Life cycle strategies of epipelagic copepods in the Southern Ocean

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Revised 8 April 1997; accepted 26 September 1997

Abstract

Twelve epipelagic copepod species were reviewed to compare their adaptations to the short primary production season and low temperatures which characterise the Southern Ocean. The species show a spectrum of adaptations, but three broad life cycle strategies were defined: (1) herbivorous in summer, a short reproductive period and winter diapause at depth (Calanoides acutus and possibly Ctenocalanus citer); (2) predominantly omnivorous/detritivorous diet, an extended period of feeding, growth and reproduction and less reliance on diapause at depth (Metridia gerlachei, Calanus propinquus, Calanus simillimus, Oithona similis, Microcalanus pygmaeus, and possibly Oncaea curvata and Oithona frigida); (3) overwintering and feeding within sea ice as early nauplii or copepodids (Stephos longipes and Paralabidocera antarctica). The large species Rhincalanus gigas appears to be intermediate between strategies 1 and 2. Contrasting species from groups 1 and 2, namely C. acutus and O. similis, were selected for more detailed comparison. For C. acutus, maximum probably food saturated feeding and egg production rates are well below equivalent values for Calanus spp. at lower latitudes. Likewise, summer growth and moulting rates are slower, and the growth season of this herbivore is only 2–4 months. Therefore, both the low summer temperatures and short primary production season seem to dictate a long (~ 1 year) life cycle for C. acutus. A collation of data on O. similis revealed that its abundance increases about tenfold from the Antarctic shelf northwards to the Polar Frontal Zone, where abundances are similar to those in temperate and tropical shelf seas. In contrast to C. acutus, O. similis appears to remain in the epipelagic and reproduce there year-round, although the food sources which sustain this are still uncertain. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Copepoda; Southern Ocean; life cycles; Calanoides acutus; Antarctica; Oithona similis

1. Introduction

Low, seasonally stable temperatures, regional ice cover and highly seasonal primary production are features common to both the Arctic and Antarctic. Both the low temperatures (Huntley and Lopez, 1992) and scarcity of food (Clarke and Peck, 1991) are factors which potentially limit zooplankton growth. Nevertheless, copepods seem to have adapted to the polar environment; in both oceans they are major zooplankton components (Conover and Huntley, 1991) with a fairly high biomass (Foxton, 1956; Hopkins, 1971; Ikeda, 1985).

Knowledge of the life cycles of Antarctic copepods at the end of the 1980s was reviewed by Smith and Schnack-Schiel (1990) and Conover and Huntley (1991). Until then, almost all of the attention had been directed towards three of the largest species,
Rhincalanus gigas, Calanus propinquus and Calanoides acutus. A prevailing view was that they were herbivorous and had similar life cycles (Vorontina, 1970). Seasonal vertical migration brought them into the surface waters in spring, when reproduction took place. Developing instars utilised phytoplankton-rich surface waters to moult to late copepodids, which descended to depth and overwintered in diapause (Vervoort, 1965). Vorontina (1970, 1978) found that the timings of these migration cycles could vary, both between species and with latitude, which she related to a delay in the onset of the spring bloom with increasing latitude (Hart, 1942). Marin (1986, 1988), however, suggested that the three large species had different life cycles, and that R. gigas may have a flexible, one or two year life cycle.

During the 1990s, studies of population structure, vertical distribution, reproduction, diet, feeding rate and lipid metabolism have been expanded to cover the more numerous smaller species. It is becoming evident that the life cycle strategy of herbivorous feeding during the short summer and winter diapause at depth is followed strictly by only a couple of the species. The others appear to have varying capabilities for either extending their feeding period into the winter months, or overwintering within sea ice.

This article highlights these recent developments by grouping twelve major epipelagic species into three broad life cycle strategies. The life cycles of a biomass dominant species, Calanoides acutus and a numerical dominant, Oithona similis contrast greatly, so these were selected for more detailed analysis. C. acutus seems to be highly adapted to a polar environment, and data on feeding, egg production, moulting rates and development times were collated to examine some of the factors which dictate its long generation time. For the ubiquitous O. similis, I have collated data on abundance, biomass, age structure and diet, to assess its regional and seasonal distribution, and how its life cycle seems to be partially decoupled from the main primary production cycle.

2. The Southern Ocean environment

The Southern Ocean, here defined as waters lying south of the Subantarctic Front, encompasses several distinct and contrasting environments for epipelagic copepods (Tréguer and Jacques, 1992). The physical zonation and regional primary production of the Southern Ocean have been reviewed extensively (see Tréguer and Jacques, 1992; Palmisano and Garrison, 1993; Savidge et al., 1996; Mathot et al., in press) so they are only summarised here.

As a whole, the Southern Ocean is now considered to exhibit modest primary production; with recently estimated annual averages in the range ~30–90 g carbon m\(^{-2}\) yr\(^{-1}\) (Smith, 1991; Lancelot et al., 1993; Mathot et al., in press). This, however, disguises a mosaic of high and low productivity sub-areas of varying area. In a recent estimate of Southern Ocean primary productivity, Mathot et al. (in press) subdivided the Southern Ocean into six zones. From north to south they are: the Polar Frontal Zone (8% of the Southern Ocean area, lying between the Polar and Subantarctic fronts) which is a region of intense eddy and frontal movement and elevated primary production. South of this is the Open Ocean Zone (36% of the Southern Ocean area) which does not experience ice cover and is characterised by low primary production. The Seasonal Ice Zone, which is highly productive in its more sheltered regions, occupies 42% of the Southern Ocean. Inside this, an area of >85% average ice cover is the Closed Pack Ice Zone (10% of the area) with very low primary production. The Coastal and Continental Shelf Zone, however, while occupying only 4% of the Southern Ocean is the most productive in the Southern Ocean. Mathot et al. (in press) estimated that sea-ice primary production only contributes ~1% of the total in the Southern Ocean, but nevertheless, sea ice appears to be important, both as a habitat and as a highly concentrated food substrate (reviews by Smetacek et al., 1990; Eicken, 1992).

Although this generalised regional picture may hold, the unpredictable and ephemeral nature of Southern Ocean phytoplankton blooms is being stressed increasingly. For example, extensive marginal ice zone blooms are now thought to be restricted mainly to sheltered parts of the Weddell and Ross seas (e.g. Savidge et al., 1996) and even in these, the environmental conditions which give rise to them are not always realised (Laubscher et al., 1993; Jochem et al., 1995). Conversely, while much of the Open Ocean Zone is oligotrophic (Banse,
Several important Southern Ocean copepods are not included here. Some epi-mesopelagic poecilostomatoids are excluded, with only the commonest and shallowest living member, *Oncaea curvata*, listed. None of the deeper living omnivores/carnivores which stray into the epipelagic (*e.g.* *Euchaeta antarctica*) is included. Information on the biology of *E. antarctica* is given by Ward and Robins (1987) and Øresland and Ward (1993). Several lower-latitude species are found in the northernmost regions of the Southern Ocean (*e.g.* *Neocalanus tonsus*; see Ohman et al., 1989), but these, together with the neritic genus *Drepanopus* (*see* Razouls and Razouls, 1988) are not included because of their more restricted regional distribution. I have also not included the harpacticoid copepod, *Drescheriella glacialis*, because it lives within sea ice throughout the year (Dahms et al., 1990).

3.1. Herbivorous feeding in summer, diapause in winter

This life cycle strategy involves reproduction in spring, with the new cohort then eating phytoplankton in the surface layer and moulting to older copepodid stages. These lay down an extensive lipid store and gradually descend to depths of over 500 m and overwinter in diapause. Many of the species in Table 1 tend to exhibit, to some extent, these features of lipid storage, seasonal vertical migration, maximum feeding and reproduction in summer and diapause in winter. However, they are only adopted strictly by *Calanoides acutus*. Table 1 suggests that Ctenocalanus citer may also belong to this category, but information on its life cycle is very limited.

Lipid storage is a recurring feature of high-latitude copepods (*e.g.* Conover, 1988; Hagen, 1988; Kattner et al., 1994). In *Calanoides acutus* its role is both to fuel overwintering without feeding and to enable reproduction to begin before the phytoplankton increase in spring (Hagen and Schnack-Schiel, 1996). Although all the species so far examined store lipid, that of the winter diapause species *Calanoides acutus* is among the highest (Donnelly et al., 1994; Hagen and Schnack-Schiel, 1996). Extensive recent studies of the large Antarctic copepods (*e.g.* Hagen et al., 1993; Graeve et al., 1994; Kattner et al., 1994; Ward et al., 1996) show that *C. acutus* stores long

1996), significant blooms have been recorded there, particularly in the Atlantic Sector (Tréguer and Jacques, 1992; Whitehouse et al., 1996).

The logistical difficulties of sampling these sub-systems on a seasonal basis has greatly hampered our understanding of the life cycles of Southern Ocean copepods. Quests for the necessary year-round coverage have forced the merging of data from several sub-systems, sometimes presenting a confusing picture of seasonal development (*e.g.* Ommanney, 1936; Voronina, 1970). Huntley and Niiler (1995) further stressed that the intense, dynamic mesoscale variability of the Southern Ocean, in conjunction with spatially variable primary production, leads to potentially great variation in subsequent feeding regimes for individual copepods spawned at any single time and place. They therefore recommended greater emphasis on mesoscale sampling on a seasonal basis. Although this approach can be applied to a few inshore environments (*e.g.* Huntley and Escritor, 1991; Lopez et al., 1995), logistical and financial restraints have so far limited seasonal coverage of the open ocean. Here ‘seasonal’ pictures have to be compiled from numerous different years of sampling (*e.g.* Andrews, 1966; Marin, 1988; Atkinson, 1991; Schnack-Schiel and Hagen, 1995). Inshore waters near research bases, however, often provide excellent opportunities for year-round coverage (*e.g.* Razouls and Razouls, 1988; Fransz and Gonzalez, 1995; Tanimura et al., 1996).

3. Life cycle strategies

Table 1 lists 12 major epipelagic copepods, with notes on aspects of their life cycles. I have emphasised seasonal feeding and diets, vertical distribution, lipid storage and the reproductive/growth season because these provide insights into how copepods use the food-rich summer months and survive the long winter when phytoplankton is scarce. The species seem to exhibit a spectrum of adaptations, ranging from herbivorous feeding, reproduction in spring/summer and winter diapause at depth (*Calanoides acutus*) to year-round feeding (*e.g.* *Metridia gerlachei*). However, I have differentiated three main life cycle strategies, and tried to categorise the species according to the pattern which they follow most clearly.
Table 1
Notes on aspects of the life cycles of major epipelagic Southern Ocean copepods

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
<th>Diet and Seasonal feeding activity</th>
<th>Seasonal vertical migration and vertical distribution</th>
<th>Lipid store</th>
<th>Reproductive period</th>
<th>Suggested life cycle duration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calanoides acutus</td>
<td>Throughout Southern Ocean, rarer in northern regions (1, 4)</td>
<td>Diatoms (22) Not feeding (5)</td>
<td>Extensive seasonal vertical migration, overwintering mainly below 500 m (46, 1, 47)</td>
<td>Extensive, mainly wax esters (39, 17, 16, 26)</td>
<td>November to March in Weddell Sea (18)</td>
<td>Mainly 1 year (46, 1, 31, 9), 2 year (12, 38) &gt; 1 year for some CVI (18)</td>
</tr>
<tr>
<td>Ctenocalanus spp.</td>
<td>Circumpolar, widely distributed (42), Two species?</td>
<td>Diatoms, occasional protozoans (20)</td>
<td>Seasonal migration near South Georgia and in Weddell Sea (7, 42)</td>
<td>Unknown</td>
<td>Spring-time reproduction (13, 42)</td>
<td>Unknown Relatively rapid development rates suggested by ref. 42</td>
</tr>
<tr>
<td>Rhincalanus gigas</td>
<td>Throughout Southern Ocean, but commonest in ACC (36, 30, 4)</td>
<td>Diatoms, occasional protozoans (22)</td>
<td>Seasonal vertical migration (47, 31, 10) Some of population can reside in surface layer in winter (32)</td>
<td>Not feeding (23), Active feeding in surface layers (32)</td>
<td>Extended in some regions/seasons (36, 32, 41) Dec to Feb in Eastern Weddell Sea (18)</td>
<td>1 year in ACC (47, 4, 10) Flexible, 1–2 years (31) Multicyrhar in Weddell Sea (10)</td>
</tr>
<tr>
<td>Metridia gerlachei</td>
<td>Mainly in middle latitudes of Southern Ocean, locally highly abundant (46, 25)</td>
<td>Diatoms, also protozoans, metazoans (20), Can eat Oncaea and eggs of C. acutus (34, 25, 3)</td>
<td>Often deeper living in summer than other large species, with diet vertical migration but not extensive seasonal migration (46, 7, 25, 43)</td>
<td>Phytolankton, metazoans, protozoans (23)</td>
<td>Long reproductive period, (Sep to March in Weddell Sea) seemingly not strictly dependent on spring bloom (46, 24, 28, 18)</td>
<td>1 year in ACC, 2 year in parts of Weddell Sea (28) Several generations per year in Gerlache Strait (24)</td>
</tr>
<tr>
<td>Calanus propinquus</td>
<td>Mainly higher latitudes of Southern Ocean (46, 4, 10)</td>
<td>Diatoms, occasional metazoans and protozoans (22), Prefers motile food (5)</td>
<td>Less extensive than for C. acutus (7, 44) Some of population can overwinter near the surface (10, 32)</td>
<td>Phytolankton, protozoans, metazoans (25, 32)</td>
<td>Extensive ston of mainly TAG (17, 26, 18)</td>
<td>1 year life cycle (47, 31) 2 year life cycle (28, 11, 27, 38)</td>
</tr>
<tr>
<td>Species</td>
<td>Distribution</td>
<td>Feeding Habits</td>
<td>Feeding Preferences</td>
<td>Reproduction</td>
<td>Life Cycle (years)</td>
<td></td>
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<td></td>
</tr>
<tr>
<td><em>Calanus simillimus</em></td>
<td>Mainly northern (Subantarctic) part of ACC (46, 30, 41)</td>
<td>Ubiquitous, more abundant in ACC than in East-Wind Drift (35)</td>
<td>Preferred motile food to diatoms (5)</td>
<td>Not feeding (23)</td>
<td>1–2 generations per year (4)</td>
<td></td>
</tr>
<tr>
<td><em>Oithona similis</em></td>
<td>Ubiquitous, more abundant in ACC than in East-Wind Drift (35)</td>
<td>Mainly diatoms, occasional protozoans (20)</td>
<td>Mainly diatoms, also amorphous debris, dinoflagellates (19, 21)</td>
<td>Not feeding (23)</td>
<td>1 year in ACC, 1.5–2 years in East-Wind Drift (35)</td>
<td></td>
</tr>
<tr>
<td><em>Oithona frigida</em></td>
<td>Unknown</td>
<td>Unknown</td>
<td>Mainly diatoms, occasional metazoans (20)</td>
<td>Not feeding (23)</td>
<td>Probably 1 year in ACC, but extended longevity of CVI (35)</td>
<td></td>
</tr>
<tr>
<td><em>Oncaea carrasi</em></td>
<td>Unknown</td>
<td>Unknown</td>
<td>Mainly diatoms, occasional protozoans (20)</td>
<td>Not feeding (23)</td>
<td>Unknown</td>
<td></td>
</tr>
<tr>
<td><em>Microcalanus pygmaeus</em></td>
<td>Unknown, but seemingly widespread (42)</td>
<td>Mainly diatoms, occasional ciliates (20)</td>
<td>Mainly diatoms, amorphous debris, occasional dinoflagellates (19, 21)</td>
<td>Not feeding (23)</td>
<td>Unknown</td>
<td></td>
</tr>
<tr>
<td><em>Paralabidocera antarctica</em></td>
<td>Antarctic regions near Antarctic coast (45)</td>
<td>As copepods on ice algae? (45)</td>
<td>As copepods on ice algae? (45)</td>
<td>Mainly in top 250 m in summer and autumn (21, 33, 35) but rather deeper in spring (33)</td>
<td>1 year in ACC, 1.5–2 years in East-Wind Drift (35)</td>
<td></td>
</tr>
</tbody>
</table>
### Table 1 (continued)

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
<th>Diet and Seasonal feeding activity</th>
<th>Seasonal vertical migration and vertical distribution</th>
<th>Lipid store</th>
<th>Reproductive period</th>
<th>Suggested life cycle duration</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Stephos longipes</em></td>
<td>Neritic, but seems to replace <em>P. antarctica</em> in Weddell Sea (44)</td>
<td>Unknown</td>
<td>Unknown</td>
<td>Unknown</td>
<td>In upper water column in summer, overwintering either as nauplii in sea ice or as CIIV at depth (44)</td>
<td>TAG (44)</td>
</tr>
</tbody>
</table>

chain wax esters (WEs) in contrast to the shorter chain WEs of *Rhincalanus gigas*. A large depot of long chain wax esters characterises the Arctic species, *Calanus glacialis* and *Calanus hyperboreus*, and this is thought to represent an efficient energy store and a specific adaptation to a long period without feeding (Lee, 1974).

*Calanoides acutus* is further distinguished from several of the other species in that a clearly defined cohort is seen during summer, which suggests a restricted period of successful spawning. The appearance of this cohort might coincide with the summer period of high chlorophyll *a* (chl *a*) concentration (see later section on generation time of *C. acutus*). The growing season of this species thus appears to be more closely keyed with the primary production season than those of other species. *C. acutus* appears to start feeding later in spring and stop feeding earlier in autumn than the other species, and it has never been observed to feed significantly in winter (Table 1). All dietary studies confirm that it eats mainly phytoplankton, unlike most of the other species in Table 1.

### 3.2. Omnivorous/detritivorous feeding, extended growth season

Species adopting this life cycle strategy tend to have broader diets than *Calanoides acutus*, a longer season of feeding, growth and reproduction which may extend into winter, and consequently less reliance on diapause. *Calanus propinquus*, *Calanus similimus*, *Metridia gerlachei*, *Oithona similis* and *Microcalanus pygmaeus* adopt this strategy. *Oncaea curvata* and *Oithona frigida* may do as well, but information on these species is sparse. *Rhincalanus gigas* appears to have life cycle traits which are intermediate between groups (1) and (2), which emphasises the artificiality of such classifications.

The literature on feeding among members of this group is often conflicting (Table 1). For example during winter, *Rhincalanus gigas* has been found either with empty guts, presumably in diapause (Hopkins et al., 1993b) or containing significant quantities of diatoms and apparently reproducing (Marin and Schnack-Schiel, 1993). *Metridia gerlachei* has been classed as predominantly herbivorous in summer (Hopkins, 1987; Huntley and Es-
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resource which can be orders of magnitude richer than the surrounding water (Eicken, 1992). A variety of metazoan groups utilise Antarctic sea ice in winter (Daly, 1990; Smetacek et al., 1990), but the life cycles of the high latitude, mainly neritic copepods, *Paralabidocera antarctica* and *Stephos longipes* involve them actually entering sea ice for part of the year. Detailed accounts of their life cycles have been published recently (Kurbjeweit et al. 1993) and Schnack-Schiel et al. (1995) for *S. longipes* and Tanimura et al. (1996) for *P. antarctica*, so I will only compare their overwintering strategies briefly.

*Paralabidocera antarctica* overwinters in sea ice as naupliar stages (Hoshiai and Tanimura, 1986; Tanimura et al., 1996). These feed on ice algae and develop from early to late stage nauplii. Tanimura et al. (1996) pointed out that this unusual overwintering strategy, with nauplii not only successfully overwintering in a protective habitat, but also feeding and growing, reflected the peculiarities of the sea-ice environment. At Syowa station where the studies were carried out, there appear to be proliferations of ice algae in both spring and autumn, which provide a highly concentrated food source (Tanimura et al., 1996).

*Stephos longipes* replaces *Paralabidocera antarctica* in the Weddell Sea, although both species appear to have circum-Antarctic distributions (Schnack-Schiel et al., 1995). Its overwintering differs from that of *P. antarctica*, being less closely associated with sea ice. Schnack-Schiel et al. (1995) describe two alternative strategies for overwintering: naupliar and early copepodid stages living in brine channels mainly in the lower part of the ice, and older copepodids either deep in the water column or near the seabed.

The extent to which other Antarctic copepods utilise sea ice is far from resolved. Under-ice feeding appears to be characteristic of some Arctic species in spring and summer, and given the high algal biomass sometimes encountered in Antarctic sea ice or on the underside of it, similar habits might be expected for their Southern Ocean counterparts (Conover and Huntley, 1991). Although large epipelagic species such as *Calanus propinquus* have been observed in the top 50 m under sea ice (Hopkins and Torres, 1988; Hosie and Stolp, 1989; Bathmann et al., 1993) and have been suggested to utilise ice algae (e.g. Kurbjeweit, 1993; Bathmann et al., 1993), its overall significance, either as a refuge or a food source is still unknown.

4. The life cycle of *Calanoides acutus*

Long generation times and slow overall growth rates are typical of polar copepods, and these are presumably dictated by the cold temperatures and/or the short primary production season. The relative importance of temperature and food in limiting growth rates is controversial (Clarke and Peck, 1991; c.f. Huntley and Lopez, 1992). Clarke and Peck (1991) pointed out that the low respiratory costs of polar organisms conferred a metabolic advantage, and suggested that their slow annual growth rates instead reflected the low annual average food availability.

For *Calanoides acutus* I have collated recent information on physiological rates, moulting rates and the length of the growing season, in order to examine some of the features of a polar environment which constrain its growth rate and generation time. *C. acutus* is an ideal candidate for this, because it is large, a major contributor to biomass, is found throughout the Southern Ocean so it is better known than any other Southern Ocean copepod. The fact that it is mainly herbivorous and that feeding is confined to the surface layer during summer mean that its food intake is more easily quantified than those of other species. Its successful reproductive season is also short, allowing clear cohorts to be followed, thus giving easier interpretations of development rates than possible for many other species.

4.1. Physiology

Some physiological data have appeared in the last five years which provide a preliminary energy budget for *Calanoides acutus* (Tables 2–4). Because most recent data on feeding and egg production have come from highly productive regions and under bloom conditions, the values in Tables 2 and 3 might approach the maximum values achievable by these copepods.

The rates in Tables 2–4 were determined for CVs and adult females (sometimes mixtures of stages),
Table 2
Ingestion rates of *Calanoides acutus* measured during summer at high ambient chl *a* concentrations

<table>
<thead>
<tr>
<th>Location</th>
<th>Temperature of mixed layer (°C)</th>
<th>Ambient chl <em>a</em> concentration (mg m⁻³)</th>
<th>Copepods used for experiment</th>
<th>Method</th>
<th>Mean daily carbon ration (% of body carbon)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bransfield Strait (Stns. 77 and 97)</td>
<td>~ 0</td>
<td>~ 3–3.8</td>
<td>CV, CVI ♀</td>
<td>incubation in natural seawater</td>
<td>3–10</td>
<td>Schnack et al. (1985)</td>
</tr>
<tr>
<td>Bellingshausen Sea</td>
<td>−1</td>
<td>3.2</td>
<td>CVI ♀</td>
<td>incubation in natural seawater</td>
<td>8</td>
<td>Atkinson and Shreeve (1995)</td>
</tr>
<tr>
<td>South Georgia shelf</td>
<td>~ 2.3</td>
<td>~ 1.8–3.7</td>
<td>CV</td>
<td>gut fluorescence</td>
<td>13</td>
<td>Atkinson et al. (1992)</td>
</tr>
<tr>
<td>South Georgia shelf</td>
<td>~ 3</td>
<td>6–12</td>
<td>CV and CVI ♀</td>
<td>gut fluorescence</td>
<td>12</td>
<td>Atkinson et al. (1996)</td>
</tr>
</tbody>
</table>

Table 3
*Calanoides acutus*: daily carbon expenditure for egg production at high ambient chl *a* concentrations

<table>
<thead>
<tr>
<th>Location</th>
<th>Time of year</th>
<th>Temperature of mixed layer (°C)</th>
<th>Ambient chl <em>a</em> concentration (mg m⁻³)</th>
<th>Daily egg carbon production rate (% of CVI ♀ carbon), mean values (max values)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gerlache Strait</td>
<td>Late November</td>
<td>0.5</td>
<td>max ~ 10</td>
<td>4.4 (6.7)</td>
<td>Lopez et al. (1993)</td>
</tr>
<tr>
<td>Bransfield Strait area</td>
<td>Late December</td>
<td>1</td>
<td>&gt; 4</td>
<td>4.1 (8.7)</td>
<td>Huntley and Escritor (1991)</td>
</tr>
<tr>
<td>South Georgia area</td>
<td>January</td>
<td>3–4</td>
<td>usually 0.5–1.5, (max: 6)</td>
<td>1.1 (6.9)</td>
<td>Ward and Shreeve (1995)</td>
</tr>
</tbody>
</table>
Tables 2 and 3 suggest a rather low carbon turnover, considering that these are likely to approach maximum rates. The large size and extensive lipid store of *Calanoides acutus* mean that physiological rates, expressed on a mass-specific basis, would tend to be less than those of smaller *Calanus* species at lower latitudes (e.g. Paffenholz, 1971; Runge, 1985; Peterson et al., 1990; Ohman and Runge, 1994; Pond et al., 1996). However, the difference is too large for allometry to be the only explanation. For example, the maximum ration of *C. acutus* in Table 2 is only about 15% of that of female *Calanus helgolandicus* at 15°C (Paffenholz, 1971) and its maximum egg production rate is only about one-quarter (Pond et al., 1996). These rates for *C. acutus* resemble those of high Arctic calaniids (see Smith and Schnack-Schiell, 1990; Nielsen and Hansen, 1995), and they are also internally consistent in the context of an energy budget. A mean egg production rate of 4% carbon per day (Table 3) would equate to a mean daily carbon intake of 12% body carbon if a conservative egg production efficiency of 33% is assumed (Hirche, 1990). This is within the range of mean values in Table 2. The summer respiration rates are also low, which is in line with overall findings of low respiratory costs of cold water crustaceans (e.g. Clarke, 1983; Ikeda, 1985).

Clarke and Peck (1991) argued that if food availability, rather than low temperature was limiting summer growth of polar ectotherms, then their growth each of which can vary greatly in lipid content and body mass (Hagen and Schnack-Schiell, 1996). Further, copepodid weights were not determined in all experiments, so to make all values more comparable, all egg production data were standardized to an adult female of dry mass 600 µg (an approximate mean of all available measurements). In a similar way, ingestion and respiration rates were standardized to a value of 520 µg dry mass (a mean literature value for CVs and adult females). Copepod carbon was assumed as 45% dry mass, from the measurements of Schnack et al. (1985). Egg carbon was calculated as 0.5 µg per egg from the equation in Huntley and Lopez (1992), based on egg membrane diameter (Ward and Shreeve, 1995). This corresponds to 42% of egg dry mass, as measured by Ward and Shreeve (1995).

Tables 2 and 3 suggest a rather low carbon turnover, considering that these are likely to approach maximum rates. The large size and extensive lipid store of *Calanoides acutus* mean that physiological rates, expressed on a mass-specific basis, would tend to be less than those of smaller *Calanus* species at lower latitudes (e.g. Paffenholz, 1971; Runge, 1985; Peterson et al., 1990; Ohman and Runge, 1994; Pond et al., 1996). However, the difference is too large for allometry to be the only explanation. For example, the maximum ration of *C. acutus* in Table 2 is only about 15% of that of female *Calanus helgolandicus* at 15°C (Paffenholz, 1971) and its maximum egg production rate is only about one-quarter (Pond et al., 1996). These rates for *C. acutus* resemble those of high Arctic calaniids (see Smith and Schnack-Schiell, 1990; Nielsen and Hansen, 1995), and they are also internally consistent in the context of an energy budget. A mean egg production rate of 4% carbon per day (Table 3) would equate to a mean daily carbon intake of 12% body carbon if a conservative egg production efficiency of 33% is assumed (Hirche, 1990). This is within the range of mean values in Table 2. The summer respiration rates are also low, which is in line with overall findings of low respiratory costs of cold water crustaceans (e.g. Clarke, 1983; Ikeda, 1985).

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Fig. 1. *Calanoides acutus*. Percentage composition of developmental stages within three regions of the Atlantic sector. Each point represents a sampling station and the trend lines link mean values of age structure from transects or groups of stations (as described in Atkinson et al., 1997).
under saturating food should match those of their temperate counterparts. Although food might not have been saturating in all of the experiments in Tables 2 and 3, the large shortfall between the maximum rates of *Calanoides acutus* and those of *Calanus* in warmer water does not support the hypothesis of Clarke and Peck (1991). Likewise, other large, Southern Ocean copepods seem to be operating on low carbon budgets, even at high chl *a* concentrations (table 5 in Atkinson et al., 1996). So possibly during the brief periods when food is super-abundant, the species are indeed limited by temperature-related factors.

At other times, however, food availability appears to have a major effect. At the start of the spring bloom in Gerlache Strait, Lopez et al. (1993) found that egg production of *Calanoides acutus* was positively related to chl *a* concentration. Also, ingestion rates recorded at low chl *a* values are lower than the values in Table 2 (e.g Schnack-Schiel et al., 1991; Pasternak et al., 1994). This suggests that food is limiting for at least part of the summer growing season, and obviously for all of the winter. So, as suggested for other species (e.g Klein Breteler et al., 1995) the seasonal interplay of both food and temperature probably constrains the production of *C. acutus*.

### 4.2. Moulting and growth rate

In a recent investigation of the life cycle of *Calanoides acutus*, Atkinson et al. (1997) compiled all oceanic data from the Atlantic Sector of the Southern Ocean (Fig. 1). These are based mainly on stratified sampling to 1000 m with 100–200 μm mesh closing nets. Because seasonal coverage in any one year is lacking in oceanic regions, this data set had to be compiled from Russian, German, American and British expeditions from 1928 to 1992 (Atkinson et al., 1997).

The study area was divided into three subregions (Fig. 1), namely Scotia Sea, Weddell–Scotia Confluence area, and eastern Weddell Sea. These contrast greatly in temperature, ice cover and summer chl *a* concentration. However, summer moulting rate estimates (Table 5) are about the same in each, with the summer cohort developing from CI to CIV in about 1.5 months (i.e. ~15 days per stage).

<table>
<thead>
<tr>
<th>Development</th>
<th>Scotia Sea</th>
<th>Weddell–Scotia Confluence</th>
<th>Eastern Weddell Sea</th>
</tr>
</thead>
<tbody>
<tr>
<td>CVI → CIV</td>
<td>122 (126)</td>
<td>128 (130)</td>
<td>133 (132)</td>
</tr>
<tr>
<td>CI to CIV</td>
<td>49 (41)</td>
<td>53</td>
<td>41 (49)</td>
</tr>
</tbody>
</table>

The values are in days using a criterion of “the time when a stage reaches 20% of the population” to define when it appears (these are based on the trend lines in Fig. 1). Values in parentheses were calculated (where possible) using a 40% criterion (Atkinson et al., 1997).

Previous estimates of summer moulting rates of *Calanoides acutus*, also based on population stage structure, have been contradictory. A similar rate to that above has been suggested by previous oceanic studies (Andrews, 1966; Atkinson, 1991) but much slower rates have been reported near the Antarctic Peninsula (Chojnacki and Weglenska, 1984; Huntley and Escritor, 1991). The reasons for these differences are not clear but in any case, the summer moulting rates of *C. acutus* are much slower than those reported for copepods in warmer water (reviewed in Kiørboe and Sabatini, 1995).

In the previous section I stressed that the large size and the lipid store of *Calanoides acutus* hindered comparisons of its physiology with that of *Calanus* from warmer water. An independent approach to assess growth rate is to estimate exponential growth rate, *g*, from development time (Huntley and Lopez, 1992):

\[
g = \ln \left( \frac{W_{\text{CIV}}}{W_{\text{egg}}} \right) / D
\]

where *W*<sub>CIV</sub> is the mass of the first diapausing stage, *W*<sub>egg</sub> is the mass of the egg and *D* is the development time from egg to CIV. For the eastern Weddell Sea data in Fig. 1, substituting values of *W*<sub>CIV</sub> = 187 μg (Schnack-Schiel and Hagen, 1994), *W*<sub>egg</sub> = 1.2 μg (Ward and Shreeve, 1995), and *D* = 60 d (a minimum realistic value from Fig. 1 and Table 5), yields a growth rate of 0.084 d<sup>−1</sup>. Whether its growth from egg to CIV approximates this exponential model is not known, but the calculated value for *C. acutus* is much less than those for *Calanus* at 15°C, which are typically in the range 0.2–0.3 d<sup>−1</sup> (see Kiørboe and Sabatini, 1995). Considering that
this Antarctic growth rate pertains to the short summer of elevated phytoplankton biomass, it provides indirect support for the earlier suggestion that the slow summer growth rate of *C. acutus* is associated with the low temperature.

4.3. Generation time

Because of the intense seasonality of the Southern Ocean, the length of growing season, as well as growth rates during summer, presumably dictate the duration of the life cycle. Because *Calanoides acutus* is herbivorous, has a seasonal migration cycle and does not feed at depth, the period when the population is in the surface layer dictates the potential period for growth and production. The durations (Fig. 2) in the Scotia Sea and eastern Weddell Sea indeed correspond to the reported timing of elevated chl *a* concentrations in these regions (Hart, 1942; Savidge et al., 1996). This latitudinal shift in life cycle timing in relation to the timing of the spring bloom was reported first in the Indian Ocean Sector by Voronina (1970, 1978) and is also clearly seen in the age structure data in Fig. 1. The ice-free months in the eastern Weddell Sea study area last only from about January to March (Gloersen et al., 1992), so this is the potential period for significant water column primary productivity (*C. acutus* has not so far been observed to utilise under ice algae: S.B. Schnack-Schiel, pers. commun.). In the Open Ocean and Polar Frontal zones of the Atlantic Sector, however, blooms can occur at any time between November and March (El-Sayed and Weber, 1982; Priddle et al., 1986; Whitehouse et al., 1996), although average summer chl *a* values may not be as high as those in the coastal and marginal ice system of the Weddell Sea (Tréguer and Jacques, 1992; Savidge et al., 1996).

The alternative models proposed for the life cycle of *Calanoides acutus* are shown in Fig. 3. The
argument for a 2 year life cycle (Drits et al., 1994; Pasternak et al., 1994) was based mainly on physiological data in autumn. These authors found two groups of late copepodids; a lipid-poor group feeding in the top 100 m and a lipid-rich group at depth, with a slower metabolism. A problem with interpretations of either physiology or stage structures from a restricted time-span is that the fate of individuals or cohorts is not known. For example a cohort observed at a certain time of year may progressively die through the rest of the year with only a small fraction successfully completing their life cycle. Knowledge of mortality therefore puts some constraints on life cycle duration (Miller et al., 1984). Population mortality, estimated from the data set in Fig. 1 for the autumn/winter period only was 0.0070 d\(^{-1}\) in the Scotia Sea and 0.0059 d\(^{-1}\) in the eastern Weddell Sea (Atkinson et al., 1997). The regression was not significant (\(p > 0.05\)) for the Weddell–Scotia Confluence area, where both abundance and vertical distributions were highly variable. These values are broadly consistent with comparable estimates for Calanus in high latitudes (Aksnes, 1996), although they are rather lower than rates for C. acutus in the Antarctic Peninsula area (Huntley et al., 1994). If two years was the normal life-span of Calanoides acutus, then at a mortality of 0.0059 d\(^{-1}\), then the CV in their first year would need to greatly outnumber (by roughly 9:1) the adults which moult near the end of their second year. (This is illustrated in Fig. 3b by the relative thickness of the two overlapping cohort lines in late winter). However, the high percentage of adult males and females in the population in late winter (Fig. 1) shows that this is not the case, and a one year cycle (Fig. 3a) fits the data more closely. A factor which complicates this analysis is that some adult females might re-enter diapause after spawning, to spawn again the following year (Hagen and Schnack-Schiel, 1996). However, in the data set in Fig. 1 they are present in only small numbers in autumn/early winter (particularly in the Scotia Sea), and it appears that over 80% of females die after their first spawning.

Conover et al. (1991) suggested that an adaptation of polar copepods to a variable environment was the ability, even of early copepodids, to overwinter. Marin (1988) likewise suggested that the life cycle of Rhincalanus gigas was flexible, and of one or two year duration depending on conditions. The stage structure of Calanoides acutus during winter varies greatly between stations: at some CV dominates and at others, CV (Fig. 1). The more striking regional difference for C. acutus is not the summer moult rate (Table 5) but rather the length of the growing season (Fig. 2). Perhaps individuals with insufficient time to moult to lipid rich CV during the first summer, or those meeting poor feeding conditions still have a chance of overwintering as CIV and completing their life cycle in two years. These non-spawning late copepodids form a significant portion of the population during late winter/early spring (Fig. 1). However, even a modest mortality of 0.0059 d\(^{-1}\) would leave only \(\sim 10\%\) of this cohort to survive a whole extra year. This severe mortality penalty for prolonging the life cycle therefore probably means that the realized life cycle of Calanoides acutus is mainly only one year. Given the highly variable and apparently unpredictable nature of Southern Ocean phytoplankton blooms (e.g. El-Sayed and Weber, 1982; Laubscher et al., 1993; Jochem et al., 1995; Whitehouse et al., 1996), perhaps a flexible life cycle strategy is needed to prevent population crashes during harsh years.

5. Oithona similis: abundance, distribution and life cycle

Oithona similis is a cosmopolitan species, abundant throughout coastal and oceanic regions of tropical, temperate and polar waters (Sabatini and Kiørboe, 1994). A realistic picture of its abundance in the Southern Ocean has only come in the last decade, with the routine use of nets finer than 200 \(\mu\)m mesh. Nevertheless, our knowledge of its life cycle and physiology in the Southern Ocean, in common with other oceans, is rudimentary (Sabatini and Kiørboe, 1994; Fransz and Gonzalez, 1995; Metz, 1996). Cyclopoids have been neglected because they are small and hard to study, and perhaps because in catches of 200–500 \(\mu\)m nets they comprise a small fraction of biomass, so are deemed unimportant. However, in the Southern Ocean a series of attempts at comparing their feeding (Atkinson and Shreeve, 1995; Atkinson, 1996; Swadling et
al., 1997), potential respiration (Fransz, 1988) and annual secondary production (Fransz and Gonzalez, 1995) have suggested that those of *Oithona* spp. can match or outweigh any of the large, biomass-dominant copepods. This presumably reflects their small size and correspondingly high metabolic rates (Ikeda, 1985; Fenchel, 1988).

Because so little is known about *Oithona* spp., I have collated some basic data on abundance and biomass provided by nets of 200 μm mesh or finer (Table 6). *Oithona* spp. are comparatively rare near the Antarctic Continental shelf (*Oncaea carvata* is often the dominant small copepod there; Metz, 1996), but it increases by about an order of magnitude towards the northern part of the Southern Ocean. Studies in the Polar Frontal Zone and near South Georgia with 100–200 μm nets have revealed abundances in excess of 6000 inds. m⁻³. These densities and standing stocks are within the range of those in coastal and oceanic locations in the Northern Hemisphere. (e.g. Dagg et al., 1980; Paffenhofer, 1983; Daro, 1988; Granéli et al., 1993; Landry et al., 1994).

Developmental stage structures for *Oithona similis* in the Antarctic have been published by Fransz (1988), Fransz and Gonzalez (1995) and Metz (1996). These authors noted that all naupliar and copepodid stages occurred throughout the year. This lack of clear cohorts, and the incomplete coverage of the oceanic region, hamper the estimation of stage durations and generation times. Naupliar stage durations in the Weddell Sea and Bellingshausen Sea were estimated as ~12 and 6–19 days per stage, respectively (Fransz and Gonzalez, 1995; Metz, 1996). Corresponding copepodid stage duration estimates are 14–28 and 30 days per stage. Both authors noted the presence of females with eggs throughout the year, so the absence of clear cohorts probably reflects more or less continuous reproduction, but with an increase prior to the main production season. Indeed Fransz (1988) observed that eggs hatched and developed through naupliar stages prior to the spring bloom in the Weddell Sea, at very low ambient chl *a* concentrations. Estimated life cycle durations for the East Wind Drift (i.e. Weddell Sea area and inner Bellingshausen Sea) are 1 year (Fransz and Gonzalez, 1995; Metz, 1996), although Metz (1996) suggested that more than one generation per year could be completed in the Antarctic Circumpolar Current to the north.

The suggestion of an extended reproductive period is supported by seasonal trends in total abundance. Fransz and Gonzalez (1995) reported only a low (about fourfold) summer–winter difference in total copepodid numbers in the Weddell Sea area. This also seems to be within the normal seasonal range of values from the sub-regions in Table 6. In contrast *Calanoides acutus* abundance changed over tenfold between winter and summer (Atkinson, 1991; Atkinson et al., 1997).

The fact that *Oithona similis* and *Calanoides acutus* contrast greatly in both size and life cycle suggests that they might be exploiting different food sources (Berggreen et al., 1988). This does not seem to be upheld, however, by studies of their gut contents (Table 1). *O. similis* from the marginal ice zone contained mainly diatoms during spring, summer and autumn (Hopkins, 1985a, 1987; Hopkins and Torres, 1989; Hopkins et al., 1993a) and no recognisable gut contents were found in winter (Hopkins et al., 1993b). The natural diet of *O. similis* remains uncertain (Paffenhofer, 1993) although they appear to prefer motile food (Uchima and Hirano, 1986; Turner and Granéli, 1992) or feed carnivously (Lampitt, 1978; Uchima and Hirano, 1986). In a prebloom study in the Bellingshausen Sea (Atkinson, 1995) and in a postbloom study in the Polar Frontal Zone (Atkinson, 1996), *Oithona* spp. (mainly *O. similis*) cleared motile taxa (ciliates, dinoflagellates and nanoflagellates) at higher rates than diatoms of similar size. Gonzalez et al. (1994) and Gonzalez and Smetsack (1994) suggested that *Oithona* spp. can eat sinking faecal pellets. So gut content analysis might not be telling the whole story of *Oithona* feeding, because
<table>
<thead>
<tr>
<th>Region</th>
<th>Location</th>
<th>Time of year</th>
<th>Sampling</th>
<th>Abundance (no. m⁻²)</th>
<th>Biomass (mg dry mass m⁻²)</th>
<th>Notes</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northern Antarctic Circumpolar Current</td>
<td>Prince Edward Islands</td>
<td>March</td>
<td>200 μm net, top 300 m</td>
<td>264000</td>
<td>—</td>
<td>—</td>
<td>Grindley and Lane (1979)</td>
</tr>
<tr>
<td></td>
<td>Prince Edward Islands</td>
<td>April/May</td>
<td>22 μm screen, top 50 m only</td>
<td>979000</td>
<td>—</td>
<td>—</td>
<td>Perissinotto (1989)</td>
</tr>
<tr>
<td></td>
<td>Polar Frontal Zone, 37°W</td>
<td>February</td>
<td>100 μm, 200 μm, top 200 m</td>
<td>&gt; 250000</td>
<td>~ 300</td>
<td>~ 3.7% of biomass and 71% of abundance of copepods in top 50 m</td>
<td>Atkinson (1996)</td>
</tr>
<tr>
<td></td>
<td>South Georgia shelf</td>
<td>January</td>
<td>100 μm net, top 200 m</td>
<td>194808</td>
<td>358</td>
<td>~ 4% of biomass and 43% of abundance of copepods in top 50 m</td>
<td>Atkinson et al. (1996)</td>
</tr>
<tr>
<td></td>
<td>South Georgia shelf</td>
<td>January</td>
<td>200 μm net, top 200 m</td>
<td>178500</td>
<td>357</td>
<td>5% of biomass of copepods and small euphausiids</td>
<td>Ward et al. (1995)</td>
</tr>
<tr>
<td></td>
<td>Ocean station north of South Georgia</td>
<td>January</td>
<td>200 μm net, top 800 m</td>
<td>199787</td>
<td>399</td>
<td>7% of biomass of copepods and small euphausiids</td>
<td>Ward et al. (1995)</td>
</tr>
<tr>
<td>Southern Antarctic Circumpolar Current</td>
<td>Outer Bellingshausen Sea</td>
<td>November</td>
<td>50 μm net, top 600 m</td>
<td>54857</td>
<td>80</td>
<td>9% of copepod biomass</td>
<td>Metz (1996)</td>
</tr>
<tr>
<td></td>
<td>Outer Bellingshausen Sea</td>
<td>February</td>
<td>50 μm net, top 1000 m</td>
<td>268155 (242704)</td>
<td>333 (260)</td>
<td>9% of copepod biomass</td>
<td>Metz (1996)</td>
</tr>
<tr>
<td></td>
<td>Outer Bellingshausen Sea</td>
<td>April</td>
<td>50 μm net, top 1000 m</td>
<td>412384 (376085)</td>
<td>579 (515)</td>
<td>—</td>
<td>Metz (1996)</td>
</tr>
<tr>
<td></td>
<td>Pacific Sector, south of Polar Front</td>
<td>Seasonal average</td>
<td>202 μm net, top 1000 m</td>
<td>—</td>
<td>61</td>
<td>4.7% of copepod biomass</td>
<td>Hopkins (1971)</td>
</tr>
<tr>
<td></td>
<td>Southern Scotia Sea</td>
<td>June–August</td>
<td>30 l bottle casts, 30 μm screened and 162 μm nets in top 1000 m</td>
<td>165333</td>
<td>71–149</td>
<td>~ 14% of biomass and ~ 46% of abundance of zooplankton</td>
<td>Hopkins et al. (1993b)</td>
</tr>
<tr>
<td>Weddell Sea area</td>
<td>Samples mainly in Eastern Weddell Sea</td>
<td>Seasonal average</td>
<td>50 μm net, top 200–300 m</td>
<td>106500</td>
<td>209 mg carbon m⁻²</td>
<td>—</td>
<td>Fransz and Gonzalez (1985)</td>
</tr>
<tr>
<td></td>
<td>Eastern Weddell Sea</td>
<td>October–November</td>
<td>50 μm net, top 200 m</td>
<td>34400</td>
<td>—</td>
<td>48% of copepod numbers</td>
<td>Fransz (1988)</td>
</tr>
<tr>
<td></td>
<td>Eastern Weddell Sea</td>
<td>January–February</td>
<td>100 μm net, top 400 or 1000 m</td>
<td>111000</td>
<td>—</td>
<td>—</td>
<td>Gonzalez et al. (1994)</td>
</tr>
<tr>
<td></td>
<td>West central Weddell Sea</td>
<td>March</td>
<td>30 l bottle casts, 30 μm screened and 162 μm nets in top 1000 m</td>
<td>120000</td>
<td>—</td>
<td>—</td>
<td>Hopkins and Torres (1989)</td>
</tr>
<tr>
<td>Location</td>
<td>Month</td>
<td>Net Size</td>
<td>Count (mg carbon m⁻²)</td>
<td>Biomass</td>
<td>Numbers</td>
<td></td>
<td></td>
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<tr>
<td>----------------------------------</td>
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<tr>
<td>Eastern Weddell Sea</td>
<td>February</td>
<td>100 μm net, top 1000 m</td>
<td>108718</td>
<td>—</td>
<td>—</td>
<td>Metz (1995)</td>
<td></td>
</tr>
<tr>
<td>Eastern Weddell Sea</td>
<td>November</td>
<td>100 μm net, top 1000 m</td>
<td>41918</td>
<td>—</td>
<td>—</td>
<td>Metz (1995)</td>
<td></td>
</tr>
<tr>
<td>Croker Passage, Antarctic Peninsula</td>
<td>March/April</td>
<td>30 l bottle casts, 30 μm screened, and 162 μm nets in top 1000 m</td>
<td>5500</td>
<td>28</td>
<td>~1% of biomass and ~5% of numbers of copepods</td>
<td>Hopkins (1985b)</td>
<td></td>
</tr>
<tr>
<td>Admiralty Bay</td>
<td>Seasonal average</td>
<td>200 μm net, top 400 m</td>
<td>23200</td>
<td>44 mg carbon m⁻²</td>
<td>only ~4 fold variation in numbers year-round</td>
<td>From and Gonzalez (1993)</td>
<td></td>
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<tr>
<td>Antarctic Peninsula</td>
<td>Average from December to March</td>
<td>86 μm net in the 75 m water column</td>
<td>1950</td>
<td>9</td>
<td>—</td>
<td>Chojnacki and Weglicka (1984)</td>
<td></td>
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<tr>
<td>Mc Mudo Sound, Ross Sea</td>
<td>February</td>
<td>162 μm net, top 800 m</td>
<td>7</td>
<td>~31–69</td>
<td>—</td>
<td>Hopkins (1987)</td>
<td></td>
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<tr>
<td>Southeast Weddell Sea</td>
<td>January–February</td>
<td>100 μm net, top 400 m</td>
<td>33632</td>
<td>—</td>
<td>—</td>
<td>González et al. (1994)</td>
<td></td>
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<tr>
<td>Bellingshausen Sea</td>
<td>November–December</td>
<td>50 μm net, top 200 m</td>
<td>23422</td>
<td>37</td>
<td>6% of copepod biomass</td>
<td>Metz (1996)</td>
<td></td>
</tr>
<tr>
<td>Bellingshausen Sea</td>
<td>February</td>
<td>50 μm net, top 1000 m</td>
<td>63872 (59666)</td>
<td>64 (57)</td>
<td>—</td>
<td>Metz (1996)</td>
<td></td>
</tr>
<tr>
<td>Bellingshausen Sea</td>
<td>April</td>
<td>50 μm net, top 1000 m</td>
<td>46634 (31410)</td>
<td>83 (57)</td>
<td>—</td>
<td>Metz (1996)</td>
<td></td>
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<td>Eastern Weddell Sea</td>
<td>November</td>
<td>100 μm net, top 400 m or 1000 m</td>
<td>71939</td>
<td>—</td>
<td>—</td>
<td>Metz (1995)</td>
<td></td>
</tr>
<tr>
<td>Eastern Weddell Sea</td>
<td>February</td>
<td>100 μm net, top 200 m or 1000 m</td>
<td>76082</td>
<td>—</td>
<td>—</td>
<td>Metz (1995)</td>
<td></td>
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</tbody>
</table>

All values refer to *O. similis* plus *O. frigida* as the two species are not usually separated. Values in parentheses refer to *O. similis* only.
Antarctic nanoplankton and protozoans are predominantly athecate forms (e.g. Kopczynska, 1992; Garrison and Gowing, 1993; Leakey et al., 1994; Archer et al., 1996). These forms are prevalent outside bloom periods, and, like detrital/faecal material are unlikely to be recognisable in gut contents.

If Oithona similis remains in the surface layers, possibly growing and reproducing, it might need to utilise low concentrations of food. Unfortunately, data to address this are very limited. In early spring in the Bellingshausen Sea, when chl $a$ was only $0.052 - 0.17 \text{ mg m}^{-3}$, Oithona spp. were feeding, with estimated daily rations of 0.5–3.5% body carbon (Atkinson and Shreeve, 1995). In the Polar Frontal Zone at post-bloom chl $a$ concentrations (∼0.7 mg m$^{-3}$), estimated daily rations were 9.5–35% of body carbon (Atkinson, 1996). Winter chl $a$ concentrations are poorly documented, but Banse (1996) drew attention to the relatively high winter values (mainly 0.10–0.15 mg m$^{-3}$) north of the Polar Front. In any case there is still insufficient knowledge of the energy budget of this species to assess the rate of food intake which might allow growth.

6. Comparisons with Arctic copepods

Conover and Huntley (1991) speculated that Southern Ocean copepods tend not to undergo the specific life history adaptations of lipid storage and winter diapause to the same extent as their Arctic counterparts. Recent work (Table 1) tends to support this view, and Calanoides acutus may be the only ‘true’ diapause species which could be likened to Calanus glacialis or Calanus hyperboreus. The others seem to vary, with diapause in some seasons, regions, or portions of the population, but possibly intermittent or opportunistic feeding extending into the winter months. The overall lower lipid levels and higher incidence of TAG rather than WE in Southern Ocean copepods is further indirect support for the occurrence of feeding in spring, autumn and winter. Marin (1988) was the first to suggest that the winter season was more biologically active for Antarctic copepods than had been supposed.

Does feeding in spring, autumn and winter simply maintain the copepods or does it allow growth? Conover and Huntley (1991) and others have stressed that the low respiratory costs in cold winter water only require low feeding rates for basic maintenance. This question is exemplified by Rhincalanus gigas, a species whose life-span is unclear and which is described variously to either enter diapause in winter (Hopkins et al., 1993b) or remain active (Marin and Schnack-Schiel, 1993; Pasternak et al., 1994). The fact that in some regions it appears to be able to grow and moult during late winter/early spring (Atkinson, 1991; Ward et al., 1997) suggests that it can do more than simply maintain basic metabolism. Several features of Rhincalanus gigas parallel those of Neocalanus cristatus in the northeast Pacific. It has a very low daily ration of algal carbon (e.g. Schnack et al., 1985), it tends to live deeper than some of the other biomass-dominant copepods in summer (Atkinson, 1991), and it appears to remain motionless for long periods. Dagg (1993) suggested that N. cristatus derived significant nutrition from intercepting sinking aggregates. Could R. gigas benefit in a similar way?

The reasons behind the different life cycles of Arctic and Antarctic copepods are intriguing. Possibly a higher average water column productivity in the Southern Ocean (Codispoti et al., 1991; Mathot et al., in press) or a tighter link with the rich protozooplankton community (Garrison, 1991) allows better growth conditions and shorter life cycles. These simplifications ignore the great heterogeneity of both regions and do not account for other, possibly major, differences. For example the literature on under ice feeding of Arctic copepods is much more extensive than that of their southern counterparts. This may reflect differences in the physics or biology of sea ice (Conover and Huntley, 1991). Alternatively the extensive observations of under-ice feeding by juvenile Euphausia superba (e.g. Daly, 1990; Smetacek et al., 1990) has simply meant that copepods under the ice have been overlooked. However, Euphausia superba seems highly adapted to the under-ice niche (Smetacek et al., 1990; Eicken, 1992) and are known to be effective predators of copepods (Price et al., 1988; Hopkins et al., 1993a; Atkinson and Snijder, 1997). Possibly euphausiids have taken over the role of feeding under sea ice in the Southern Hemisphere.
Acknowledgements

I thank Professor S.B. Schiel for her comments which improved the structure of this article, and Dr. A. Hirst for his discussions of copepod growth. Constructive comments on the manuscript were provided by P. Ward, Dr. J. Priddle and Professor A. Clarke.

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