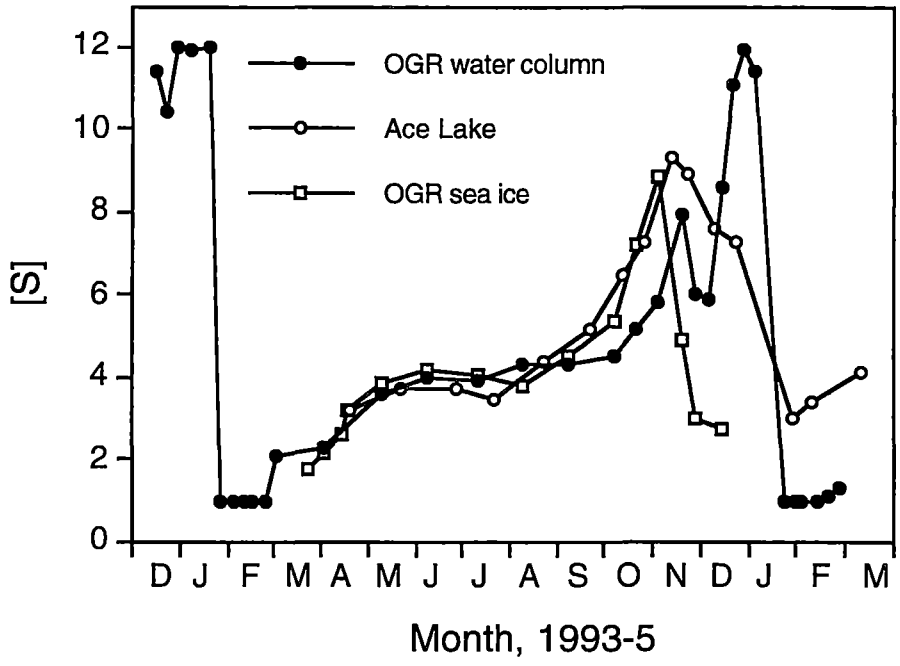


Figure 7.14. Mean population stage ([S]) of *Paralabidocera antarctica* calculated for both sites, December 1993 to March 1995. O'GR = O'Gorman Rocks. [S] 1 = naupliar stage 1, [S] 12 = copepodite stage 6.

7.3.2.4 Egg production by *Paralabidocera antarctica* at O'Gorman Rocks

The results of the egg production experiment are presented in Table 7.1. The maximum egg production rate for one female was 27 eggs in one 24 hour period. That female was collected on 29/12/93 and was fed on the < 200 µm fraction. The rate of faecal pellet production suggested that newly collected (29/12/93) females were

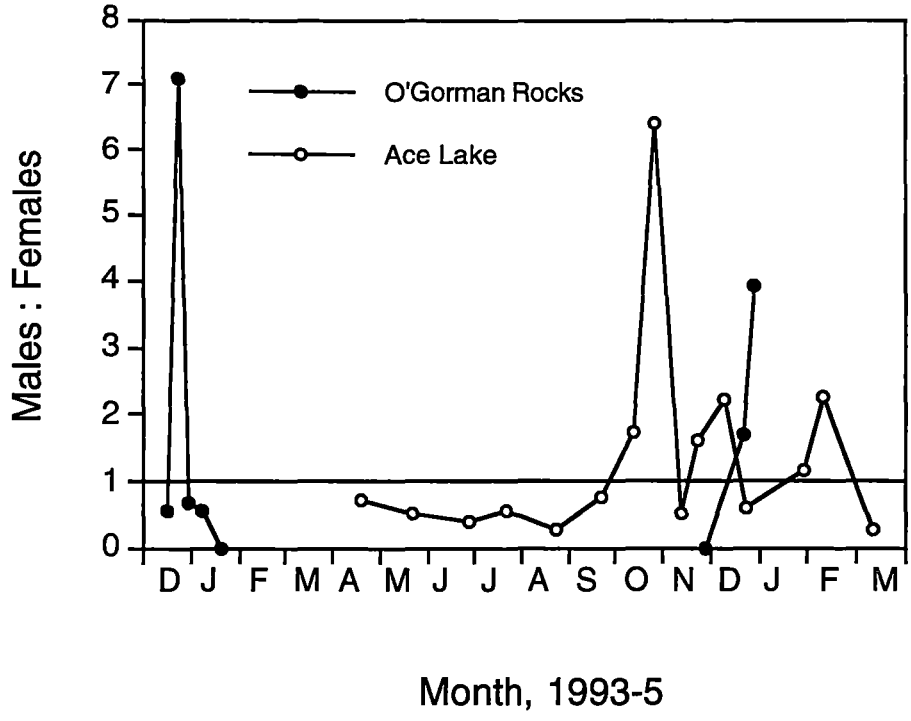


Figure 7.15. Sex ratio (males : females) of *Paralabidocera antarctica* in the water column at the O'Gorman Rocks site and in Ace Lake, December 1993 to March 1995. Horizontal line shows ratio of 1 : 1.

Table 7.1. Egg production rates for female *Paralabidocera antarctica* collected from the O'Gorman Rocks site in December 1993.

Date of collection	15/12/93		29/12/93	
Food size, µm	> 200	< 200	> 200	< 200
No. females	20	20	20	20
Total eggs	10	10	1555	1010
Mean eggs/female	0.5	0.5	77.8	50.5
Eggs/female/day	0.1	0.1	13.0	8.4
Faecal pellet/female/day	6.5	0.5	12.8	6.9

feeding more heavily than those collected on 15/12/93, and that they were feeding more heavily in the > 200 μm fraction than in the < 200 μm fraction.

7.3.2.5 Lipids of *Paralabidocera antarctica*

Lipids were stored in sacs of varying sizes distributed throughout the body. The globules were pale yellow to bright orange in colour and comprised a large proportion of the body (Figure 7.16). The main lipids extracted from the specimens were triacylglycerols and polar lipids, with small amounts of hydrocarbons, sterols and free fatty acids. Trace amounts of wax esters were measured on only three occasions.

Figures 7.17 to 7.24 show (a) changes in dry weight and (b) the variation in proportion of triacylglycerols and polar lipids over time. At O'Gorman Rocks nauplii in both the ice and the water column increased in weight from May to late October (Figure 7.17). The reduction in weight of specimens collected from the ice in early November probably reflects the fact that only underdeveloped nauplii remained in the ice at that time. Polar lipids accounted for less than 10 % of the dry weight, whereas triacylglycerols contributed from 1 to 22 % of the dry weight. As *Paralabidocera antarctica* at O'Gorman Rocks developed rapidly through copepodite stages I to IV, there were few opportunities to collect enough specimens for analysis, however, stage III was analysed on three separate dates (Figure 7.18). Copepodites increased in weight from CI to CIV. Animals collected from the water column were slightly heavier than those collected from the ice. The copepodite stages all contained between 5 and 11 % polar lipid (dry weight). These stages stored very little, if any, triacylglycerols.

Figure 7.16. Stage IV nauplius of *Paralabidocera antarctica* showing lipid sacs distributed throughout the body (scale: 1 cm = 60 μm).

Males were slightly heavier at the peak of their abundance than towards the end of their reproductive period (Figure 7.19). They contained less than 8 % polar lipids and no more than 3 % triacylglycerols. Females lost substantial weight during the breeding period (Figure 7.20). The amount of triacylglycerols stored varied considerably, and during both summers there was a large decrease in the percentage of triacylglycerols with time. CV females were collected on only one date and contained very little lipid overall.

The weight of nauplii of the lacustrine population increased from May to late November before dropping again in late December (Figure 7.21). Substantial amounts of triacylglycerols were recorded from these specimens, ranging from 10 to 35 % of dry weight. Low concentrations (< 10 %) of polar lipids were recorded. Copepodites increased in weight from the CI to the CIV stage (Figure 7.22). In comparison with the O'Gorman Rocks population these copepodites stored substantially more triacylglycerols, especially in the CI stage and late season CIV.

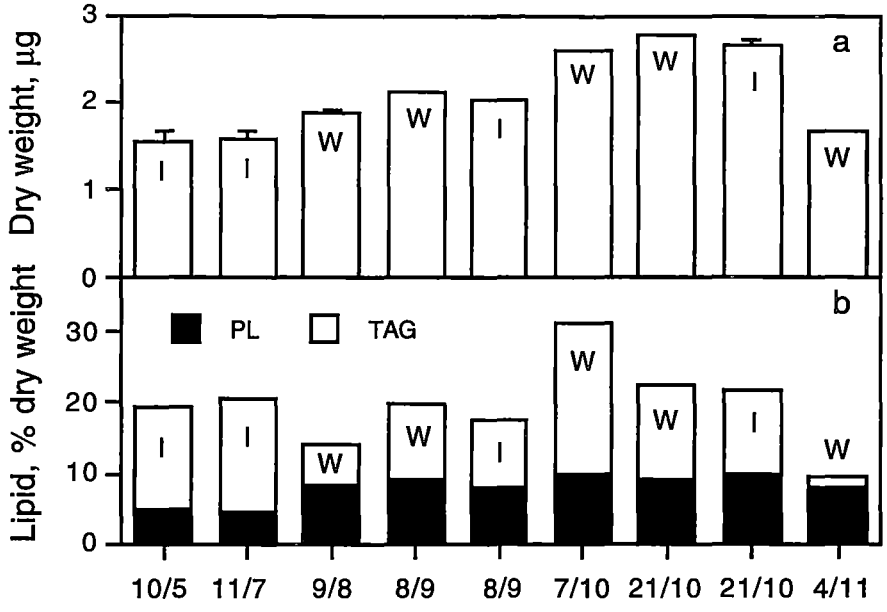


Figure 7.17. Lipids in nauplii collected from the O'Gorman Rocks site. a) shows dry weight as mean ± s.e. (n=6); some error bars are too small to be shown. b) shows ratio of triacylglycerols (TAG) to polar lipids (PL) as % of dry weight. Abbreviations are: I = samples collected from sea ice cores; W = samples collected from the water column.

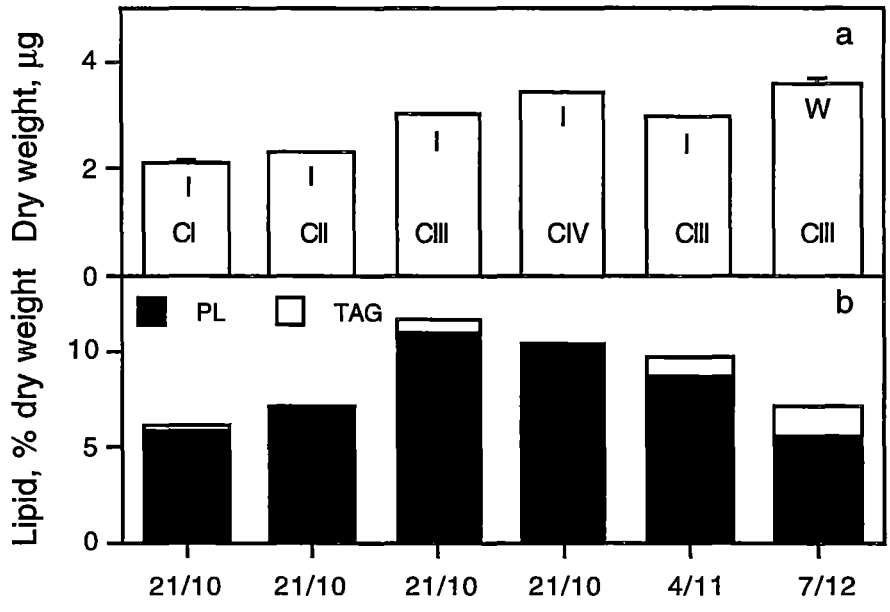


Figure 7.18. Lipids in copepodite stages CI to CIV collected from the O'Gorman Rocks site. a) shows dry weight as mean ± s.e. (n=3); some error bars are too small to be shown. b) shows ratio of triacylglycerols (TAG) to polar lipids (PL) as % of dry weight. Abbreviations are: I = samples collected from sea ice cores; W = samples collected from the water column.

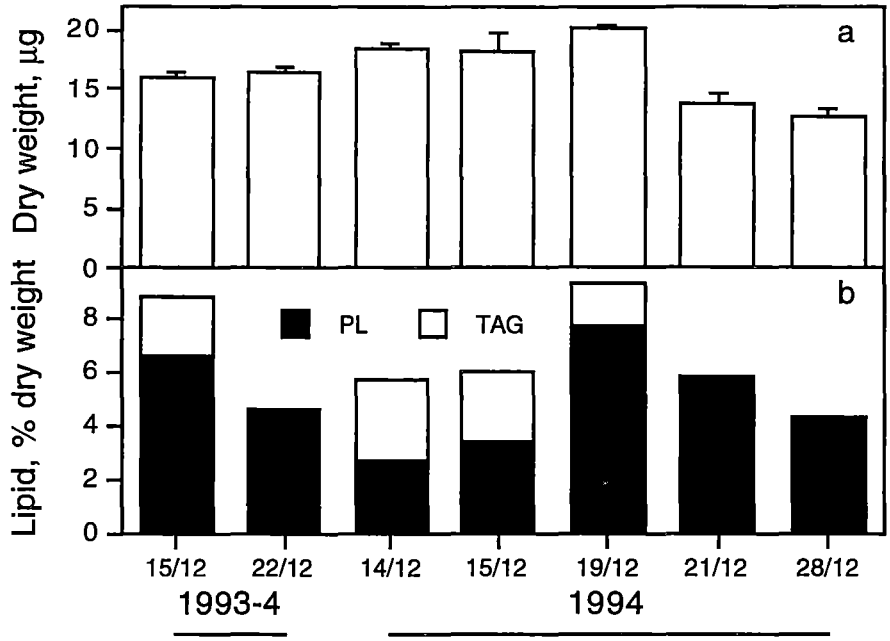


Figure 7.19. Lipids in adult males collected from the O'Gorman Rocks site. a) shows dry weight as mean ± s.e. (n=3); some error bars are too small to be shown. b) shows ratio of triacylglycerols (TAG) to polar lipids (PL) as % of dry weight.

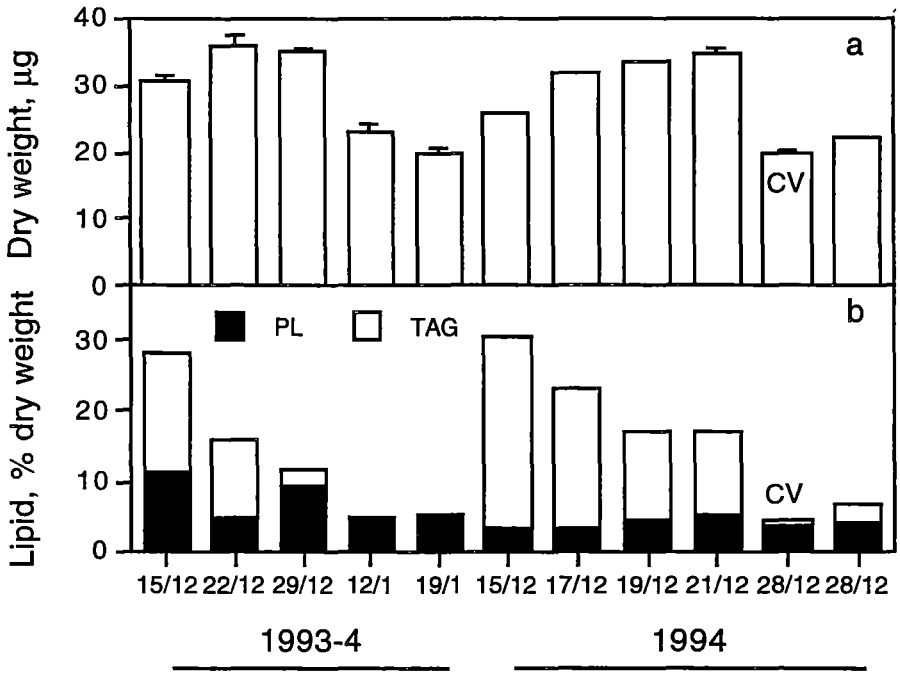


Figure 7.20. Lipids in adult females collected from the O'Gorman Rocks site. a) shows dry weight as mean ± s.e. (n=3); some error bars are too small to be shown. b) shows ratio of triacylglycerols (TAG) to polar lipids (PL) as % of dry weight. One analysis of CV females was made on 28/12/94 and is added for comparison.

Males in Ace Lake were considerably smaller than the neritic population (Figure 7.23). Furthermore, they stored substantial amounts of triacylglycerols in both the CV and CVI stages. However, the proportion of triacylglycerols present decreased to zero in late December and early January. Females of the lacustrine population were also smaller than the coastal population (Figure 7.24). CV females stored small amounts of triacylglycerols that increased as females matured and became reproductive in mid-November. There was a dip in the amount of triacylglycerols present in mid-December, then another rise in late December. In mid January the females did not contain any triacylglycerols and the total amount of lipid was very low.

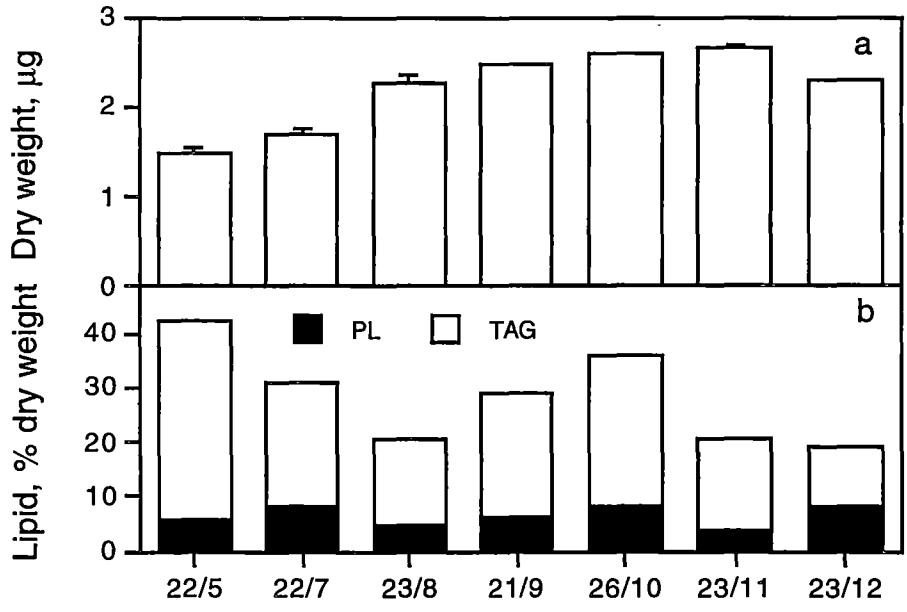


Figure 7.21. Lipids in nauplii collected from Ace Lake. a) shows dry weight as mean ± s.e. (n=3); some error bars too small to be shown. b) shows ratio of triacylglycerols (TAG) to polar lipids (PL) as % of dry weight.

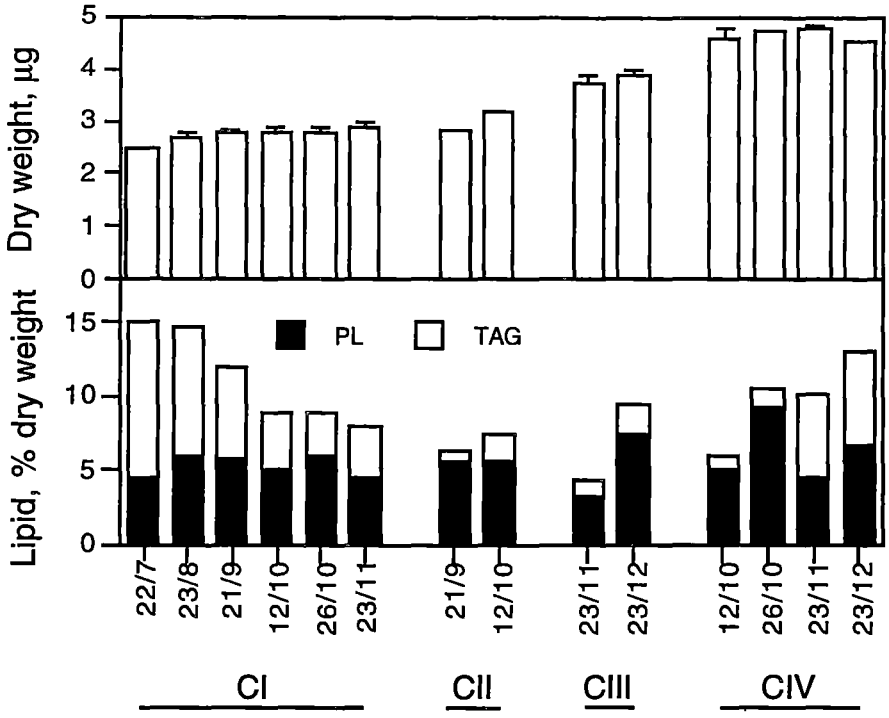


Figure 7.22. Lipids in copepodite stages I to IV collected from Ace Lake. a) shows dry weight as mean ± s.e. (n=3); some error bars are too small to be shown. b) shows ratio of triacylglycerols (TAG) to polar lipids (PL) as % of dry weight.

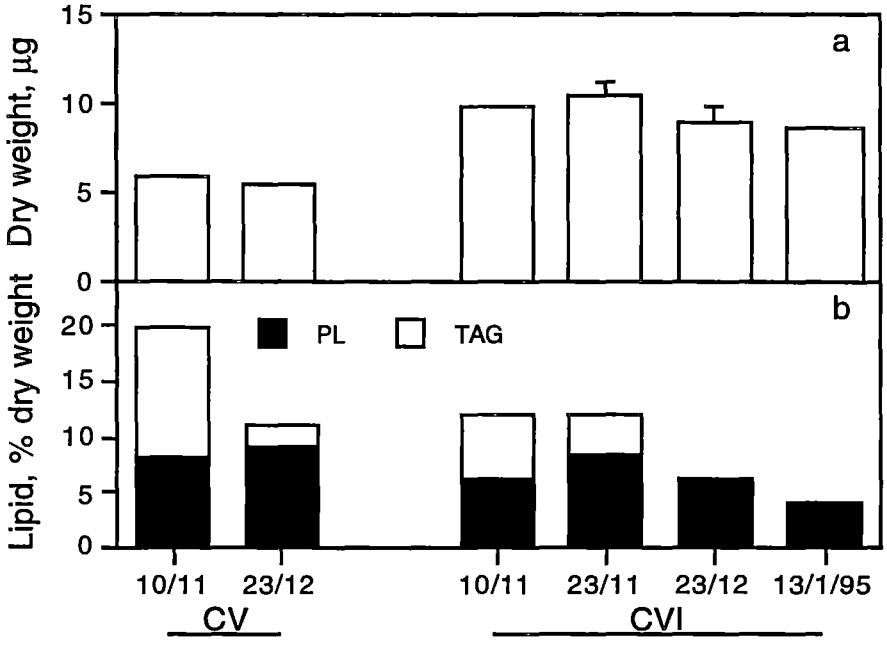


Figure 7.23. Lipids in male copepodite stages V and VI collected from Ace Lake. a) shows dry weight as mean ± s.e. (n=3); some error bars are too small to be shown. b) shows ratio of triacylglycerols (TAG) to polar lipids (PL) as % of dry weight.

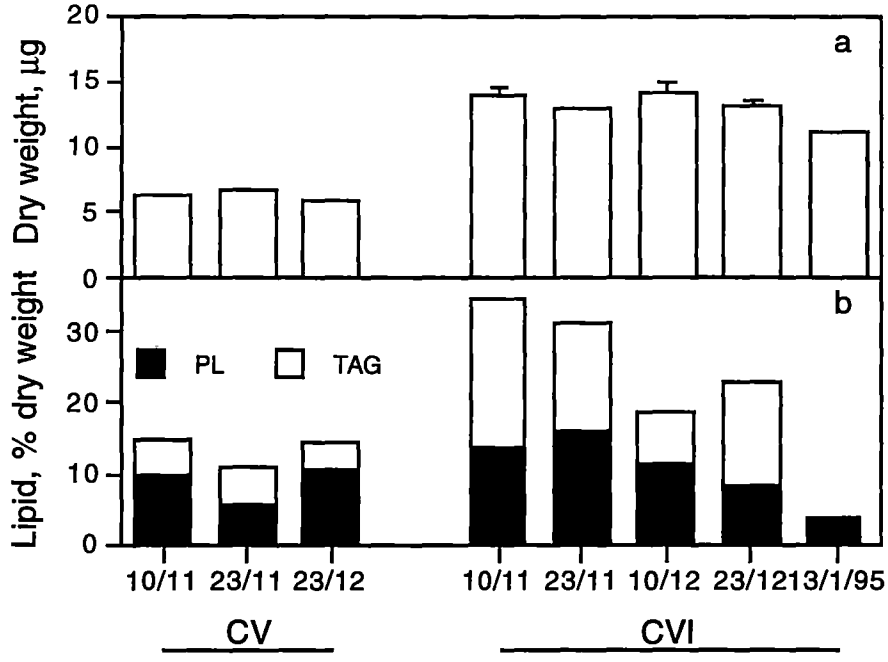


Figure 7.24. Lipids in female copepodite stages V and VI collected from Ace Lake. a) shows dry weight as mean ± s.e. (n=3); some error bars are too small to be shown. b) shows ratio of triacylglycerols (TAG) to polar lipids (PL) as % of dry weight.

7.4 Discussion

7.4.1 Life cycle of *Paralabidocera antarctica*

The neritic population of *Paralabidocera antarctica* completed one life cycle every year. Adults appeared in late December 1993, and spawned before disappearing from the water column. The new generation emerged into the water column as the NI stage in late January, well before the beginning of sea ice formation. The first two naupliar stages colonised the sea ice as it formed, and there was rapid development to naupliar stage NIV by May. From May to September nauplii overwintered in the sea ice and very few individuals were collected from the water column. The development from late naupliar stages to copepodite stages I to IV occurred from September to early

November and coincided with an increase in the biomass of ice algae. Between 4 and 19 November the population shifted from the sea ice to the water column. Very few CV males and females were observed. Adults appeared again in mid-December 1994, spawned and were not collected again after early January 1995.

The life cycle for *Paralabidocera antarctica* outlined above concurs with that described by Tanimura and co-workers (Tanimura et al. 1984 a,b, 1996). While the importance of sea ice to the life cycle of neritic populations of *P. antarctica* is clear, several questions remain. Tanimura et al. (1996) suggested that eggs were spawned at the ice-water interface in late summer when the sea ice was thinnest and, presumably, the eggs then became incorporated into the ice. Certainly the large number of eggs reported in sea ice cores from Syowa in March 1970 (Hoshiai and Tanimura 1986) supports this assumption, although the eggs were not identified. However, in the present study very few eggs were ever observed in the ice cores, and they did not resemble copepod eggs (Chapter 5). During the period of open water in the 1993-4 summer, several trips were made to the O'Gorman Rocks site with the aim of establishing the location of eggs of *P. antarctica*. Bottom sediments were sampled with a small Eckman grab, the water column was sampled with the 'umbrella' net, and pieces of thin ice cover were collected and melted in the laboratory. Eggs were not found in the water column or the sea ice. However, examination of the sediments revealed the presence of large numbers of eggs that closely resembled those collected during the egg production experiments (Section 7.3.2.4). The presence of those eggs in the sediments, coupled with the appearance of naupliar stage NI in late January, suggests that at the O'Gorman Rocks site *P. antarctica* underwent a short (approximately one month) period of diapause as the egg stage. The role of diapause at this stage of the life cycle might have been to ensure that the NI stage did not appear in the water column too soon, i.e. before the sea ice reformed. Surviving unfavourable periods as a diapausing egg is a common strategy amongst members of the family Acartiidae (Marcus 1990, 1991), to which *P. antarctica* belongs (see Section 7.4.5).

It has also been postulated that the adults of *Paralabidocera antarctica* die immediately after spawning (Tanimura et al. 1996). Results of the present study support this conjecture as regular sampling at the O'Gorman Rocks site following both December spawning periods revealed that the number of *P. antarctica* adults had dropped sharply to zero by mid-January. Evidence from the lipid analysis presented below further supports this contention. Therefore, it is inferred that the need to feed at or near the under-ice surface constrains *P. antarctica* to complete spawning before the sea ice breaks out. It would be of interest to test the hypothesis that premature break-out of sea ice prevents *P. antarctica* from completing its life cycle. Under those circumstances it would be useful to determine whether resting eggs in the sediments were a source of recruitment in the following year.

The life cycle of *P. antarctica* living in Ace Lake was broadly similar to that at O'Gorman Rocks. Naupliar stages predominated from April to September, then developed rapidly through the copepodite stages in October and early November. However, the lacustrine population differed from the neritic population in several ways. Firstly, the dry weight determinations revealed that the lacustrine animals were considerably smaller. This difference was first reported by Bayly (1978), who found that adults of the lacustrine population were approximately 60 % of the length of the coastal specimens. Secondly, the Ace Lake population did not have a strong association with the lake ice and they were not found in the ice cores except on one occasion. Thirdly, copepodites in Ace Lake matured to the adult stages about one month earlier than the neritic population. Finally, the presence of most stages throughout the year, albeit sometimes in low numbers, suggests that the synchrony in the life cycle of the neritic population has begun to diminish in the lacustrine population.

The similarities and differences between the life cycles of the neritic and lacustrine populations of *Paralabidocera antarctica* have been listed above. Before considering

what factors might be responsible for these observations it is useful to review the physico-chemical nature of both habitats.

7.4.2 Habitat differences between the two sites

The salient features of the two habitats under discussion are compared in Table 7.2. The ice cover at O'Gorman Rocks was present from March until December or January. The underlying water column was thermally quite stable and there was little variation in salinity. The bulk salinity of the sea ice was comparatively high, suggesting greater porosity and therefore more potential habitat space (Eicken et al. 1991a). There were peaks in primary productivity in the water column during both summers, and in the winter the main site of production shifted to the sea ice. Copepods and other small invertebrates were present in both the ice and the water column, although, overall, the macrofaunal diversity of the ice was lower (Chapter 5). Predators, in the form of ctenophores and medusae, were present in the water column at various times. No predators were present in the sea ice itself, however *Pagothenia borchgrevinkii* is known to inhabit the ice-water interface in the inshore regions (Tucker 1983, Kirkwood 1993).

The ice cover on Ace Lake lasted for more than 11 months and the ice was much harder in texture, as indicated by the low salinity. The waters of the oxylimnion experienced a temperature difference of 11 °C, and a maximum salinity difference of 23 psu. There were low but measurable quantities of chl *a* present throughout the year however chl *a* concentration in the ice was always very low. Predators were absent from the lake and the only potential competitor was the small, rarely observed harpacticoid, *Idomene scotti*, that inhabited the fringing algal mats.

Table 7.2. Similarities and differences between the two habitats sampled for *Paralabidocera antarctica.*

		O'Gorman Rocks	Ace Lake
Temperature (°C)	Water	-1.91 to 1.43	- 1.0 to 10.0
Salinity (psu)	Ice	3 to 9	0. 4 to 3
	Water	32 to 34	7 to 30
Chl *a* ($\mu g\ L^{-1}$)	Ice	0.5 to 26	0.3 to 1.0
	Water	0.1 to 23.7	0.5 to 3.3
Potential predators	Ice	Present	Absent
	Water	Present	Absent
Potential competitors	Ice	Present	Absent
	Water	Present	Absent

7.4.3 The role of lipids in the life cycles of *Paralabidocera antarctica*

The lipid content of the two populations was similar. Lipids were stored in many small sacs distributed throughout the body, and the main energy reserves were triacylglycerols. This was first noted by Volkman et al. (1988) in specimens collected from Ace Lake during February 1984. Although wax esters are the primary form of storage in many copepods living at high latitudes, as originally hypothesised by Lee et al. (1971), at least two other Antarctic copepod species, *Calanus propinquus* and *Euchirella rostromagna*, are now known to store triacylglycerols in high concentrations (Hagen et al. 1993, 1995). These two species switch to an omnivorous diet during periods of low primary productivity and might also feed on algae at the ice-water interface (Hagen et al. 1993, 1995, Schnack-Schiel and Hagen 1994).

The presence of triacylglycerols indicates short term (within one week) feeding by copepods (Hakånson 1984). However, Hoshiai et al. (1987) present evidence that *Paralabidocera antarctica* might not begin feeding until naupliar stage IV. Therefore, it is concluded that triacylglycerols present in naupliar stages I to III were sufficient to fuel their development to the fourth stage when feeding begins. That the later stage nauplii also contained many lipid sacs suggests that, although food was available during the winter, patchiness in its distribution might require the animals to undergo short periods of fasting until they locate another patch. Copepodite stages CI to CIV at O'Gorman Rocks stored very little triacylglycerols. Their period of growth and development coincided with the beginning of the spring bloom of ice algae and food was plentiful. Therefore, they did not have to endure periods of starvation. In contrast, those same stages in Ace Lake continued to store some triacylglycerols, which might indicate that successful bouts of foraging were still sporadic.

The total lipid content of males and females was high at the beginning of the reproductive period and then declined over time. The high proportion of triacylglycerols present in CV males in Ace Lake in early November might have been accumulated to fuel the beginning of spermatogenesis in adult males. Similarly, in adult females the concentration of triacylglycerols was high early in the reproductive season when spawning was occurring. Experimental evidence suggests that females spawn for several days and then die. Hagen and Schnack-Schiel (1996) also concluded that lipid storage by large Antarctic copepods was used more as an energy source for fuelling reproduction than for surviving the winter. The decline in the total lipid content stored is further evidence that adults die after spawning. A similar strategy has been suggested for adult male *Euphausia superba* (Virtue et al. 1996), based on their finding of negligible amounts of triacylglycerols present.

7.4.4 The role of habitat in the life history strategies of *Paralabidocera antarctica*

In discussing the differences between the life cycles of the two populations of *Paralabidocera antarctica* the following biotic and abiotic influences will be considered: temperature, salinity and porosity of ice, food availability, competition and predation. The smaller size and somewhat faster developmental rate of *P. antarctica* in Ace Lake was probably strongly related to temperature. That copepods are larger at colder temperatures is a commonly observed phenomenon (Abdullahi and Laybourn-Parry 1985, Jamieson and Burns 1988). Developmental rate also increases with increasing temperature (Miller et al. 1977). Whether food or temperature is the primary factor affecting developmental rate of copepods is under some debate (Huntley and Lopez 1992), however the temperature difference of approximately 11 °C experienced by the two populations in this study is likely to be the most important factor in determining developmental rate and size.

The lacustrine population of *Paralabidocera antarctica* has experienced a 10 °C rise in the temperature of its habitat within a 20 year period. When Ace Lake was first sampled in 1974, the temperature of the water column was around 1 °C (H. Burton, unpublished data). When sampled again in 1979 it had reached 8 °C (Burch 1988), and by the present study in 1994 had risen another 2 °C. As it is highly improbable that the population has become adapted to increased temperature in only 20 generations, it must be concluded that the species was already strongly eurythermal. Coupled with its euryhaline characteristics, this has enabled *P. antarctica* to successfully colonise some of the saline lakes of the Vestfold Hills, whereas other species common in the inshore waters have failed.

The salinity of the ice cover at O'Gorman Rocks was greater than that of Ace Lake. Higher salinity results in greater porosity which, in turn, suggests a greater availability

of habitat space. The complex nature of the sea ice habitat provides a refuge from predation for those organisms which are small enough to live within the interstitial spaces. In contrast, the lower salinity, and subsequent reduced porosity, of the ice cover on Ace Lake suggests that the amount of available habitat space is considerably reduced.

Biotic factors are probably also important in influencing the life cycles of the two populations. As shown in the study of lipids present in *Paralabidocera antarctica*, the species is able to feed on a regular basis throughout the year. By alternating between the ice and the water column at O'Gorman Rocks, *P. antarctica* maximised its foraging success. In Ace Lake, a comparatively low but constant supply of food was available in the water column, whereas very little food was present in the lake ice. Thus, the lake ice was not providing an especially important source of nourishment.

In the coastal sea ice, *Drescheriella glacialis* was probably the main potential competitor for resources, though this species was only dominant in those areas where unstable ice conditions prevented *Paralabidocera antarctica* from establishing populations (Chapter 4). In contrast, in the water column other species (such as *Oncaea curvata*, *Oithona similis*, *Pelagobia longicirrata*, *Ctenocalanus citer* and larvae of benthic invertebrates) might have competed with *P. antarctica* for resources. Interspecific competition is not important in Ace Lake, however the degree of intraspecific competition has not yet been assessed. Bayly and Burton (1987) noted some vertical separation between the life stages over the 11 m of the oxylimnion, and suggested this as a mechanism for avoiding intraspecific competition. *Idomene scotti*, primarily an inhabitant of the benthic algal mats, is unlikely to be an important competitor.

Finally, the complete lack of predators in Ace Lake means that the ice cover no longer need function as a refuge. The threat of predation imposes many behavioural and

morphological constraints on a species (Verity and Smetacek 1996), and has often been postulated as a primary reason behind vertical migration by copepods (Gliwicz 1986). The neritic population of *Paralabidocera antarctica* near Syowa Station was found to be preyed on quite heavily by *Pagothenia borchgrevinkii* (Hoshiai and Tanimura 1981, Hoshiai et al. 1989). *Paralabidocera antarctica* possibly responded to this pressure by undergoing vertical migration in which they moved into the interstitial cavities during the night (Tanimura et al. 1984a).

In conclusion, it is likely that a combination of biotic and abiotic factors, including ice hardness, reduced threat of predation, and a constant food supply, has freed the Ace Lake population from the constraints of living within the ice cover.

7.4.5 Phylogenetic relationships of *Paralabidocera antarctica*

Paralabidocera antarctica was originally described by Isaac C. Thompson from specimens collected for Professor D'Arcy W. Thompson by the crew of a whaling vessel working in the vicinity of the South Shetland Islands (Thompson, 1898). It is endemic to Antarctic waters, being most common in nearshore waters, and has never been definitely recorded north of 64°29'S (the precise origin of Thompson's material is unknown) (Bayly 1978). Two other species closely related to *P. antarctica* have been described: *Paralabidocera grandispina* from sea ice near White Island in McMurdo Sound (Waghorn 1979), and *Paralabidocera separabilis* from a fjord adjacent to the Bunger Hills (66°17'S, 100°47'E) (Brodsky and Zvereva 1976). There have been very few observations made about these latter two species. Bayly (1978) raised the question of whether the lacustrine form of *P. antarctica* should be recognised as a distinct subspecies (or species). He based this proposal on the size differences between the two populations and on several morphological differences in the fifth leg of the males. However, Waghorn (1979) believed that the differences between the fifth legs of the

two populations were apparent rather than real, and should not be considered a point of difference between them. Modern molecular techniques would help to resolve this question (e.g. Bucklin et al. 1995, Dahms and Schminke 1995)

The genus *Paralabidocera* has morphological characteristics that place it between the families Acartiidae and Pontellidae (Tanimura 1992). However, it is more closely related to members of the family Acartiidae (which includes the genera *Acartia*, *Paracartia* and *Acartiella*), although it is somewhat more primitive and there is less reduction in segmentation (Bradford 1976, Bayly 1978). Members of the family Acartiidae, including *Acartia tonsa* and *Acartia clausi*, are ecologically very successful and are distributed widely throughout marine inshore waters and estuaries (Paffenhöfer and Stearns 1988, Tester and Turner 1988). The euryhaline nature of *P. antarctica* led Bayly (1978) to suggest that the ancestors of *Acartia* and its close relations might have evolved in poikilosaline waters of a comparatively restricted region, perhaps in cold inshore waters deep in Gondwanaland. It is possible, therefore, that radiation of the family Acartiidae has been from the poles to the tropics.

The taxonomic affinities of *Paralabidocera antarctica* raise interesting questions about the storage of lipids, as discussed earlier. The limited information available suggests that *Acartia* species are capable of storing wax esters, although triacylglycerols are generally the predominant form of storage (Lee and Hirota 1973, Conover and Huntley 1991). Lee et al. (1971) postulate that lipid-class composition reflects evolutionary processes among closely related species. An inability to synthesise large quantities of wax esters might have restricted *P. antarctica* to living in association with the sea ice where the food supply is more plentiful. Conversely, inhabiting the sea ice, perhaps firstly as a refuge from predation, might have resulted in the species not venturing far along the evolutionary pathway of lipid development.

7.5 Conclusions

The life cycles of the neritic and lacustrine populations of *Paralabidocera antarctica* were similar in many ways. There was a long overwintering period as the naupliar stages, development was rapid through the copepodite stages and adults appeared in late spring or early summer, spawned and presumably died. The lake population experienced considerably warmer temperatures, which resulted in smaller body size and a faster developmental rate. Both populations primarily stored triacylglycerols, a feature that has also been described for several other Antarctic species. The implication was that *P. antarctica* was able to graze throughout the year. The sea ice provided both a food source and refuge from predation for the neritic population, whereas neither of these functions was fulfilled by the lake ice. The lack of association with the lake ice is one reason why the timing and reproduction of that population appears to have become less synchronised.

Chapter 8
Conclusions

At the beginning of this thesis several broad objectives were defined which had the aim of elucidating the influence of seasonal sea ice formation on the life history strategies of Antarctic copepods. This chapter briefly summarises the main conclusions from the study, and presents ideas for the directions of future studies.

The sympagic macrofauna of fast ice around the Vestfold Hills was characterised by low taxonomic diversity and high abundance of one or two dominant species. *Paralabidocera antarctica* was the most common copepod sampled from the fast ice, except at one site in Ellis Fjord where the small harpacticoid *Drescheriella glacialis* was dominant. The latter species possessed several life history strategies, in particular year-round reproduction and relatively rapid developmental rates, that provided an advantage for colonising disturbed habitats. In contrast, *P. antarctica* was a successful coloniser of sea ice which underwent predictable cycles of formation. A third sympagic species, *Stephos longipes*, which is common in the Weddell Sea, was rarely recorded in ice around the Vestfold Hills.

The above three species of copepods differ in their relationship with the sea ice. *Paralabidocera antarctica* lives within brine channels during the winter and stays closely associated with the under-ice surface in the late spring and summer. The life history of this species in the neritic waters around the Vestfold Hills was similar to that described by Tanimura et al. (1996). These authors, however, provided little information about the crucial ice free period. In the present study it was found that *P. antarctica* undergoes a short period of diapause as the egg stage at this time.

In contrast to *Paralabidocera antarctica*, *Stephos longipes* is associated with sea ice only during short autumn periods, and during winter enters diapause, as stages CIV

and CV, on the bottom sediments (Kurbjeweit et al. 1993). It is possible that this species requires deeper water to complete its life cycle and, therefore, could not establish resident populations in the nearshore system.

It has been postulated that the third species, *Drescheriella glacialis*, inhabits the sea ice throughout its entire life cycle, and that reproduction occurs year-round in areas where sea ice persists (Dahms et al. 1990, Tanimura et al. 1996). However, in the present study *D. glacialis* occurred in reasonable density in several coastal areas that would have been devoid of sea ice during the summer (i.e. Walkabout Rocks, Offshore Site 2; Chapter 4). Therefore, it is hypothesised that this species persists either as a resting stage, or in an active state, in the sediments during periods of open water, and has a brief pelagic phase in which it is able to colonise the newly formed ice. As copepodites of *D. glacialis* have been shown to be efficient swimmers (Dahms et al. 1990), active colonisation of the sea ice is possible. Alternatively, the presence of abundant *D. glacialis* in first year sea ice situated over shallow water (i.e. Ellis Narrows, Long Fjord; Chapter 4) suggests that turbulent mixing might be adequate to transport either nauplii or eggs from the sediment to the ice cover. Either scenario suggests that, in areas where sea ice breaks out regularly, *D. glacialis* has a benthic component to its life cycle. As such, the life cycle of the population found in ice around the Vestfold Hills might differ markedly from the populations in the Weddell Sea.

There was a strong degree of spatial patchiness in the horizontal distribution of the sympagic biota, especially at scales of less than one metre. Patchiness in the vertical distribution of the biota was not examined in the present study, and forms a logical extension to the studies of horizontal patchiness. Sea ice is a heterogeneous habitat and the current methods used for sampling the ice result in a discrete core that is difficult to interpret in relation to an entire ice sheet. The biologically important scales for copepods are probably on the order of centimetres or less. Therefore, recent technologies, such as under-water video cameras deployed *in situ*, might provide a

means of studying the animals at appropriate scales. Alternatively, the development of sea ice microcosms in the laboratory could enable observations of the settlement behaviour, and movement, of animals within the brine channels.

The neritic zooplankton assemblage was characterised by low species diversity but seasonally high abundances. Small copepods, including *Oncaea curvata*, *Oithona similis*, *Stephos longipes*, *Paralabidocera antarctica*, Harpacticoids, and *Ctenocalanus citer*, were found to be the numerically dominant species at various times of the year. This assemblage is typical of the zooplankton communities of coastal eastern Antarctic waters. Conover and Huntley (1991) suggested that Antarctic copepods have no special adaptations for a seasonally limited food supply (compared to those in the Arctic). However, as these authors themselves suggested, their hypothesis has not been supported by the results of recent studies. Adaptations to the limited food supply in the water column, and the extended period of ice cover, that was experienced by the inshore assemblage include: (i) association with the sea ice; (ii) timing reproduction to coincide with the phytoplankton bloom; (iii) accumulation of wax esters to survive periods of starvation; and (iv) lateral migrations from deeper offshore waters.

Only a few species of copepod, including those discussed above, possess the physiological tolerance necessary to access an environment - the sea ice - that provides both food and refuge, yet appears to be relatively free of the pressures of competition. Other species, such as *Oithona similis* and *Ctenocalanus citer*, might not live within the brine channels but possibly use under-ice algae as a food source to fuel reproduction before the spring bloom begins. Furthermore, these species appear capable of ingesting a range of organisms and are likely to undergo seasonal switches in diet. A possible winter food source for small copepods such as *Oncaea curvata* and *O. similis* are bacteria and other heterotrophic microorganisms that are associated with aggregates ('marine snow') in the water column. While bacteria are often discounted as a viable food source for marine copepods, the feeding apparatus of nauplii and small

copepodites is such that filtering particles of 3 μm or less is probably within their capabilities. Lipid analysis can provide insights into the metabolic pathways of species, and further analysis of ontogenetic changes in lipid storage by small copepods would be very useful. In particular, fatty acids and sterols can be used as dietary biomarkers.

When the under-ice material dislodges from the surface and sediments to the benthos in late spring it may trigger the release and development of benthic larvae. While meroplanktonic larvae of benthic species are seasonally abundant in the nearshore zooplankton assemblage, their grazing potential on the phytoplankton bloom has not been established. In the present study copepods grazed only 1 to 5 % of the primary production. A further 10 % sedimented to the benthos (Gibson 1997) and approximately 25 % was consumed by heterotrophic dinoflagellates (Archer et al. 1996b). Therefore, about 60 % of the production was either removed from the area via water circulation or was consumed by other taxa such as polychaetes, larvaceans, euphausiids and echinoderm larvae. Quantifying the grazing impact of these other taxa would furnish a more complete picture of carbon cycling in the inshore marine system.

Comparative studies of neritic and lacustrine *Paralabidocera antarctica* indicated that there were marked differences between the populations. Firstly, the species was not an obligate ice dweller when conditions favoured living in the water column. For example, the constant food supply and lack of predators in Ace Lake resulted in the copepods maintaining a pelagic lifestyle. Secondly, the copepods in Ace Lake were smaller than the neritic animals. It appears that higher temperatures alone have resulted in this difference. Alternatively, fluctuating environmental conditions in Ace Lake might have forced the population through a genetic bottleneck, thus producing a founder effect whereby the population has become skewed towards those individuals that show faster development to a smaller size. Thirdly, the reproductive cycle of the neritic population was more focussed as a result of its dependence on the sea ice. The

decreased synchrony of reproduction in the lake reflected the loss of dependency on the ice habitat.

The populations of *Paralabidocera antarctica* isolated in the lakes of the Vestfold Hills provide an excellent opportunity to examine the relative roles of genetic and environmental controls on the life cycle strategies of a species. Furthermore, it would be of interest to examine the extent of genetic divergence of the populations in the three lakes from the coastal and fjord populations. Modern molecular techniques provide appropriate tools to explore these questions.

Appendix A
Sampling Protocols and Experimental Methodology

A.1 Introduction

This appendix provides details of the routine sampling and experimental methods used during this study. Where necessary, further methodological details have been given in specific chapters.

A.2 Sampling Dates

Sampling dates for the O'Gorman Rocks and Ace Lake sites are listed in Tables A.1 and A.2 respectively. The sampling sites were marked by poles frozen into the ice. Sampling was usually undertaken between 10 am and 1 pm (0300 hrs to 0600 hrs UTC). Throughout most of this study, access to the water column was gained by drilling 25 cm diameter holes through the ice covering with a petrol powered "Jiffy" ice auger. When ice broke out at O'Gorman Rocks, sampling was performed from a small boat anchored at the site.

Table A.1. Sampling dates, O'Gorman Rocks, December 1993 to March 1995

15 Dec 1993	24 Feb 1994[1]	9 Aug 1994	28 Dec 1994[5]
22 Dec 1993	2 Mar 1994[1]	8 Sep 1994[4]	4 Jan 1995
29 Dec 1993[1]	16 Mar 1994[2]	7 Oct 1994	16 Jan 1995[1]
6 Jan 1994[1]	23 Mar 1994[2]	21 Oct 1994	23 Jan 1995[1]
12 Jan 1994[1]	2 Apr 1994	4 Nov 1994	30 Jan 1995[1]
19 Jan 1994[1]	14 Apr 1994[2]	19 Nov 1994	2 Feb 1995[1, 5]
26 Jan 1994[1]	17 Apr 1994[3]	28 Nov 1994	11 Feb 1995[1, 5]
2 Feb 1994[1]	10 May 1994	7 Dec 1994	20 Feb 1995[1, 5]
9 Feb 1994[1]	9 Jun 1994	14 Dec 1994	27 Feb 1995[1]
15 Feb 1994[1]	11 Jul 1994	21 Dec 1994[5]	6 Mar 1995[2]

[1]Sampling from boat anchored at site; [2]Sea ice only sampled; [3]Sea ice sampled for horizontal patchiness study; [4]Only three sea ice cores collected; [5]Grazing experiments performed.

Table A.2. Sampling dates, Ace Lake, April 1994 to March 1995

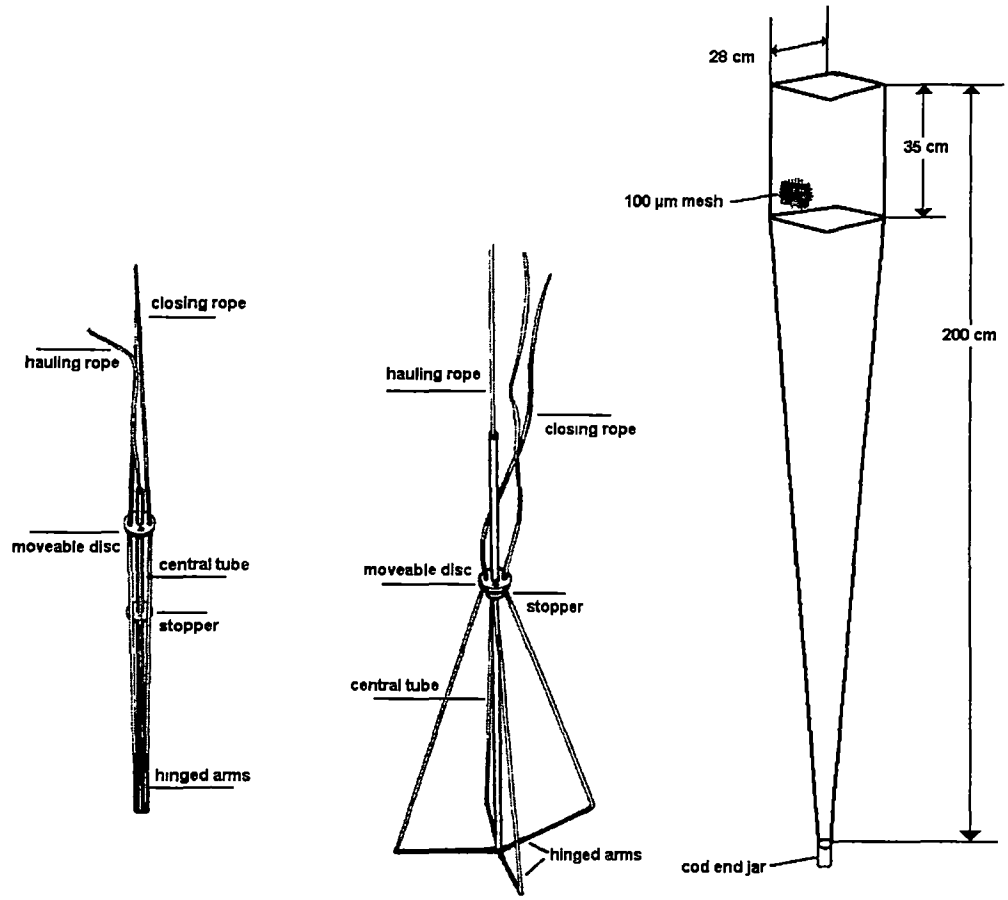
20 Apr 1994	23 Aug 1994	10 Nov 1994	28 Jan 1995
22 May 1994	21 Sep 1994	23 Nov 1994	10 Feb 1995
28 Jun 1994	12 Oct 1994	10 Dec 1994	13 Mar 1995
22 Jul 1994	26 Oct 1994	23 Dec 1994	

A.3 Zooplankton Sampling

Zooplankton were sampled with a 2 m long collapsible net (mesh size: 100 μm; mouth area: 784 cm^2; net open area: 13,820 cm^2) that was designed to be deployed through small holes drilled in ice (Kirkwood and Burton 1987). The net frame consisted of

four hinged arms around a central pole. A calibrated hauling rope was threaded through the central pole. The arms were opened and closed by means of a second line attached to the frame (Figure A.1).

Figure A.1. Diagram of the 'umbrella' net used in the study (from Kirkwood and Burton 1987)



A weighted cod-end kept the net in a vertical position as it passed through the water column. The cod-end was constructed using a 500 mL plastic jar that was lined on the bottom with lead weights. Mesh windows (80 μm) around the upper third of the jar enabled the sample to be concentrated. The net was lowered to the required depth, allowed 60 sec to stabilise, then hauled steadily back to the surface. When the net reached the under-ice surface, the hinged arms were closed, and the net brought back through the ice hole. Four replicate samples were collected at random on each date. At O'Gorman Rocks the net was lowered to 20 m only, thus the bottom 3 m at this site were not sampled. Ace Lake was sampled to just above the oxycline at 11 m.

After the net was retrieved the contents of the cod-end were poured into a 100 mL glass jar. The net was rinsed twice with sea or lake water and any remaining material also transferred to the glass jar. Material in the jar was preserved with 10% borax-buffered Steedman's solution (formaldehyde 50 %, propylene glycol 45 %, propylene phenoxetol 5%; v/v/v) (Steedman 1976). Some advantages of using propylene glycol and propylene phenoxetol as additives to formaldehyde fixative are: 1) improved penetration of fixative; 2) slower evaporation rate and subsequent prevention of dehydration; 3) reduction of freezing point; 4) increased anti-bacterial and anti-fungal properties; and 5) maintenance of softness and flexibility of tissues (Steedman 1976).

The volume filtered by the plankton net was determined by multiplying the mouth area by the depth of sampling. To calculate zooplankton densities a filtration efficiency of 100 % was assumed. The filtration efficiency of a net can be influenced by mesh size, the ratio of net area : mouth area, net shape, towing speed and clogging (Tranter and Smith 1968). Clogging of the net was only evident at O'Gorman Rocks under strong phytoplankton bloom conditions in summer, and never at Ace Lake. At those times it was likely that the filtration efficiency of the net was less than 100 % and, thus, the population densities were somewhat underestimated.

In the laboratory, samples were concentrated onto a 53 μm mesh sieve, then back-washed into a sorting tray with filtered seawater, and examined using a Wild M7 S stereomicroscope (62x magnification). In some instances staining the specimens with rose bengal (A.P.H.A. 1976) facilitated the sorting. Where necessary, subsamples (of at least 1000 specimens) were split from the total sample using a Kott whirling plankton splitter (Kott 1953). Copepods were identified to species and, where possible, to developmental stage. Stages of *Paralabidocera antarctica* were identified using the taxonomic description of Tanimura (1992). Nauplii of *Oncaea curvata* and *Oithona similis* could not be distinguished from one another and were pooled. All other specimens were identified to the lowest taxonomic level possible.

A.4 Ice Coring

Sea and lake ice were sampled using a 76 mm diameter SIPRE ice auger that had been modified by the attachment of a small electric motor. The ice was cored through its entire thickness. When the thickness was greater than 1 m (the length of the barrel of the SIPRE corer), sections of ice were cored in sequence. As air temperatures became lower the hardness of the ice meant that the corer did not function efficiently, and the ice broke into small pieces as it was being sampled. Therefore the vertical stratigraphy of the ice cores was obscured and it was not possible to study the detailed vertical distribution of the biota within the ice.

Loss of the fragile bottom ice community is possible when sampling with a SIPRE corer (Horner et al. 1992). However, a distinct, 2 to 4 cm thick, dark brown layer was often observed at the bottom of the cores, which suggested that they were being collected intact. Furthermore, some specimens might be lost when brine flows from the ice as the core is withdrawn and, therefore, densities might be somewhat underestimated.

Immediately after collection the cores were wrapped in opaque black plastic, stored horizontally to prevent leaching of brine and transferred to a - 20 °C freezer in the Davis laboratory. At O'Gorman Rocks five cores were usually collected, although on 8 September 1994 only three cores could be taken due to malfunction of the corer. The hardness of the ice on Ace Lake meant that coring was very time consuming, especially when air temperatures were below -15 °C. Therefore only one or two cores were collected on most sampling dates. The thickness of the ice and the snow cover was measured at each hole produced by the SIPRE corer. Water depth was measured using a Humminbird Echosounder.

As discussed above it was not possible to examine the vertical structure of the ice, so entire cores were melted in the dark in plastic containers that ranged in volume from 5 to 30 L (depending on the size of the core). The cores were treated in one of two ways. Those cores which were to be subsampled for salinity, nutrients and DOC concentration were melted at temperatures of less than 4 °C without the addition of filtered seawater. The 54 sea ice cores collected for the study of horizontal patchiness (Chapter 3) were all treated in this way except that melting temperature was between 4 and 8 °C. Cores which were used for determinations of chlorophyll, particulate lipid and POC concentrations were melted in prefiltered seawater (GF/F) so as to minimise the impact of osmotic stress on soft-bodied organisms (Garrison and Buck 1986). Dilution factors of between 1:3 and 1:4 ice to filtered seawater (GF/F) were used.

The melted core water was thoroughly mixed, then subsamples extracted with beakers (200 to 2,000 mL). Subsamples were weighed to determine the exact dilution factor. Once the melted cores had been subsampled for the required measurements, the remaining water was filtered through a 53 μm mesh sieve. Metazoans collected by the sieves were preserved as outlined in section A.3.

A.5 Dry Weights of Copepods

Dry weight determinations of copepods were made on specimens that had been stored in Steedman's fixative between six months and two years. As any weight loss due to preservation in formaldehyde tends to occur within the first few weeks of storage (Bayly 1986), the difference in storage times is unlikely to have affected the results. Mass was determined by weighing specimens with a Mettler (M3) microbalance (± 1 µg). Only those specimens which appeared intact were used for weighing. Between 10 and 300 individuals (depending on size) were pooled for each measurement. The animals were rinsed with a small volume (< 300 µL) of distilled water to remove attached salts and excess fixative (Böttger and Schnack 1986), and sorted onto preweighed aluminium pans (15 mm diameter). The specimens were dried at 60 °C until constant mass was attained. A factor of 30 % was used to correct for weight lost due to preservation in formaldehyde (Böttger and Schnack 1986).

Carbon concentration was assumed to be 50 % of corrected dry weight for the smaller species (Båmstedt 1986) and 45 % of corrected dry weight for *Calanoides acutus* (Schnack 1985).

A.6 Temperature and Salinity

Water temperature and electrical conductivity were measured using a Platypus Submersible Data Logger (SDL) (Platypus Engineering, Hobart, Australia). The SDL was kept at each depth for at least 40 s to allow stabilisation of the temperature and conductivity outputs. The data were stored internally in the SDL, and were recovered later using a personal computer-based interrogation program. Salinity (psu) was calculated from measured temperature and electrical conductivity using the equation of Fofonoff and Millard (1983).

Bulk salinity (psu) of the melted ice cores was determined with the following method. Density of a subsample was measured at 20 °C (± 0.00001 kg m^{-2}) using an Anton Paar DMA55 density meter, and salinity calculated using the following equation:

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

where S is salinity in psu and ρ_{20} is density at 20 °C (S. Stark, personal communication 1995).

A.7 Water Sampling

Water samples for chlorophyll analysis, phytoplankton identifications, etc. were collected with a 0.5 m long, polycarbonate 2 L Kemmerer bottle attached to a calibrated line (Roberts and Burton 1993). The bottle was lowered open to the required depth, then closed by dropping a brass messenger down the attached line. On being hauled to the surface, the contents were transferred to 2 L plastic or glass bottles, stored in the dark in insulated containers and returned to the laboratory.

A.8 Phytoplankton and Ice Algae Pigments

Subsamples from the water column, or melted cores, were filtered onto 47 mm Whatman GF/F glass fibre filters, and the volume of the filtrate recorded (± 10 mL). Between 1,800 and 2,000 mL of water was usually filtered. However, during conditions of strong phytoplankton blooms, the filters clogged rapidly and 800 to 1,000 mL was filtered. Filters were air dried, wrapped in aluminium foil, and stored frozen at - 20 °C until further analysis.

Photosynthetic pigments (chl *a*, *b*) were extracted from the water samples using a technique adapted from that of Parsons et al. (1984). Briefly, the filter was sliced up, placed in 90% (v/v) aqueous acetone, sonicated for 5 minutes, extracted overnight in a freezer at - 20 °C, resonicated, and centrifuged for 5 minutes at 3,000 rpm.

The supernatant was transferred to a 4 cm glass cuvette and the absorbance measured at 664, 647 and 630 nm using a GBC 916 Spectrophotometer with 90% (v/v) aqueous acetone in the reference beam. Absorbance at 750 nm was also measured to correct for turbidity in the samples. The equations of Parsons et al. (1984) were used to calculate the concentrations of chl *a* and chl *b*. The detection limit of the method was 0.1 mg m^{-3} and the estimated error was less than 1 % for chl *a* and chl *b* (Parsons et al. 1984).

A.9 Phytoplankton and Ice Algae Identification

Samples for identification of phytoplankton and ice algae were stored in 1 L glass bottles and preserved with 0.25% Lugol's Iodine solution (prepared as per Parsons et al. 1984). Known volumes of the samples were allowed to sediment in measuring cylinders, and then in 10 mL Utermöhl counting chambers (Utermöhl 1958). Cells were examined with a Leitz Laborlux inverted microscope at 400 x magnification and identified to the lowest possible taxon. Diatoms were identified using the taxonomic guides of Priddle and Fryxell (1985) and Medlin and Priddle (1990).

A.10 Nutrients in Sea Ice

Samples for analysis of macronutrients (silicate, phosphate and nitrate) in sea ice cores were stored in acid-washed, high-density polyethylene bottles (125 mL) and kept

frozen at -20 °C until analysis (within four weeks of sampling). Standard wet chemical techniques as provided by Parsons et al. (1984) were used in the analyses and are summarised in Table A.3.

Table A.3. Summary of methods used for analysis of nutrients. Estimates of the detection range and accuracy (at the concentration given in brackets) are also given.

Analysis	Method	Detection Range	Accuracy
Nitrate	Cadmium reduction column/sulphanilamide/N-(1-naphthyl)-ethylenediamine	0.05 - 45 μM	± 0.5 μM (20 μM)
Phosphate	Molybdic acid/ascorbic acid/Sb(III)	0.03 - 5 μM	± 0.03 μM (3 μM)
Silicate	Molybdic acid/metol/oxalic acid/sulfite	0.1 - 140 μM	± 0.25 μM (10 μM)

A.11 Organic Carbon

A.11.1 Particulate organic carbon

Subsamples from melted core water used for the determination of POC concentration were first passed through a 100 μm mesh sieve to remove any zooplankton present. Samples were then concentrated onto pre-muffled, pre-weighed (to 10 μg), 47 mm GF/F filters. Filters were rinsed firstly with a few mL of 1 M HCl to remove carbonates and then with deionised water to wash out any water soluble salts. The filters were dried at 80 °C overnight and reweighed to determine total particulate matter. The filters were then heated for 16 hours at 525 °C in a muffle furnace to oxidise any organic material, and reweighed. Particulate organic matter (POM) was

determined by difference. POC was calculated by assuming that carbon made up 35.8 % of POM, which assumed an average POC composition of $C_{106}H_{263}N_{16}O_{110}P$ (Libes 1992).

A.11.2 Dissolved organic carbon

Subsamples from melted core water used for the determination of DOC concentration were filtered through an all glass filtering system that was muffled before each use. After allowing 30 mL of sample to pass through the system the next 60 mL of filtrate was collected in pre-muffled 125 mL amber bottles, to which 100 µL concentrated HCl was added as a preservative. The bottles were sealed with screw caps and virgin teflon lined inserts and stored upright at - 20 °C until analysis.

Analysis of DOC was performed using a Shimadzu 5000-TOC total organic carbon analyser, which determined OC by oxidising a sample to CO_2 in a column of platinum-coated zeolite balls at a temperature of 680 °C. The gas produced in the reaction column was dried and any halogen present was removed with chemical scrubbers. The amount of CO_2 produced, and thus the concentration of organic carbon, was determined by an internal non-dispersive infra-red gas analyser, the output of which was integrated by the instrument. Inorganic carbon was removed automatically by the instrument from the acidified samples by stripping with CO_2-free gas prior to injection in the reaction column.

A.12 Lipids

Phytoplankton and ice algal samples were filtered onto pre-extracted (methanol/chloroform) filters, air dried, wrapped, and stored frozen until analysis.

Zooplankton were transported alive to the laboratory in insulated containers filled with sea or lake water. Sympagic macrofauna were isolated from the ice cores as soon as possible after melting. Batches of up to 200 animals were sorted from the samples, under conditions of low light and cool temperature, and stored frozen. Because of the need to keep the sorting time as short as possible, nauplii of *Paralabidocera antarctica* were pooled for analysis. Similarly, because of the difficulty in sorting, copepodites of *Oncaea curvata* and *Oithona similis* were pooled for analysis without attempting to distinguish between the developmental stages. Samples for lipid analysis were stored either in liquid nitrogen or in a - 70 °C freezer, thus ensuring minimal, if any, alteration of lipid classes (Ohman 1996).

Lipids were extracted from the samples by a modified one-phase $CHCl_3$-MeOH-H_2O Bligh-Dyer method (White et al. 1979). Filters were sliced up, added to separatory funnels (125 mL) with the solvent, and allowed to stand overnight. The next day, the phases were separated by adding further $CHCl_3/H_2O$ (1:1; v/v) to the separatory funnel. The bottom $CHCl_3$ layer containing the lipids was transferred into a round bottom flask (100 mL), and the mixture evaporated to dryness on a rotary-evaporator. The dried lipid was then transferred into a small glass vial with $CHCl_3$ where, if necessary, it could be stored overnight at - 20 °C. Finally, the sample was blown down to dryness under N_2 and redissolved in a known volume of $CHCl_3$.

Separation of the main lipid components was by thin layer chromatography - flame ionisation detection (TLC-FID) (Volkman et al. 1989, Volkman and Nichols 1991). A portion of the total lipid solution was applied to a silica coated chromarod-SIII (Iatron Laboratories, Japan), and developed for 30 minutes in hexane/diethyl ether/glacial acetic acid (60/17/0.2; v/v/v). Alternatively, a non-polar system of hexane/diethyl ether (96/4; v/v) was used to resolve wax esters from triacylglycerols. The chromarods were oven-dried for 8 minutes at 100 °C, placed in an Iatroscan Mark III TH-10 TLC-FID analyser, equilibrated for one minute and scanned at 30 cm min^{-1}. The resulting chromatogram was integrated using Chart and Peaks (AD Instruments) software on a

Macintosh LCII. External standards were applied to one or two rods so that lipids could be identified by comparison to Retention factors. Separate response curves were constructed for each lipid class over the range of concentrations used in the study (0.5 to 5 μg).

Appendix B
Composition of Lipid Classes

B.1 Introduction

This appendix provides details of the major lipid classes measured from the water column and ice core samples using the TLC-FID.

Table B.1. Lipid class composition of the water column at O'Gorman Rocks. Polar lipids are those which remained at the origin of the TLC rod and include phospholipids and glycolipids. Abbreviations are: TAG = triacylglycerols; FFA = free fatty acids; ST = sterols.

Date	Depth (m)	Total polars	Total non-polars	TAG	FFA	ST
		($\mu g\ L^{-1}$)		(%)		
22/12/93	2	30	65	68	nd	nd
	10	6	nd	nd	nd	nd
6/1/94	0	44	28	11	16	12
	10	61	15	nd	19	nd
12/1/94	0	49	99	23	43	nd
	10	66	32	nd	24	9
19/1/94	0	133	20	nd	3	10
	10	164	6	3	nd	nd
26/1/94	0	109	63	nd	37	nd
	10	156	228	1	58	nd
2/2/94	0	53	11	nd	17	nd
	10	100	283	nd	74	nd
9/2/94	0	51	235	1	81	nd
	10	17	4	nd	20	nd
15/2/94	0	10	nd	nd	nd	nd
	10	13	7	13	22	nd
24/2/94	0					
	10	59	40	nd	nd	7
2/3/94	0	8	nd	nd	nd	nd
	10	15	nd	nd	nd	nd
2/4/94	2	21	19	23	24	nd
	10	6	2	nd	14	10
10/5/94	2	9	8	8	10	nd
	10	2	1	35	nd	nd
9/6/94	2	2	2	33	14	nd
	10	3	2	15	26	3
11/7/94	2	6	14	57	11	1
	10	6	1	4	15	nd
9/8/94	2	10	13	32	24	nd
	10	4	6	33	26	nd
8/9/94	2	12	4	nd	24	nd

	10	36	14	nd	26	1
7/10/94	2	36	7	7	9	nd
	10	5	4	12	30	nd
21/10/94	2	23	10	17	14	nd
	10	10	11	14	40	nd
4/11/94	2	29	11	9	18	1
	10	17	9	12	22	nd
19/11/94	2	38	30	43	nd	1
	10	17	5	nd	24	nd
28/11/94	2	20	8	4	25	nd
	10	14	6	6	24	nd
7/12/94	2	326	157	3	28	2
	10	106	101	4	44	1
14/12/94	2	69	72	5	45	1
	10	13	3	6	12	nd
21/12/94	2	64	8	nd	11	1
	10	59	10	1	13	1
28/12/94	2	38	11	1	20	3
	10	60	18	1	21	1
4/1/95	2	77	23	1	21	1
	10	63	18	nd	22	1
16/1/95	2	29	17	1	35	1
	10	47	11	1	17	1
23/1/95	2	48	9	1	14	1
	10	64	3	1	4	nd
30/1/95	2	25	12	2	30	nd
	10	16	14	47	nd	nd
13/2/95	2	61	52	10	36	1
	10	47	31	nd	39	1
20/2/95	2	58	17	7	16	1
	10	40	10	7	12	1
27/2/95	2	43	19	10	20	nd
	10	39	9	1	17	nd

nd = not detected

Note that the hydrocarbon fraction of the lipids present in the water column at O'Gorman Rocks was not included because in some of the samples there was uncertainty about contamination, and it was impossible to determine the source. Green et al. (1992) and Skerratt et al. (1995) both recorded lipids from the water column in the vicinity of O'Gorman Rocks during summer months between 1989 and 1993. In many cases hydrocarbons were not detected in their samples and, when they were, reached no more than 5 % of the total lipid.

Table B.2. Lipid class composition of the sea ice at O'Gorman Rocks. Polar lipids are those which remained at the origin of the TLC rod and include phospholipids and glycolipids. Abbreviations are: HC/WE = hydrocarbons and wax esters that co-eluted; TAG = triacylglycerols; FFA = free fatty acids; ST = sterols.

Date	Core	Total polars	Total non-polars	HC	TAG	FFA	ST
		($mg\ m^{-2}$)		(%)			
23/3/94	1	67	89	7	38	11	1
	2	43	57	7	45	4	tr
	3	48	81	8	47	5	3
2/4/94	1	877	379	7	21	2	nd
	2	568	247	10	18	2	nd
	3	543	336	6	31	2	nd
10/5/94	1	593	426	7	24	10	1
	2	1397	394	7	8	5	2
	3	635	354	7	20	8	1
9/6/94	1	1604	452	tr	22	nd	nd
	2	558	302	4	31	1	nd
	3	1225	399	2	20	3	nd
11/7/94	1	2051	538	nd	12	5	2
	2	1686	669	nd	22	5	2
	3	2128	837	nd	22	4	2
9/8/94	1	1399	609	nd	28	2	nd
	2	2290	624	nd	18	3	nd
	3	1266	323	nd	16	4	nd
7/10/94	1	1152	315	tr	15	6	nd
	2	735	159	1	9	8	nd
	3	632	324	1	26	6	nd
19/11/94	1	44	15	4	18	2	1
	2	169	70	tr	29	tr	nd
	3	49	16	1	22	1	tr
28/11/94	1	1484	315	4	4	8	2
	2	1080	151	5	3	5	nd
	3	1917	449	2	9	9	nd
14/12/94	1	89	109	4	23	24	4
	2	11	15	2	40	14	2
	3	26	18	2	21	13	4

nd = not detected

tr = trace, < 1%

Table B.3. Lipid class composition of the water column in Ace Lake. Polar lipids are those which remained at the origin of the TLC rod and include phospholipids and glycolipids. Abbreviations are: HC/WE = hydrocarbons and wax esters that co-eluted; TAG = triacylglycerols; FFA = free fatty acids; ST = sterols.

Date	Depth (m)	Total polars	Total non-polars	HC/ WE	TAG	FFA	ST
		($\mu g\ L^{-1}$)				(%)	
20/4/94	2	147	47	2	22	1	nd
	5	88	147	3	56	3	nd
	10	37	12	5	13	7	nd
22/5/94	2	51	156	tr	74	1	tr
	5	18	73	1	76	3	nd
	10	33	12	2	19	6	nd
28/6/94	2	38	30	3	37	24	1
	5	20	34	2	36	36	2
	10	58	2	2	11	1	nd
22/7/94	2	50	40	1	29	33	tr
	5	80	40	3	27	21	nd
	10	71	9	2	12	7	1
23/8/94	2	22	23	5	10	36	nd
	5	10	12	5	5	43	nd
	10	8	4	9	8	16	nd
21/9/94	2	100	26	7	10	4	nd
	5	56	18	8	1	15	nd
	10	51	11	9	5	3	nd
12/10/94	2	103	28	11	3	7	tr
	5	57	20	12	3	10	1
	10	43	8	11	1	5	nd
26/10/94	2	45	34	7	27	10	nd
	5	39	28	11	19	11	2
	10	31	6	7	3	7	nd
23/11/94	2	52	61	3	1	48	1
	5	21	14	4	2	35	nd
	10	22	10	nd	nd	32	nd
10/12/94	2	48	35	1	6	36	nd
	5	3	3	5	2	45	1
	10	19	6	4	nd	21	tr
23/12/94	2	84	145	1	7	55	tr
	5	67	88	nd	17	40	tr
	10	65	92	tr	8	50	tr
28/1/95	2	62	22	4	4	16	3
	5	36	16	3	1	25	nd
	10	29	34	nd	7	47	tr
10/2/95	2	62	78	nd	9	11	tr
	5	29	46	5	4	27	1
	10	16	26	4	2	31	0

nd = not detected

tr = trace, < 1%

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