

AN OVERVIEW OF SOUTHERN OCEAN ZOOPLANKTON DATA: ABUNDANCE, BIOMASS, FEEDING AND FUNCTIONAL RELATIONSHIPS

A. Atkinson✉* and P. Ward
British Antarctic Survey
Natural Environment Research Council
High Cross, Madingley Road
Cambridge CB3 0ET
United Kingdom
Email – aat@pml.ac.uk
*New address: Plymouth Marine Laboratory
Prospect Place, The Hoe
Plymouth PL1 3DH
United Kingdom

B.P.V. Hunt and E.A. Pakhomov
Department of Earth and Ocean Sciences
University of British Columbia
6339 Stores Road
Vancouver, B.C.
Canada, V6T 1Z4

G.W. Hosie
Department of Sustainability, Environment,
Water, Population, and Communities
Australian Antarctic Division
203 Channel Highway
Kingston, Tasmania 7050
Australia

Abstract

There is an enormous amount of data on Southern Ocean (SO) zooplankton, mostly on their distribution with a minority addressing rate processes. This review aims to summarise these data and show where it resides, to assist SO food-web modellers or those with limited specialist knowledge of SO zooplankton. First, a brief overview is provided of the diversity and basic biology of SO zooplankton, with an emphasis on abundance, distribution and feeding. Second, advice is provided on the uses, strengths and limitations of zooplankton data as inputs to SO data compilations or food-web models. Copepods overall comprise >75% of the SO zooplankton biomass (excluding *Euphausia superba*). Total mesozooplankton biomass density differs little between the Antarctic sectors, but latitudinally it is maximal in the Polar Frontal Zone and declines to the north and south. Those compiling data on numerical density (no. m⁻² or no. m⁻³) need to allow for differences in the extent of identification of early larval stages. Likewise, the time of year, depth of sampling and mesh size of sampler greatly influence the recorded abundance, since the populations can make seasonal vertical migrations and their pulsed reproduction causes great seasonal changes in size structure and abundance. Other issues are specific to polar environments, for example, lipid storage which leads to significantly different length-mass and mass-rate relationships than are reported in global literature compilations. Likewise, stenothermy (narrow temperature tolerance) means that fixed (Q₁₀-type) temperature relationships based on global literature compilations must be applied with great caution in SO-specific studies. Protozoa/micrometazoa (<200 µm) are the main grazers in the SO, since mesozooplankton typically remove <30% of primary production. This emphasises the dominant role of microbial food chains involving small metazoans, relative to the classic short diatom-krill-whale type food chains. Even within regions of abundant krill, copepod production in summer roughly triples that of postlarval *E. superba*. This fact reflects a large flow of energy through multiple trophic levels, via copepods and their major invertebrate predators such as other predatory copepods, chaetognaths, small omnivorous euphausiids, amphipods up to myctophid fish and birds.

Introduction

During the 80-year history of active research on Southern Ocean (SO) zooplankton, several thousand papers have been published in a wide variety of journals. The data behind these publications are mainly outside of central databases, being scattered widely in publications and logbooks and largely unsynthesised. Given the increasing efforts to compile zooplankton data for databases, meta-analyses and models, there is a need to summarise the plethora of data, with their associated caveats, to a non-specialised user group.

This review is aimed primarily at modellers, data compilers, or those outside SO- or zooplankton research fields. First, the basic biology of the component taxa is summarised, with an emphasis on their diet and feeding. Second, the main features of bulk zooplankton properties, the seasonal and circumpolar distribution of total biomass and numerical density are described. Third, insights are provided for modellers of caveats in data compilations and in the functional rate processes available for SO zooplankton. The large bibliography includes key references from outside the *Web of Knowledge* search arena, and might be a useful starting point for literature searches. For more detailed reviews of ecology, life cycles and controls on distribution (including group-specific ecology and bipolar comparisons) the reader is referred to Conover and Huntley (1991), Smith and Schnack-Schiel (1990), Atkinson (1998), Pakhomov et al. (2002a) and Hunt et al. (2008).

The review is structured firstly around a brief introduction to the main epipelagic taxa that dominate SO zooplankton. *Euphausia superba* has been reviewed recently (Siegel, 2005; Nicol, 2006; Atkinson et al., 2008) and is included here for comparison. The issue of sampling method is critical to solid and comparable data. The space-time distribution of total meso- and macrozooplankton biomass and abundance is then summarised. The last section summarises diet, feeding, key rate processes such as production and functional relationships to food and temperature. Functional relationships are in great demand by modellers but seldom produced by SO ecologists. It is therefore shown where these limited data lie and, where non-SO-specific data need to be used instead, and advice is provided on the use of globally derived relationships from the literature.

Overview of the major zooplankton groups

Zooplankton include a great diversity of planktonic invertebrate metazoans of contrasting body form and life style. Common zooplankton in the SO range over four orders of magnitude in body size, from tiny (<100 µm) copepod nauplii to giant (well over 1 m) jellyfish or salp chains. Their generation times can range from a few days to several years (Figure 1). Typically, gelatinous or jelly-like organisms that filter or ambush prey tend to have more energy efficient lifestyles than rapidly moving crustaceans and consequently tend to have faster growth rates for a given size (Clarke and Peck, 1991).

This review defines mesozooplankton (mainly copepods) as those caught with the 200 µm mesh ring net, Bongo net or Continuous Plankton Recorder (CPR) (270 µm mesh) and macrozooplankton as the larger organisms (e.g. amphipods, small euphausiid species, salps, large chaetognaths, cnidarians etc.) that are more effectively sampled with commonly used 4 mm mesh trawls such as the 8 m² rectangular midwater trawl (RMT 8). The main taxa are described below, particularly their feeding ecology and how they fit into the food web. The 'big three', namely copepods, euphausiids and salps, are addressed first, before summarising briefly the other taxa that are regionally important.

Copepods

As in other oceans, copepods dominate the total mesozooplankton across most of the SO in terms of biomass, abundance, grazing activity and secondary production. They typically comprise >75% of biomass and are only exceeded by *E. superba* or salps in some subregions in some years (Conover and Huntley, 1991; Voronina, 1998; Pakhomov et al., 2002a; Shreeve et al., 2005). Their great range in body length (100 µm to 10 mm) and feeding habits (on ~5 µm autotrophs up to other copepods several mm long) means that this single group contributes to the food web in multiple ways.

Epipelagic copepods have a broadly similar body form and lifestyle, with a series of nauplii and copepodite stages usually feeding in the upper reaches of the water column in the productive season, followed by reproducing adults. Most studies address the species that are large and dominate biomass, namely *Calanoides acutus*, *Rhincalanus*

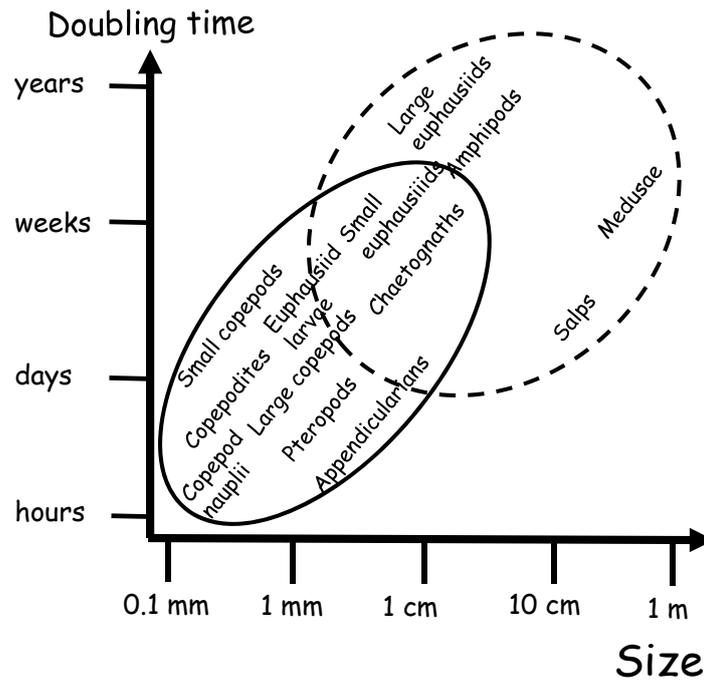


Figure 1: Schematic representation of the relationship between zooplankton size and growth rates. The solid bounded ellipse provides a representation of the organisms caught with a 200 μm mesh size Bongo or ring net (here defined as mesozooplankton). The broken ellipse represents those caught with an RMT8 net (here defined as macroplankton). The intercept represents the size of organisms typically caught by both nets but under-represented in both of their catches due to avoidance and net mesh selection. The gelatinous ambush or filter feeding members such as medusae, salps, small pteropods and appendicularians often have faster growth rates than crustaceans of similar size.

gigas, *Calanus simillimus*, *C. propinquus* and *Metridia gerlachei*. Their life cycles involve reproduction and early larvae feeding in summer, with later lipid-rich stages less active, spending the winter in diapause, or at least with reduced activity, and often at depth (Andrews, 1966; Ommanney, 1936; Voronina, 1970). Later workers emphasised the considerable variability even within these few species (Atkinson, 1991; Schnack-Schiel et al., 1991; Schnack-Schiel and Hagen, 1995; Ward et al., 1997) and that true winter diapause-at-depth was actually the exception, being probably performed strictly only by *C. acutus* (Schnack-Schiel and Hagen, 1995; Atkinson, 1998; Pasternak and Schnack-Schiel, 2001).

A global analysis of copepod diets showed that ciliates comprise on average ~30% of the ciliate plus phytoplankton diet component (Calbet and Saiz, 2005). This underlines the importance of alternative (non-diatom) energy pathways to copepods. Much of the work on SO copepod feeding

has been on the biomass dominants plus the important small species *Oithona similis*. The general consensus is that *C. acutus* and *R. gigas* are the most 'herbivorous' species of this group (Hopkins and Torres, 1989; Atkinson et al., 1996a; Schmidt et al., 2003). They are suspension feeders that ingest both motile and non-motile particles broadly according to their abundance (Schnack, 1985; Atkinson et al., 1996a). Despite the very large and colonial diatoms that characterise SO blooms, these indeed appear to be ingestible by the copepods, although food size increases with copepod size (Atkinson, 1994). *Calanus simillimus*, *C. propinquus* and *M. gerlachei* appear to be slightly more omnivorous, possibly able to switch between suspension and raptorial feeding as does *Acartia tonsa* (Kjørboe et al., 1996). Consequently they ingest a higher proportion of motile prey (Hopkins and Torres, 1989; Atkinson, 1995; Burghart et al., 1999; Schmidt et al., 2003). Further along the spectrum

is *Paraeuchaeta antarctica*, a cruising raptor and predator of other copepods (Yen, 1991; Øresland and Ward, 1993).

Considerable work has now been done on the carbon budgets of these largest copepod species. In productive environments, daily expenditure for egg production of *C. acutus*, *C. simillimus* and *C. propinquus* is 1.6–4.5% (Lopez et al., 1993; Kosobokova, 1994; Ward and Shreeve, 1995) with 3.4–3.8% of their body C lost via respiration. This fits broadly with measured ingestion rates of 10–11% (Atkinson et al., 1996a). The larger *R. gigas* seems to be a less active, efficient species, with corresponding energy budget terms perhaps one-third to one-half of those above.

A change in the view of SO copepods in the last 20 years has followed an increase in the use of fine-mesh nets and in experimentation. Small copepods, such as *O. similis*, *Ctenocalanus citer* and *Microcalanus pygmaeus*, were realised to be both highly abundant and important in energy flow (Schnack et al., 1985; Schnack-Schiel and Mizdalski, 1994; Atkinson, 1996; Atkinson, 1998; Dubischar et al., 2002; Ward and Hirst, 2007). Their life cycles and distributions do not follow the pattern of the biomass dominants (Metz, 1996) and their role in the food web is still being discovered. *Oithona similis* can exploit protozoans and detrital food colonised by bacteria as well as large diatoms (Lonsdale et al., 2000; Atkinson, 1996; Pond and Ward, 2011). Its feeding, growth and thus production may therefore be less seasonal than those of more herbivorous species (Fransz and Gonzalez, 1995). *Ctenocalanus citer* has been proposed to exploit sea-ice and thus feed throughout the dark season (Pasternak and Schnack-Schiel, 2007). The ice-specialist copepods *Stephos longipes* and *Paralabidocera antarctica* have had their life cycles documented (Schnack-Schiel et al., 1995; Tanimura et al., 1996) but the extent to which *C. propinquus* and smaller copepods interact with sea-ice is still unclear.

Nauplii and early copepodite (larval) stages are often hard to identify and experiment on, so most rate process work has focussed on CV and adult stages, as well as on the larger species. Because small organisms have higher feeding, respiration and growth rates on a mass-specific basis, simple scaling-up of the energy budget terms outlined above, to the whole copepod assemblage will lead to underestimates. For this reason, allometric

considerations, as well as appropriate sampling gear, are needed to estimate the total contribution of the copepod group (see 'Energy flows through zooplankton' section).

Euphausiids

Euphausiids (often given the generic name 'krill') are particularly important in the more productive SO systems (e.g. Hunt et al., 2011; Brinton, 1985; Parker et al., 2011). Because their postlarvae are larger than adult copepods, this group can provide a more direct link from primary production to vertebrates. Six species of euphausiid are numerous south of the Antarctic Polar Front (APF), all with circumpolar distributions and broadly overlapping ranges (Dilwyn-John, 1936; Baker, 1954; Gibbons et al., 1999). The largest, *E. superba* (often called 'Antarctic krill' or simply 'krill') has the largest total biomass of this group and is a key Antarctic species, supporting a commercial fishery and a high biomass of specialist predators, including baleen whales, seals, penguins, flying seabirds and fish.

Smaller krill species, such as *E. frigida*, *Thysanoessa macrura*, *T. vicina* and *E. triacantha* are widespread and more evenly distributed than the swarming species *E. superba* (Nishikawa et al., 2009). *Euphausia crystallorophias* differs in having a neritic-based distribution, mainly around the Antarctic continent where it is an important component of the high-latitude shelf ecosystem (Pakhomov and Perissinotto, 1996a; Pakhomov et al., 1998).

Most euphausiids have been found in greater abundance where temperature discontinuities arise, primarily at frontal zones of major water mass boundaries. Thus, *E. frigida*, *T. macrura* and *E. superba* have all been recorded as being more abundant at the Weddell-Scotia confluence frontal zone, and *E. triacantha* in the region of the APF, than further north or south. Such areas are thought to be of great significance for euphausiid recruitment (Brinton, 1985). *Euphausia superba* is unusual compared to the other species in having a distribution centred in the productive Atlantic sector (0–90°W; Marr, 1962), which holds ~75% of the total stock (Atkinson et al., 2008).

Despite the importance of *E. superba*, only the broadest features of its diet are known, and opinions have changed over how carnivorously it feeds.

First it was simply classed as a herbivore (Marr, 1962) but later studies increasingly emphasised the role of zooplankton, protozoans and marine snow in its diet (e.g. Price et al., 1988; Marchant et al., 1996; Perissinotto et al., 1997; Atkinson and Snýder, 1997). This generated the hypothesis that the species ‘switched’ to copepods when phytoplankton food was in short supply (Atkinson et al., 1999), for example in winter (Huntley et al., 1994a). However, subsequent quantitative volumetric gut content analyses, while upholding the role of protozoans as alternative food items, have found that copepods form only about 7% of the diet volume of post-larvae averaged across a range of habitats throughout the year (Schmidt et al., 2006, 2011, 2012). This copepod ingestion coincided with feeding on benthically derived foods, such as phytodetritus and associated bacteria and benthic diatoms, and so they were possibly predated on during vertical migrations (Schmidt et al., 2011). However, studies contrast during the autumn/winter period of low food, with some suggesting extensive omnivory of post-larvae (Atkinson et al., 2002; Huntley et al., 1994a) or larvae (Wickham and Berninger, 2007; Meyer et al., 2009). Others emphasise greatly reduced food intake of post-larvae (Quetin and Ross, 1991; Meyer et al., 2010) and use of large seasonal lipid stores (Hagen et al., 2001).

The larvae and post-larvae of *E. triacantha*, *Thysanoessa* spp. and *E. frigida* are not ice-associated, as compared with the larvae and often the juveniles of *E. superba* (Flores et al., 2011). These smaller euphausiids are also more omnivorous than *E. superba*, based on stable isotope studies (Schmidt et al., 2003, 2004; Stowasser et al., 2012). This result is also consistent with a series of comparative gut contents studies showing that metazoans often comprise >40% of *Thysanoessa* spp. diet (see Hopkins and Torres, 1989).

Most SO euphausiids are long-lived, with *E. superba* having a life span of 5–7 years (Siegel, 1987). Two years has been suggested for *E. frigida* (Brinton, 1985; Siegel, 1987; Ward et al., 1990), up to 3 years for *E. triacantha* (Baker, 1959; Siegel, 1987), and up to 4–5 years for *E. crystallorophias* (Pakhomov and Perissinotto, 1996a). Most growth rate data have been assembled for *E. superba*, which grows at roughly 0.1 mm per day during the spring/summer, equivalent to an increase of roughly 1% of its body mass per day (Atkinson et

al., 2006; Kawaguchi et al., 2006; Atkinson et al., 2009). This would be consistent with a mean daily ration of roughly 5% (Pakhomov et al., 1997a) and a maximum of perhaps ~13% (Perissinotto et al., 1997).

Salps

Salps are tunicates, a group of large macroplankton organisms, often termed ‘gelatinous’ due to their mainly transparent bodies, but which are actually formed of tunicin. Two species prevail in Antarctica: *Salpa thompsoni* and *Ihlea racovitzai*, the former being more numerous. Both have broad circumpolar distributions (Foxton, 1966; Foxton, 1971; Atkinson et al., 2004; Casareto and Nemoto, 1987), with *I. racovitzai* characteristic of higher latitudes.

Salp life cycles are complex, involving an alternation of generations between a solitary sexual form and an aggregate (chaining) form that grows by budding asexually (Foxton, 1966). Chains of the latter may reach over 1 m in length and contain several hundred individuals. This contributes to explosive population growth and regionally dense salp concentrations in some years. These ‘salp blooms’ have the potential to remove a large amount of the phytoplankton and possibly out-compete other grazers (Loeb et al., 1997; Dubischar and Bathmann, 1997; Pakhomov et al., 2002a).

Contrary to its impression of a rather helpless jelly floating in the currents, a salp can swim sufficiently well to perform diel vertical migrations (DVMs) of >500 m each way per night (Perissinotto and Pakhomov, 1998a, 1998b; Nishikawa and Tsuda, 1991; Gili et al., 2006), as well as a seasonal vertical migration cycle akin to that of biomass-dominant copepods (Foxton, 1966). However, unlike diapausing copepods, a recent study in the Lazarev Sea reported feeding year-round, albeit with gut pigment concentrations proportional to surface chl *a* concentrations (von Harbou et al., 2011).

In common with appendicularians, salps appear to be ‘efficient’ species, with low energetic costs and an effective mechanism for feeding unselectively at low food concentrations. This is done by pumping water through an internal net filter, which achieves a very high ingestion rate (Pakhomov et al., 2002a, 2006; von-Harbou et al., 2011),

potentially removing a large percentage of the algal stock. The sinking rates of the salp faecal pellets (Pakhomov et al., 2006; Phillips et al., 2009) are generally faster than those of *E. superba*, and both groups have been assigned significant roles in vertical biogeochemical fluxes (Fortier et al., 1994; Dubischar and Bathmann, 1997; Pakhomov et al., 2002a; Schmidt et al., 2011; Atkinson et al., 2012).

The undoubted regional importance of salps in the food web has led to an increase in studies of their distribution and biology in the last few decades (Chiba et al., 1998; Perissinotto and Pakhomov, 1998a, 1998b; Pakhomov et al., 2011). A series of ‘salp years’ has been described in recent decades (e.g. Chiba et al., 1998; Huntley et al., 1989; Nishikawa et al., 1995; Ward et al., 2012) coinciding with an increase in their abundance in high Antarctic latitudes last century (Loeb et al., 1997; Pakhomov et al., 2002a; Atkinson et al., 2004).

Studies are slowly starting to determine how salps fit into the food web. Rather than being an ‘ecological dead end’ with few predators, Pakhomov et al. (2002a) showed that a variety of species (mainly across amphipods, midwater fish and seabirds) feed on salps. Almost certainly the dietary role of such soft-bodied items has been under-represented due to the much greater ease in identifying crustaceans in predator diets. Other studies (Huntley et al., 1989; Donnelley et al., 1994; Dubischar et al., 2006, 2011) have examined the biometry and elemental composition of salps, and these, coupled to growing datasets for example on feeding rate in relation to body size, has led to a much better appreciation of salp biology.

Themisto gaudichaudii

This predatory amphipod is an important macroplankton of low Antarctic latitudes (Mackintosh, 1934, 1937; Labat et al., 2005; Mackey et al., 2012). It is especially numerous over productive shelves surrounding islands in the Antarctic Zone/Polar Frontal Zones such as South Georgia and Marion, Heard and Kerguelen Islands, where it can remove a significant fraction of zooplankton production (Pakhomov and Perissinotto, 1996b; Froneman et al., 2000b). In turn, its large maximum size of over 25 mm makes it important prey for some myctophid (Shreeve et al., 2009) and flying seabird species (Ridoux, 1994; Croxall et al., 1999; Bocher et

al., 2001). In years of low *E. superba* availability at South Georgia, they can act as an alternative prey for macaroni penguins (Waluda et al., 2010).

Themisto gaudichaudii is a highly adapted predator, with large compound eyes and grasping mouthparts. They occur in dense swarms in surface waters and appear to feed opportunistically on whatever zooplankton is available. Their average daily C rations are ~6–7%, similar to those of krill (Pakhomov and Perissinotto, 1996b), making *T. gaudichaudii* one of the main predators of copepods in the productive island ecosystems where they are abundant. Interestingly, stable isotopic analyses place adults of this species at a similar level to mainly herbivorous copepods (Wada et al., 1987; Gurney et al., 2001; Stowasser et al., 2012). This is clearly not true and is an example of the utility of using multiple feeding methods to arrive at consensus over diet (Schmidt et al., 2004, 2006).

The population dynamics, growth rates and energy budget of *T. gaudichaudii* are still not well known. Spawning is in spring/summer (Barnard, 1932; Kane, 1966; Labat et al., 2005; Watts and Tarling, 2012), perhaps allowing small juvenile stages to utilise food associated with the seasonal phytoplankton bloom. The number of generations per year appears flexible, being one at Kerguelen (Labat et al., 2002) and one to two (Watts and Tarling, 2012) at South Georgia. Growth rates are high (0.07–0.1 mm d⁻¹), commensurate with the substantial ingestion rate. This, combined with a biomass reaching 50 mg dry mass m⁻³ in the productive shelf waters of Kerguelen and South Georgia (Ward et al., 1995; Labat et al., 2005) mean an annual production of 3.6 mg C m⁻³ y⁻¹ estimated for South Georgia (Watts and Tarling, 2012).

Pteropods

Pteropods are gastropod molluscs with an entirely pelagic lifecycle. Broadly, SO pteropods fall into two orders (van der Spoel et al., 1999); the Thecosomata (shelled pteropods: *Limacina helicina antarctica*, *L. retroversa australis*, *Clio pyramidata* and *C. piatkowskii*) and Gymnosomata (naked pteropods *Clione limacina antarctica* and *Spongiobranchaea australis*).

The role of pteropods in SO ecosystems has been emphasised by recent predictions that, due to acidification resulting from a business-as-usual

approach to CO₂ emissions (IS92a), SO surface waters may begin to become uninhabitable for aragonite shelled thecosome pteropods by 2050 (Orr et al., 2005). However, it must be stressed here that, despite some suggestions to the contrary within the ocean acidification literature, pteropods account for far lower biomass and energy flow than SO copepods, euphausiids or salps.

A recent review of SO pteropods (Hunt et al., 2008) provides a more comprehensive appraisal of the taxonomy, ecology and role of SO pteropods, concluding that they are, on occasion, significant components of some of its sub-systems. The two *Limacina* species are most abundant, with autumn densities of *L. retroversa australis* of 60 ind. m⁻³, ~11% of total mesozooplankton densities at the sub-Antarctic Prince Edward Islands. South of the APF, *L. helicina antarctica* predominates, reaching ~20% of abundance and ~11% of mesozooplankton biomass at South Georgia (Atkinson et al., 1996a; Pakhomov et al., 1997b) and up to 63% of total mesozooplankton abundance at a coastal site in the Ross Sea (Foster, 1989; Knox et al., 1996). Macrozooplanktonic pteropods comprise mainly *Clio* species, adult *L. helicina antarctica* and *Clione antarctica*. Combined pteropods contributed <5% to total zooplankton in the Lazarev Sea, but 15% (max = 93%) to macrozooplankton in the East Antarctic (Hunt et al., 2008).

Trophically, gymnosomes are specialist predators on thecosomes, while thecosomes are considered predominantly herbivorous, capturing food with a mucous web. The ingestion rates of *L. r. australis* are high (Bernard and Froneman, 2005; Bernard, 2006), and those of *L. h. antarctica* and *C. pyramidata* can account for >40% of community grazing impact (Pakhomov and Froneman, 2004b). Carnivory occurs in thecosomes, appearing to increase with the size of the specimen, and may play a role in winter survival. As well as being major consumers of phytoplankton when they are abundant, they can also be important in the diet of carnivorous zooplankton, benthic invertebrates and fish (Hunt et al., 2008).

Life histories of SO pteropods are limited to a single study for *L. r. australis* (Bernard, 2006) making population studies a priority area for future research on this group. Pteropods play a significant role in biogeochemical cycling, through the production of fast sinking faecal pellets and mucous

flocs, and rapid sinking of dead animals ballasted by their aragonite shells (Howard et al., 2011).

Appendicularians

Appendicularians, also known as larvaceans, are planktonic tunicates that are widespread in the world oceans. Their body is divided into a trunk (usually <3mm long) and a muscular tail that is several times longer than the trunk. They are filter feeders, using a secreted mucous structure known as a 'house' to extract particles from the water. The house completely encloses the animal, and water is pumped through it by the tail. Appendicularians have high grazing rates (e.g. Deibel, 1988, 1998) and are able to retain particles of <0.2 µm. This fraction includes pico- and nanoplankton, bacteria and colloidal dissolved organic carbon (DOC) so they are capable of partially bypassing the microbial food chain (e.g. Deibel and Powell, 1987; Bedo et al., 1993).

Appendicularians are inconsistently reported in the Antarctic literature, probably due partly to net mesh selectivity and under-counting of their fragmented remains by inexperienced analysts. However, densities over 300 ind. m⁻³ have been reported in the seasonal ice zone of East Antarctica (Hunt and Hosie, 2006a; Tsujimoto et al., 2007).

Appendicularian growth rates are very high and strongly related to temperature (e.g. Deibel, 1998; Hopcroft et al., 1998a; Sato et al., 2001). Further, their houses are discarded and renewed regularly (Fenaux, 1985). As some of the filtered particles remain trapped in the discarded house (Alldredge, 1976; Bedo et al., 1993) they contribute to marine snow and carbon export (e.g. Fortier et al., 1994). Appendicularians can also be important in the diet of pelagic animals, including copepods, chaetognaths, medusae, ctenophores, and larval and adult fish (e.g. Alldredge and Madin, 1982; Ohtsuka and Onbé, 1989; Fortier et al., 1994). This plankton group, like pteropods, may therefore have a regionally significant role in the SO.

Carnivorous macroplankton

The diverse macroplankton comprise, in addition to euphausiids, salps, amphipods and large pteropods, an array of other, mainly carnivorous organisms, including siphonophores, mudusae, polychaetes and chaetognaths. Fish larvae are

also important inshore predators (North and Ward, 1990). These macroplankters are diverse but comprise some important taxa such as chaetognaths and siphonophores (Pakhomov et al., 1999; Hunt et al., 2011). The pioneering studies on these were done during the *Discovery Expeditions* (David, 1955) and since then several studies on their biology have appeared (e.g. Hagen, 1985; Pakhomov et al., 1999; Froneman et al., 1998, 2002; Kruse et al., 2010a, 2010b).

Estimating zooplankton abundance and biomass

Nets are still the most commonly used zooplankton sampler, but no single net type or mesh size is suitable to capture the full size spectrum of metazoan plankton (Fraser, 1968; Voronina et al., 1994). Voronina et al. (1994) concluded that only a combination of water bottles, plankton nets and trawls are able to cover the entire metazoan plankton community. The factors influencing net performance include avoidance behaviour, clogging of meshes by particulates and mesh selectivity (i.e. escape of animals through the meshes).

Net mesh selectivity

A mesh size of 75% of the width of the smallest animal retains ~95% of individuals of that width (Vannucci, 1968; Nichols and Thompson, 1991). Gallienne and Robins (2001) estimated the percentage retention of abundance, biomass and production of Atlantic plankton according to mesh size, using equation (4) of Nichols and Thompson (1991). From their data (Figure 2a) 50 μm mesh nets are clearly needed to retain the entire metazoan assemblage. In Figure 2(b), SO abundance data have been added and it was found that the basic trend is similar. Overall, a standard WP-2 net equipped with a 200 μm net (UNESCO, 1968; Sameoto et al., 2000) retains ~10% of mesozooplankton abundance, ~70% of total biomass and may miss ~50% of total production (see also Hopcroft et al., 1998b).

Macroplankton trawls such as the RMT8 also suffer from net mesh selectivity (Beaumont and Hosie, 1997). For example, Siegel (1986) compared krill abundances/length frequencies from 4.5 mm mesh RMT8 and 330 μm mesh RMT1 towed just above it. The RMT8 retained 63% of *E. superba* of 20 mm length, with 100% efficiency only achieved

when the krill were ≥ 25 mm. The same would clearly apply to small macroplankton that can also avoid small mesozooplankton nets. So even though small euphausiids might be counted 'twice' in meso- and macroplankton nets (Figure 1), they are underestimated by both methods.

Clogging of mesozooplankton nets will also influence net catches, by reducing the effective mesh aperture and thus the volume of water passing through it. Clogging is greater when using fine meshed nets and in productive waters. Clogging with dense phytoplankton can make sorting of samples difficult and make it virtually impossible to obtain accurate estimations of phytoplankton or zooplankton biomass.

Net avoidance

For larger macroplankton and especially *E. superba*, net avoidance is a problem. This is particularly serious with nets of small diameter that are towed slowly, such as vertical hauls with Bongo or ring nets. Based on samples collected from the upper 20 m of the water column with a vertically hauled 0.45 m diameter NORPAC net and a CPR (mouth size of 12.7 \times 12.7 mm), Hunt and Hosie (2003) showed that the CPR undersampled large fast moving crustaceans during the day relative to the NORPAC net.

Variable resolution of abundant larval stages

Depending on the requirements and expertise of the analyst, the degree of identification of early larval stages varies greatly. Reports of zooplankton in the literature or in databases might include numerical densities (no. ind. m^{-2}) but often without indicating which larval stages these include. This problem is especially serious when attempting to interpret 'mined' or retrieved data from global databases, old reports or sampling sheets. It could make comparisons between workers almost meaningless unless both the sampling method and the level of taxonomic resolution were very specifically defined.

Zooplankton, numbers, biomass and converting between them

There is current interest in large-scale or circumpolar meta analyses (e.g. www.iced.ac.uk)

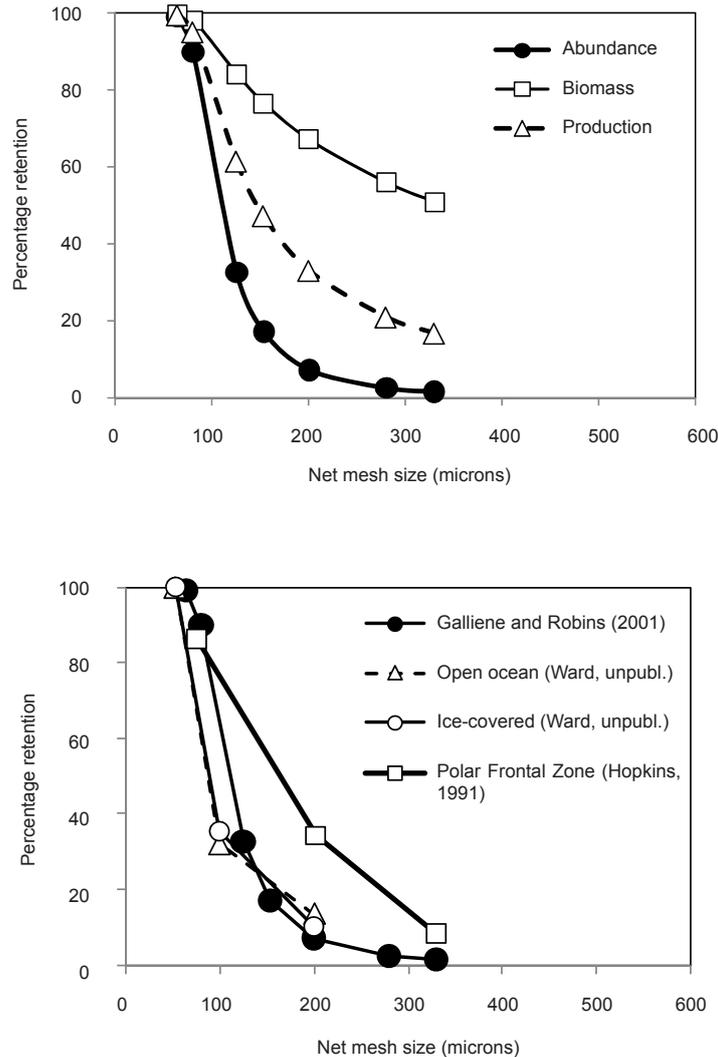


Figure 2: (a) Data taken from Gallienne and Robins (2001) to show estimated percentage retention of zooplankton abundance, biomass and production across a range of net mesh sizes. These data are from the Atlantic (50°N to 50°S). (b) Abundance data taken from Figure 2(a) with the addition of Antarctic data from 200, 100 and 53 μm nets in a south–north transect across the Scotia Sea (Ward et al., 2012). Data from Hopkins (1971) were obtained using nets of 330, 202 and 76 μm in the Polar Frontal Zone.

which often requires the merging of dispersed datasets collected with different methods. This requires care since conversion factors, sometimes even obtained outside the SO, may need to be used. A more general overview on biomass conversion factors is presented in Postel et al. (2000), with a summary of conversions for modellers provided by Frangoulis et al. (2010).

A variety of methods have been used to estimate zooplankton biomass (Table 1). Early workers often used simple displacement volumes, wet masses or settled volumes. However, these could

lead to an imprecise estimate of the energy content of that biomass because of the different proportions of water, for example between jellies and crustaceans. Therefore, dry masses have been derived more frequently, being nowadays the most frequent currency of mesozooplankton biomass. Wet masses are however more commonly used for *E. superba* biomass, especially from acoustic methods.

Table 2 shows some of the diversity of SO-specific conversions. Care is needed in using externally derived conversion factors because polar zooplankton are not comparable to ‘global’ zooplankton

Table 1: Some examples of the methods used to determine zooplankton biomass in the Southern Ocean. Numerous variants to the ones shown exist.

Unit	Author	Method used
Volume	Foxton (1956)	Measurement of formalin-preserved catches in settling chamber, having excluded large, rare organisms
	Labat et al. (2002)	Volume determined by optical plankton counter and compared with direct dry-mass determinations from nets in the same study
Wet mass	Fukuchi et al. (1985)	Direct wet-mass determinations of fresh aliquots of samples
	El Sayed and Taguchi (1981)	Direct wet-mass determinations of fresh aliquots of samples
	Ashjian et al. (2004)	Silhouette photography, converted to wet mass using non-regional-specific regressions and compared with displacement volume from the same sample set, also converted to wet mass
Dry mass	Alcaraz et al. (1998)	Direct weighing of whole dried sample aliquot from frozen material
	Froneman et al. (1997)	Direct weighing of whole dried sample aliquot from formalin-preserved material, no correction for tissue loss due to formalin preservation
	Sertorio et al. (2000)	Direct weighing of whole dried sample aliquot from frozen material, values increased by 30% to allow for tissue loss due to formalin preservation
	Ward and Shreeve (1999)	Direct weighing of selected groups, plus length-mass regressions for remaining (often smaller) zooplankton derived for same geographic region.
	Hopkins (1987)	Use purely of length mass regressions derived from the same geographic region
Ash-free dry mass	Franz and Gonzalez (1997)	Measurement on whole frozen aliquots
Carbon mass	Cabal et al. (2002)	Direct CHN analysis of frozen catch aliquots

due to their increased but highly seasonal degree of lipid storage (Hagen and Schnack-Schiel, 1996; Hagen et al., 2001). This leads to radically differing body compositions throughout the year. Storage lipids do not contain N and are C rich, being built up among the biomass-dominant large copepods as a storage depot for winter. This means a dramatic change in lipid content, from ~10% of dry mass at the end of winter to ~50% at the end of summer (Hagen and Schnack-Schiel, 1996; Hagen et al., 2001), and has a large influence on the C content of an equivalent mass of zooplankton.

Zooplankton distribution

Data sources

A large amount of data on SO zooplankton either precede, or are not captured by *Web of Knowledge* searches, so this section, together with the bibliography and appendices, provides some clues to data sources. The *Discovery Investigations* in the 1920s

and 1930s laid the groundwork for understanding of SO zooplankton distributions. They confirmed the circumpolar distributions of most species (Baker, 1954), defined the broad zonations and seasonal distributions of species assemblages (Mackintosh, 1934, 1937) and then focused on the life cycles and distributions of major species. These included copepods (Andrews, 1966; Ommanney, 1936), salps (Foxton, 1956), chaetognaths (David, 1955), amphipods (Kane, 1966) and euphausiids (Baker, 1959; Marr, 1962).

Subsequently, Soviet and Japanese investigations continued these large-scale surveys, often outside the Atlantic sector. These provide valuable documentation of large-scale distributions (e.g. Voronina and Naumov, 1968; Chiba et al., 2001) and further comparative work on the life cycles of the biomass-dominant copepod species: *C. acutus*, *R. gigas*, *C. propinquus* and *C. simillimus* (Voronina, 1970, 1972). Unfortunately some of these datasets are inaccessible and have not yet had

Table 2: Examples of inter-conversion factors between total body length (BL, mm), dry mass (DM, mg), wet (fresh) mass (WM, mg) and Carbon mass (CM, mg) derived specifically for Southern Ocean taxa. Note that this list is not exhaustive and original publications should be consulted for further details, provisos and information. The values here are reflective of the time of capture and may not represent a seasonal mean value. For information on seasonal change in *Euphausia superba* see Siegel (1992) and large copepod composition see Hagen and Schnack-Schiel (1996). Some of these references also report proximate N- and energy-based composition.

Units	Factor used	Taxon	Notes	Reference
BL:DM	$DM = 0.0026e^{1.3608BL}$	Copepods	Early copepodites	Mizdalski (1988)
	$DM = 0.0822e^{0.4079BL}$	Copepods	Late stage copepodites/adults	Mizdalski (1988)
	$DM = 0.002BL^{2.804}$	Amphipods	<i>Themisto gaudichaudii</i> in summer	Pakhomov and Perissinotto (1996b)
	$DM = 0.04BL^{2.39}$	<i>Euphausiids</i>	Euphausiid larvae	Siegel (1987)
	$DM = 6.45785 \times 10^{-5}L^{3.89}$	<i>E. superba</i>	Post-larvae (mixed sex/maturity stage in summer)	Atkinson et al. (2006)
	$DM = 0.0598BL^{2.204}$	<i>Salpa thompsoni</i>	Length is oral-atrial length	Huntley et al. (1989)
BL:WM	$WW = 3.85 \times 10^{-3}L^{3.20}$	<i>E. superba</i>	Overall summer value for all sex/maturity stages	Morris et al. (1988)
WM:DM	WM = 8DM	mesozooplankton	Copepod dominated assemblage	Hagen (1988)
	WM = 5DM	zooplankton	Euphausiid-dominated assemblage	Hagen (1988)
	WM = 6.25DM	mesozooplankton	This conversion used in Rujakov (1996)	Vinogradov and Shuskina (1985)
	WM = 4.23(DM-0.004)	<i>E. superba</i>	Overall summer value for all sex/maturity stages	Morris et al. (1988)
	WM = 6.15DM	Large copepods	Mean for 3 species derived from this reference	Mizdalski (1988)
	WM = 15.9DM	<i>Salpa thompsoni</i>	Average of summer, autumn and winter	Dubischar et al. (2011)
	WM = 23.7(DM-0.113)	<i>Salpa thompsoni</i>	Summer/autumn data	Huntley et al. (1989)
CM:DM	CM = 0.44DM	Copepods	Mean of two large species	Ikeda and Mitchel (1982)
	CM = 0.44DM	Copepods	Spring/summer average	Schnack (1985)
	CM = 0.27DM	Chaetognaths	Autumn/winter average	Donnelly et al. (1994)
	CM = 0.50DM	<i>E. superba</i>	Mixed sexes/stages	Färber-Lorda et al. (2009)
	CM = 0.42DM	<i>E. superba</i>	Mixed sexes/stages	Atkinson et al. (2012)
	CM = 0.15DM	<i>Salpa thompsoni</i>	Summer/autumn/winter average	Dubischar et al. (2011)
	CM = 0.0369DM + 0.0655	<i>Salpa thompsoni</i>	Summer/autumn data	Huntley et al. (1989)
	CM = 0.074DM	Salps	Autumn/winter average	Donnelly et al. (1994)

the impact that they deserve. A variety of efforts are currently under way to retrieve these data and make them more widely accessible.

In the last few decades, national sampling programs have become more regional, often focusing on sectors of national interest or near national bases. This has led to rapid advances in the understanding of specific systems (e.g. reviews by Hosie, 1994; Schnack-Schiel and Mujica, 1994; Ducklow et al., 2007; Atkinson et al., 2001; Murphy et al., 2007; Pakhomov and Froneman, 1999a). However, it has also led to some over-generalisation, particularly in the krill literature. Recent initiatives have attempted to broaden the geographical extent of sampling, for example the BROKE and BROKE-WEST studies (Hosie et al., 2000; Swadling et al., 2010) or the SO-CPR Survey (Hosie et al., 2003; McLeod et al., 2010; Pinkerton et al., 2010a). An alternative approach is the meta-analysis of compiled historical data (e.g. Rudjakov, 1996; Atkinson et al., 2004, 2008) or circumpolar syntheses using satellite data (e.g. Constable et al., 2003; Grant et al., 2006).

Most SO zooplankton abundance and biomass data are not in any central database, but reside within the individual publications, logsheets or electronic databases of the individual institutes. However, some global- and SO-scale initiatives are starting to 'mine' or compile data from multiple sources. Examples are www.scarmarbin.be, www.nodc.noaa.gov, www.st.nmfs.noaa.gov/plankton, www.iced.ac.uk/science/krillbase.htm. The SO-CPR Survey provides a database of approximately 30 000 CPR samples for about 240 taxa over about 70% of the SO using a consistent methodology (McLeod et al., 2010, <http://data.aad.gov.au/aadc/cpr/>). Using data taken from any such central database needs great care to ensure that any regional and temporal differences reflect real variability rather than differences in method or time of year of sampling.

Large-scale distribution

Appendices 1 and 2 include studies across a variety of regions and productivity regimes. These specific studies support the main trends in biomass and abundance revealed by larger-scale surveys. Thus most species have circumpolar distributions and total biomass is surprisingly similar between sectors (Foxton, 1956) in contrast to *E. superba*. The main trends are latitudinal, with an increase

in diversity, abundance and biomass from high latitudes towards the APF area, where total abundances and biomasses are often maximal (Foxton, 1956; Rudjakov, 1996; Fransz and Gonzalez, 1997; Atkinson and Sinclair, 2000; Pakhomov and McQuaid, 1996; Pakhomov et al., 2000; Woodd-Walker et al., 2002; Pollard et al., 2002). This trend is strongest in the small species such as *O. similis* (Atkinson, 1998; Pinkerton et al., 2010a).

These large-scale latitudinal distributions of zooplankton have often been related to water temperature (Hosie, 1994; Chiba et al., 2001; Ward et al., 2012; Mackey et al., 2012). The various species thus have a series of broad, albeit overlapping biogeographic distributions. However, the APF does not appear to mark a strong biogeographic separation between 'sub-Antarctic' and 'Antarctic' assemblages (Pakhomov et al., 2000; Atkinson and Sinclair, 2000; Froneman et al., 2000a; Hunt and Hosie, 2005, 2006a, 2006b). Within the Antarctic Zone of the SO, a biogeographic transition lies roughly at the latitudes of Southern Antarctic Circumpolar Current Front (SACCF) and the northernmost limit of influence by sea-ice (Grant et al., 2006; Ward et al., 2012).

Within this broad pattern, certain iron-fertilised areas have unusually high biomass. These include the low latitude, broad island shelves of South Georgia (Ward et al., 1995; Atkinson et al., 1996a, 2001) and the Kerguelen archipelago/plateau (Razouls et al., 1998; Carlotti et al., 2008). By contrast, smaller volcanic seamounts such as Crozet, Marion and Prince Edward Islands have elevated phytoplankton concentrations, but very little shelf area and a more flow-through system (Perissinotto, 1989; Pollard et al., 2007). While this may not allow time for zooplankton biomass to build up, it provides a 'life support system' for the island-based predators (Froneman and Pakhomov, 1998; Pakhomov and Froneman, 1999a; Perissinotto and McQuaid, 1992).

In contrast to South Georgia and Kerguelen, low mesozooplankton biomass is the rule near some well-studied productive shelves to the south. Good examples are the Antarctic Peninsula (Mackintosh, 1937; Hernández-Léon et al., 2000; Ward et al., 2004) and parts of the Ross Sea (Foster, 1987; Biggs, 1982). The low biomass in these highly

productive, retentive regions is surprising and the reasons remain unclear (Tagliabue and Arrigo, 2003).

Seasonal reproductive cycles of mesozooplankton

With the exception of inshore waters (e.g. Chojnacki and Wegleńska, 1984; Fukuchi et al., 1985; Razouls et al., 1998), seasonal time series are sparse in the SO. Authors have instead compiled data from multiple cruises at different times of year, albeit in different years (e.g. Schnack-Schiel and Hagen, 1995; Hagen and Schnack-Schiel, 1996; Fransz and Gonzalez, 1995; Atkinson et al., 1997; Ward et al., 1997). These have shown that reproduction coincides roughly with the spring/summer bloom. Given the high mortality of larvae, this produces a sharp summer increase in total zooplankton abundance (Atkinson, 1991; Hunt and Hosie, 2006a, 2006b), with abundances often increasing ~10-fold. Not all species reproduce so synchronously; *O. similis* reproduces year-round, leading to only a three-fold seasonal difference in its abundance (Fransz and Gonzalez, 1995; Metz, 1996).

Given the large summer increase in mesozooplankton abundance, perhaps surprisingly their total biomass changes little throughout the year. Winter biomass within the top 1 000 m layer is ~80% of that in summer (Foxton, 1956; Hopkins, 1971; Atkinson and Peck, 1988). This reflects the life cycle of the biomass-dominant copepods. Their overwintered copepodites are much larger than the growing summer larvae, so larger individual size in winter compensates for greatly reduced abundance.

Seasonal vertical migration

Several of the biomass-dominant zooplankton, including the large copepods, chaetognaths and salps, undergo a seasonal vertical migration. In autumn the population descends from the top 200 m layer to overwinter at depth, returning to surface layers in spring (Mackintosh, 1937; Foxton, 1956, 1966; Andrews, 1966; Marrari et al., 2011). Thus about 50% of the total (0–1 000 m) mesozooplankton biomass is above 250 m in the months November–March, decreasing to 20% in the mid-winter months of July–August (Figure 3a). The corresponding figures for the top 100 m layer, as proportions of the top 1 000 m layer in summer and winter are one-third and one-tenth respectively

(Figure 3b). This seasonal change (which differs in timing according to latitude (Figure 3)) must be allowed for when interpreting regional changes based on epipelagic net samples (Voronina, 1970; Ward et al., 2006a).

Diel vertical migration (DVM)

The DVM of zooplankton, generally towards the surface at night, is also found in the SO (e.g. Hardy and Gunther, 1935; Perissinotto and McQuaid, 1992; Atkinson et al., 1992a, 1992b; Ward et al., 1995). Some taxa show much stronger DVM than that of the biomass-dominants. These include the copepod family Metridiidae (Lopez and Huntley, 1995; Atkinson et al., 1996b), *E. superba* larvae (Marr, 1962), salps (Nishikawa and Tsuda, 1991) and *E. triacantha* (Piatkowski et al., 1994; Pakhomov, 1995). Adults of *E. superba* have also been found to regularly migrate right down to the seabed to feed, although whether this is a diel behaviour is still unclear (Schmidt et al., 2011).

Generally, nets that sample the top 200 m should encompass most of the diel ranges of mesozooplankton that dominate biomass (although not for some macrozooplankters such as *E. triacantha*, salps and *E. superba*). However, some of the population may be missed during shallower daytime hauls, due to a combination of DVM and daytime avoidance. The DVM cycle is often linked to a diel feeding cycle, which is important to monitor over a full diel cycle to estimate grazing impact.

Decadal and longer-term changes in abundance

Several standardised SO monitoring surveys in the Atlantic sector are now ~20 years in length, enabling decadal and sub-decadal trends in zooplankton, including *E. superba*, to be determined (Ross et al., 2008; Loeb et al., 2010; Murphy et al., 2007). Likewise, the broader-scale SO-CPR Survey commenced in January 1991 (Hosie et al., 2003) and has passed the 20-year milestone. The Japanese National Institute of Polar Research (NIPR) commenced a standardised monitoring program in 1972 south of Australia using the NORPAC net (Hosie, 2004; Takahashi et al., 2008) and like the CPR survey it still continues. Twenty years is slightly too short to gain convincing evidence for long-term trends or ‘regime shifts’, since such signals may be confused with decadal- or intra-decadal

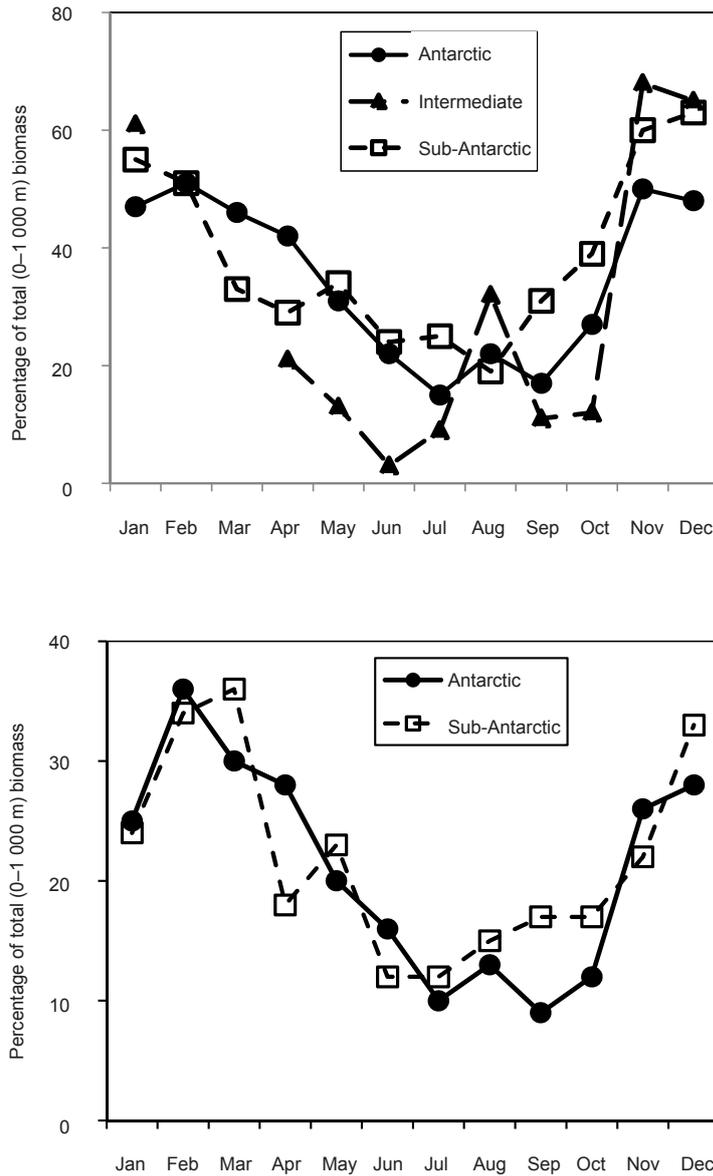


Figure 3: (a) Percentages of the total (0–1 000 m layer) mesozooplankton biomass located within the top 250 m layer. Foxton’s (1956) data (recalculated from his Table 3) are based on 2 185 samples from 366 circumpolar stations. Hopkins’ (1971) data are based on 375 samples from about 90 stations in the SE Pacific, extracted from his Figure 3. His designation of the intermediate zone comprises surface water temperatures of 2°–4°C. (b) Percentages of the total (0–1 000 m layer) mesozooplankton biomass located within the top 100 m layer, based on the data in Table 3 of Foxton (1956).

variability such as El-Niño-Southern Oscillation (ENSO) events (Loeb et al., 2010; Murphy et al., 2007).

For this reason there have been several attempts to splice datasets spanning longer periods of time to determine whether major changes have occurred since the *Discovery* sampling era of the 1920s and 1930s. Evidence for long-term changes in

copepods is equivocal (Kawamura, 1986; Ward et al., 2008). However, there is some evidence that salps have expanded into high latitudes of Antarctica (Pakhomov et al., 2002a; Atkinson et al., 2004) and that *E. superba* recruitment and numerical density decreased within the southwest Atlantic sector during the last two decades of last century (Loeb et al., 1997; Atkinson et al., 2004; Trivelpiece et al., 2011). Several factors may have caused this,

Table 3: Very simple and pragmatic division of krill and zooplankton into four functional groups. This division is based on biomass not numerical density, since biomass is far less sensitive to slight differences in sampler or regional and seasonal changes in sampling. The four groups are selected also because data on each are available from different surveys by various nations throughout Antarctica, allowing the construction of large datasets and meta-analyses. The grouping however very broadly preserves functional group attributes, so may be tractable as inputs to certain food-web modelling approaches.

Functional group	Composition	Composition and ecological function
Mesozooplankton	Biomass density from 200 μm Bongo or ring net-type nets, excluding post-larval <i>E. superba</i> and salps	Comprising mainly the biomass-dominant copepods and other mainly suspension-feeding taxa
Salps	Biomass density of salps	Filter-feeding taxon with unique biology, often enumerated separately in catches
<i>Euphausia superba</i> post-larvae	Biomass density of post-larvae of <i>E. superba</i>	Another species with unique biology, often enumerated from acoustics or surveys with large nets
Remaining macroplankton	Biomass density of remaining macroplankton (amphipods, chaetognaths, adults of small euphausiids, large pteropods, large predatory polychaetes, cnidarians plus the largest copepods such as <i>Euchaeta antarctica</i>)	Mainly carnivorous taxa retained on the 4 mm meshes typifying an RMT8 net

including a large-scale reduction in sea-ice in the middle decades of last century (de la Mare, 1997; Cotté and Guinet, 2007), a wide-scale increase in water temperature (Gille, 2002; Meredith and King, 2005; Whitehouse et al., 2008) and possible changes in higher or lower levels within the food web (Montes-Hugo et al., 2009).

The SO-CPR Survey has already identified two major changes in zooplankton composition in eastern Antarctic waters. The first was in the sea-ice zone (SIZ) around year 2000 when smaller zooplankton became more dominant instead of Antarctic krill (Hosie and Raymond, unpublished data). The second change occurred in 2004/05 north of the SIZ when pelagic foraminiferans exceeded 50%, and at times 80%, of the numerical abundance instead of the 8% long-term average, replacing *Oithona* as the dominant species (Takahashi et al., 2010a). Such changes in food size and type could have a major impact on the survival of higher predators.

Conclusions: compiling comparable zooplankton data

Because the abundance (no. m^{-2} or no. m^{-3}) of zooplankton yielded by nets is highly sensitive to the sampling and analysis method, and to the depth

and time of year of sampling, compilations of such data can be hard to interpret. The same also applies to biomass density (g dry mass m^{-2}), but the potential errors are not nearly as severe as for abundance comparisons (Figure 2a), and some major issues, such as the time of year of sampling (Figure 3), can even be broadly adjusted for.

The most widely used large sampler is the RMT8, making it one choice for regional-based comparisons of biomass of mesozooplankton. For mesozooplankton, the mostly commonly-used net is a ring net or Bongo, usually of diameter 0.5–0.75 m with around 200 μm mesh size. These are typically towed from 200 m to the surface, so this sampling method forms a pragmatic starting point for mesozooplankton comparisons. The SO-CPR Survey offers a very large dataset over much of the Southern Ocean using a consistent methodology. In Table 3, four important groups of meso- and macroplankton whose biomass density is routinely quantified by the variety of surveys around the SO are suggested. These could be described loosely as ‘functional groups’ and which could form the basis of some wider-scale zooplankton meta analyses or broad-scale modelling inputs.

Energy flows through zooplankton

Diet composition

Buitenhuis et al. (2006) incorporated mesozooplankton into a biogeochemical model of the world ocean, and found that a major requirement for improved models was better data on food selectivity. A key input to mass balance food-web models such as *Ecopath* is the percentage contribution (in units of mass or energy) of the various food items to the taxon's total food intake throughout the year, averaged across the area of the model (Cornejo-Donos and Antezana, 2008; Pinkerton et al., 2010b). Given the difficulty of year-round sampling, measuring diet and feeding rate and the fact that functional groups can contain multiple species and maturity stages, solid estimates hard to deliver, even for well-known species.

A good example of a careful seasonal comparative study on the complete pelagic food web is the work by Hopkins et al. (1993a, 1993b). He found profound seasonal and regional changes in diet, the fact that comparatively few species in the food web were mainly herbivorous, and that a complex network of trophic linkages exists (Hopkins, 1985b, 1987; Hopkins and Torres, 1989; Hopkins et al., 1993a, 1993b). These studies were based entirely on the numerical incidence of food items in the stomach rather than on a mass or volumetric basis, so would not be amenable as direct inputs to an *Ecopath* model, for example. As the authors stress, the results are susceptible to variable size, digestion speed and ease of identification of the food items.

The small body sizes of zooplankton, patchy distribution of predators and prey, and variable turbulence still hamper any approach to study diet and feeding rate (Table 4). Each provides different information: gut contents indicate what a zooplankton has just eaten, incubations show what it is willing to eat and at what rates, gut fluorescence quantifies the herbivorous component, while biomarkers indicate what it assimilated over the last weeks to months. No one approach is entirely satisfactory, but since they are independent, have their specific strengths and weaknesses, and integrate over different time periods, the most powerful approach is to use multiple methods (Båmstedt et al., 2000; Schmidt et al., 2006).

Table 5 compiles these different types of approaches for SO zooplankton. The main study

species are *E. superba* and copepods and the commonest methods are feeding incubations, gut contents analysis and the gut fluorescence technique. Molecular approaches are still in need of some development before they can provide quantitative analysis of relative ingestion rates across the dietary spectrum (Martin et al., 2006).

Impact on prey populations

The most common measurement of grazing impact has been the percentage of primary production removed per day by zooplankton groups (Table 6). Obtaining a solid estimate of this is difficult, and some of the studies have been excluded from Table 6 where key variables have not been measured, such as gut passage time, diel periodicity or primary production. Several issues may mean that metazoan grazing impact is underestimated in Table 6. First, most studies only encompass the organisms caught by 200 μm Bongo-type nets (the typical sampler used for these studies) and the important smaller fraction and the larger macrozooplankters (e.g. salps, *E. superba* and other euphausiids) are often under-represented. Second 'bottle effects' may lead to underestimates of grazing rates on phytoplankton from bottle incubations (Båmstedt et al., 2000; Nejstgaard et al., 2001) and conversely 'pigment destruction' yielding overestimates of phytoplankton ingestion where gut pigment destruction was erroneously corrected for (Durbin and Campbell, 2007).

Notwithstanding these issues, the general consensus from Table 6 is that mesozooplankton grazing generally removes <30% of primary production. Exceptions exist, for example when salps or *E. superba* are abundant (Dubischar and Bathmann, 1997; Pakhomov et al., 1997a; Perissinotto et al., 1997; Perissinotto and Pakhomov, 1998a). The generally low grazing impact of meso-macrozooplankton fits well with global literature compilation of mesozooplankton (mean 23% of primary production removed per day; Calbet, 2001). Calbet and Landry (2004) found that instead microzooplankton were the main grazers, based on a global literature compilation. This also held for polar waters, where on average they removed ~ 60–70% of primary production. In non-bloom conditions of the SO, copepods may instead act as a 'top predator' of protozoans (Atkinson, 1996), controlling their populations.

Table 4: The most commonly used methods to determine diet/feeding rate of Southern Ocean zooplankton.

Method	Aspect of feeding measured	Principle	Advantages	Disadvantages	Integration time
Feeding incubations	Diet and feeding rate	Confinement in grazing bottle Quantification of food removal rates	Allows direct calculation of feeding rates Shows what animals are capable of eating No incubation artefacts. Informs on size selectivity	Artefacts of confinement Hard to recreate realistic turbulence regimes and prey encounter rates Soft/rapidly digested items underrepresented Need separate throughput experiments to derive feeding rates (or use lit value)	Hours
Gut content analysis	Diet or feeding rates	Visual examination of food items in gut			Hours
Gut fluorescence analysis	Feeding rate	Using chl <i>a</i> derivatives to quantify ingestion rates of phytoplankton	Provides insights into in-situ variability in feeding	Only informs on herbivorous component of diet Uncertainties over several issues in this method	Hours
Faecal egestion rates	Egestion (and feeding rate)	Egestion rate of freshly-caught animal and converting to ingestion rate	Minimum of laboratory artefacts Direct measure of C output	Conversion to ingestion rate is very sensitive to assimilation efficiency value used Only practical for large macrozooplankters	Hours
Fatty acid biomarkers	Diet	Fatty acid signatures of foods are incorporated into consumer	Indicates assimilated food No incubation artefacts	Internal transformations hinder interpretations Signatures not always taxon-specific	Days to weeks
Stable isotope analysis	Trophic level	Heavier isotopes are enriched in consumer	Indicates assimilated food No incubation artefacts	Indicates trophic level not specific diet Variable food-web baseline and variable fractionation	Weeks to months

Table 5: Examples of diet and feeding rate papers addressing Antarctic zooplankton. *Euphausia superba* (both adults and larvae) are included in this table for completeness. The examples are sub-divided by species and by diet method. Note that the grazing studies which determine grazing impact on phytoplankton stocks (Table 5) are not included here, for clarity.

Method	Copepods	Small euphausiids	Salps	Amphipods	Chaetognaths	<i>Euphausia superba</i>	Multiple taxa
Feeding incubations	Metz and Schnack-Schiel, 1995					Ishii et al., 1985	Schnack, 1985
	Atkinson, 1994, 1995					Price et al., 1988	Granéli et al., 1993
	Atkinson and Shreeve 1995					Ross et al., 1998	Froneman et al., 1996
	Razouls et al., 1998					Meyer et al., 2003	
	Sarthou et al., 2008					Wickham and Berminger, 2007	
	Lonsdale et al., 2000						
	Voronina and Sukhanova, 1976				Froneman et al., 1998, 2002	Ligowski, 2000	Hopkins, 1985b
	Øresland and Ward, 1993				Øresland, 1990	Martin et al., 2006	Hopkins, 1987
	Pasternak, 1995				Øresland and Ward, 1993		Hopkins and Torres, 1989
	Pasternak and Schnack-Schiel, 2001						Hopkins et al., 1993a, 1993b
Gut fluorescence	Atkinson et al., 1992a, 1992b, 1996b						Pakhomov et al., 1997b
	Lopez and Huntley, 1995					Daly, 1998	Pakhomov et al., 1997b
	Drits et al., 1993					Pakhomov et al., 2004	Bradford-Grieve et al., 1998
	Mayzaud et al., 2002a, 2002b						Froneman et al., 2000a
	Huntley and Escritor, 1992						Pakhomov et al., 2002b
							Pakhomov and Froneman, 2004b

(continued)

Table 5 (continued)

Method	Copepods	Small euphausiids	Salps	Amphipods	Chaetognaths	<i>Euphausia superba</i>	Multiple taxa
Faecal egestion rates	Calbet and Irigoien, 1997					Clarke et al., 1988 Pond et al., 1995 Nordhausen and Huntley, 1990 Pakhomov et al., 1997a Atkinson et al., 2012	
Fatty acid biomarkers	Graeve et al., 1994 Pond and Ward, 2011	Nicol et al., 2004 Stübing and Hagen, 2003				Virtue et al., 1993 Cripps et al., 1999 Stübing et al., 2003 Pond et al., 2005 Schmidt et al., 2004	Phleger et al., 1998 Ju and Harvey, 2004
Stable isotopes							Wada et al., 1987 Rau et al., 1991 Stowasser et al., 2012 Cherel et al., 2010
Multiple methods	Zeldis et al., 2002 Urban-Rich et al., 2001 Atkinson, 1996 Atkinson et al., 1996a	Gurney et al., 2001, 2002 Pakhomov et al., 1998 Pakhomov and Perissinotto, 1996a	Pakhomov et al., 2002a Pakhomov et al., 2006 Von Harbou et al., 2011	Pakhomov and Perissinotto, 1996b Froneman et al., 2000b	Kruse et al., 2010b	Perissinotto et al., 1997 Atkinson and Snyder, 1997 Atkinson et al., 2002 Meyer et al., 2002 Schmidt et al., 2006, 2011 Huntley et al., 1994a	Perissinotto, 1992 Dubischar and Bathmann, 1997 Zeldis, 2001 Schmidt et al., 2003

Table 6: Estimates of grazing impact by mesozooplankton and salps, expressed as a proportion of primary production removed per day. APF – Antarctic Polar Front, Meso – mesozooplankton, Macro – macrozooplankton, I – bottle incubation methods, G – gut fluorescence methods, R – radiotracer methods, O – ingestion rate determined from oxygen consumption, SIZ – Sea-ice zone, POOZ – permanently open ocean zone.

Province	Study area	Month	Method	Organisms measured	% of primary production eaten	Reference
Open ocean north of APF	Subtropical Convergence area	Jun, Oct	G	Meso	<4	Bradford-Grieve et al. (1998)
	Subantarctic/Subtropical Frontal Zone Along 0° meridian	Oct–Nov, Aug Jan–Feb	I G	Copepods Meso and macro	3.0–8.0 53–89	Zeldis et al. (2002) Froneman et al. (2002)
Open ocean near APF	Polar Frontal Zone, Atlantic sector	Feb	I, G	Meso	<3	Atkinson (1996)
	6°E (Atlantic/Indian sector) 170–175°E, S of New Zealand	Dec–Jan Dec–Mar	G I, G	Meso plus salps Copepods, juv. krill	28 3.0–21	Pakhomov et al. (2004) Urban-Rich et al. (2001)
Near productive islands/shelves in proximity to APF	Kerguelen area	year-round	I, O	Copepods	<13	Razouls et al. (1998)
	Kerguelen area	Oct–Nov	O, G	Copepods	23 (SIZ), 41 (POOZ)	Mayzaud et al. (2002a,b)
	South Georgia shelf	Jan	I, G	Copepods	<2.5	Atkinson et al. (1996a)
	South Georgia shelf/slope	Feb–Mar	I, G	Meso	36	Pakhomov et al. (1997b)
Open ocean south of APF	Kerguelen area	Jan–Feb	I	Copepods	3.0–50	Sarthou et al. (2008)
	Prince Edward Island area	Apr–May	G	Meso	9–17 (high PP), 76–81% (low PP)	Perissinotto (1992)
	Along 6°W (SE Atlantic sector)	Oct–Nov	I, G	Large copepods	0.1–3.7 (large copepods) >100 (salps)	Dubischar and Bathmann (1997)
	Lazarev Sea	Dec–Jan	G	Meso plus salps	23	Pakhomov et al. (2002b)
Antarctic Peninsula area	6°E (Atlantic/Indian sector)	Dec–Jan	G	Meso plus salps	17	Pakhomov et al. (2004)
	Along 0° meridian	Dec–Jan	G	Meso plus macro	29	Froneman et al. (1997)
	Along 0° meridian	Jan–Feb	G	Meso plus macro	<20	Froneman et al. (2000a)
	S of Australia, Indian sector	Feb	G	Copepods	8	Zeldis (2001)
High Antarctic shelf	Bellingshausen Sea	Oct–Dec	I	Copepods	<2.9	Atkinson and Shreeve (1995)
	Bransfield Strait, S Drake Passage	Dec	I	Copepods	19	Schnack et al. (1985)
	Bransfield Strait, Drake Passage	Dec–Feb	G	Meso	10	Cabal et al. (2002)
	Tip of Antarctic Peninsula Bransfield Strait	Jan Jan	O G	Meso Meso	6 0.4–4.8	Alcaraz et al. (1998) Hernandez-Leon et al. (2000)
	Coastal site near Davis Station	Dec–Feb	R	Copepods	1.0–5.0	Swadling et al. (1997)

In common with other oceanic regions, small grazers with high basal metabolic rates are trophically important in the SO (Schnack et al., 1985; Metz, 1996; Atkinson, 1994, 1996). These studies show that metazoan grazing is seriously underestimated if grazing is just based on the fraction retained on 200 µm mesh nets. However, this does not draw into question the above-mentioned division between micro- and mesozooplankton impact. Microzooplankton grazing is measured in dilution experiments typically with 200 µm pre-screening to exclude mesozooplankton. The microzooplankton component included in dilution experiments thus includes micro-metazoa as well as protozoans.

Predation and mortality losses

There are two sorts of studies that have estimated predation and mortality loss terms. First, there are estimates of grazing impact on zooplankton by large copepods (e.g. Øresland, 1990; Øresland and Ward, 1993), chaetognaths (e.g. Froneman et al., 1998), amphipods (e.g. Pakhomov and Perissinotto, 1996b), *E. superba* (Price et al., 1988; Atkinson and Snýder, 1997) and myctophid fish (Pakhomov et al., 1996; Shreeve et al., 2009). Second, there are estimates of mortality losses of copepods from population dynamics of single species (Huntley et al., 1994b; Ward et al., 1997; Atkinson et al., 1997; Tarling et al., 2004; Hirst and Ward, 2008) or assemblages from direct time-series observations (Zhou et al., 2004). SO studies are not yet sufficiently advanced to partition mortality, for example into predation, death through injury, starvation, pathogens, etc. A global synthesis of copepod mortality has inferred that predation accounts for about 75% of overall mortality (Hirst and Kiørboe, 2002).

Predation mortality is not just from pelagic predators. *Euphausia superba* have been found to interact regularly with the seafloor to feed (Ligowski, 2000; Schmidt et al., 2011) and they can form a substantial part of the diet of some benthic predators (references in Schmidt et al., 2011). Both underwater photographs and benthic samples show this also to be the case for *E. crystallorophias* (author's unpublished data). For those biomass-dominant copepods with seasonal migration cycles, their autumn descent in shelf waters would bring increased predation from the rich predatory and suspension-feeding fauna inhabiting shelf sediments (Dearborn et al., 1986; Dahm, 1996; see Schnack-Schiel and Isla, 2005 for review). The

extensive DVM cycle of salps as well as their seasonal die-off were also found to bring them into contact with benthic predators, and contribute both to salp mortality and to benthic-pelagic coupling (Gili et al., 2006).

During the summer season, however, it is likely that pelagic invertebrates are the main source of copepod mortality. This means that energy channelled through copepods and then through the macroplanktonic carnivores tends to go through more trophic steps to vertebrate predators than those going directly through *E. superba* (Figure 4).

Krill–salp–copepod interactions

Given the prominent role of krill, salps and copepods, there is a surprising degree of uncertainty about competitive and predator-prey relationships between them. Krill have been shown to be able to eat both copepods (e.g. Price et al., 1988; Atkinson et al., 2002; Schmidt et al., 2011) and salps (e.g. Kawaguchi and Takahashi, 1996), but the importance of copepods in their diets have since been questioned (Schmidt et al., 2006, 2012). Likewise, a degree of interaction (possibly competitive) has been suggested to occur between krill and salps (Loeb et al., 1997) and between krill and copepods (Atkinson et al., 1999).

However, it is surprisingly hard to demonstrate that one species is out-competing another in the pelagic realm, and both the krill-copepod and krill-salp competition hypotheses have since been questioned (Kawaguchi et al., 1998; Pakhomov et al., 2002a; Shreeve et al., 2002; Pakhomov, 2004). In the Prydz Bay region, for example, there is a substantial spatial separation in salp and krill distributions (Hosie, 1994), although this may not always be the case in the Atlantic sector. Clearly these are central issues to resolve through fine-scale distribution and feeding studies, as for instance krill functioning as a phytoplankton feeder or as a predator on copepods or salps have fundamentally different roles within the food web.

‘Alternative’ energy pathways through zooplankton

Several local and large-scale comparisons have been made of the overall SO production by copepods, *E. superba* and salps (Conover and Huntley, 1991; Voronina, 1998; Pakhomov et al., 2002a;

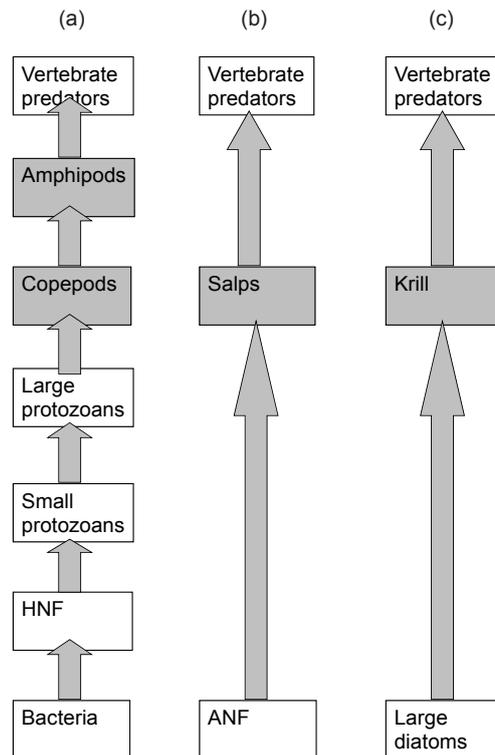


Figure 4: Examples of radically different food-chain lengths found most typically in (a) most of the SO, especially its northern reaches, (b) moderately productive regions, and (c) more productive regions, but north of the continental shelf of high Antarctica. HNF – heterotrophic nanoflagellates, ANF – autotrophic nanoflagellates. ‘Small protozoans’ include 10–20 μm ciliates and flagellates. Shaded boxes represent mid trophic levels connecting microplankton to vertebrates.

Shreeve et al., 2005). Importantly, these calculations are all based on the summer period and they do not include production by larval *E. superba*. Both adults and larvae of this species are able to feed and grow through large parts of the year, unlike the biomass-dominant copepods which may be only active for three to four months. Notwithstanding these important issues and the fact that a whole diverse taxon is being compared with a single species, post-larval *E. superba* production in summer has been found to be ~ 30% of that of copepods (Shreeve et al., 2005).

Smetacek et al. (2004) recently highlighted the contrast in food chain types between subsystems of the SO. Put simplistically and in very general terms, krill inhabit phytoplankton-rich areas characterised by ‘the food chain of the giants’, namely very large diatoms→krill→whales (Figure 4). This is the often-quoted food chain involving large species, only two trophic steps and massive size ratios

between grazer and food. This type of food chain is the textbook example of an efficient food chain, because it has only two transfers of energy and thus a minimum of energy loss along the route from primary producer to top predator. While this krill food chain is often criticised as an oversimplification, the large stock of krill-specialist predators testifies to efficient energy transfer in krill-rich systems.

Other types of food chains have been described in the much larger, iron-stressed ‘High Nitrate Low Chlorophyll’ areas of the SO, often at lower latitudes (Figure 4). These, very broadly, comprise the small copepods or ephemeral salp blooms and regenerating communities dominated by the microbial food chains. Figure 4 shows just three examples of a wide range of food chain types, but we stress that the real-world situation is more complex, with a range of longer, microbial food webs operating alongside shorter salp and krill food webs.

While this food web complexity is widely known, a common misconception is that diatom blooms are ephemeral events, superimposed against a fairly constant 'background' energy flow through the microbial food web. This is not the case (Barber and Hiscock, 2006) and SO studies show that protozoans increase sharply in numbers within blooms (Leakey et al., 1994), remaining an important food supplement to copepods and krill (Atkinson et al., 1996a; Schmidt et al., 2006).

Allometric relationships

Body size has long been recognised as an important determinant of critical rate processes of organisms, and has been used in a variety of ways to determine feeding relationships (e.g. Jennings et al., 2002). In common with the general relationship between generation time and body size (Figure 1), stable isotope analysis shows a significant positive relationship between trophic level and organism size (Stowasser et al., 2012). *Salpa thompsoni* and the large medusa *Stygiomedusa gigantea* (as well as *E. superba*) were outliers from this relationship, having much lower trophic levels that would have been predicted from size (Stowasser et al., 2012). Being able to eat food much smaller than themselves helps to make salps and *E. superba* key players in SO biogeochemical cycles (Fortier et al., 1994).

Numerous compilations of literature data now quantify rate processes of zooplankton in relation to body mass (e.g. Peters and Downing, 1984; Hansen et al., 1997; Huntley and Lopez, 1992; Kiørboe and Sabatini, 1995; Hirst et al., 1998; Ikeda et al., 2001; Hirst and Kiørboe, 2002; Hirst and Bunker, 2003; Bunker and Hirst, 2004). These are very useful as they provide a very rough indication of what the expected range of rate processes might be for a grazer of any given size.

However, such data compilations are often used for purposes other than what they were intended for. The important point about many of these relationships is that they are based on compilations over many ecological systems, often based on late-stage larvae or adults, with measurements typically made at roughly the ambient water temperature from which the animal was collected. Such global relationships are poor for addressing specific questions, for example concerning a species at the northern limit of its range in a warm summer, an

assemblage dominated by early larvae or one entering the diapause season. Some examples of such limitations are provided below.

A typical finding of global data compilations is that the mass-specific rates decrease sharply with increasing body size, such that the slope, b , of the log-log regression between animal size and its vital rate is close to 0.75, in accordance with theoretical considerations. While the use of such values is tempting, studies in specific systems have shown substantial variation about the global mean body mass scaling coefficient. One such example is the SO, where b -values for feeding and excretion appear to be much lower within specific copepod assemblages; nearer 0.6 than 0.75 (Atkinson and Shreeve, 1995; Atkinson, 1996; Atkinson and Whitehouse, 2001). The reason appears to reflect the storage of lipids, a prevalent feature of high-latitude systems. The larger larvae (particularly of the larger species) have an increasingly large fraction of their body mass being non-metabolically active tissue. When the allometry is based on N mass (reflective of metabolically active tissue, since fat does not contain N), then the scaling coefficient is closer to the value of 0.75 more commonly observed (Atkinson and Whitehouse, 2001). This is one example where using global relationships does not work for specific polar ecosystems.

Rate processes in relation to temperature and food

Surprisingly few SO studies have examined how feeding, respiration or growth rates of zooplankton or *E. superba* relate to food or temperature (Quetin and Ross, 1989; Schnack-Schiel et al., 1991; Calbet and Irigoien, 1997; Ward and Shreeve, 1998; Ross et al., 1998, 2000; Shreeve et al., 2002; Atkinson et al., 2006; Tarling et al., 2006; Meyer et al., 2009; Brown et al., 2010). Using global-scale literature compilations instead may sometimes be the only option, but two major problems must be stressed with this approach. First, the predictive power of the relationships is often weak, as evidenced by the orders of magnitude of scatter about the regression lines (e.g. Peters and Downing, 1984; Hirst and Bunker, 2003). This is not a criticism of the approach or the models, but it highlights the fact that ecosystems are variable and that adapting a global model to a specific ecosystem may not be appropriate.

The second issue concerns scale of measurements. Taking temperature effects on growth rate as an example, the copepods were incubated at temperatures approximating those in situ, so they were presumably adapted to those temperatures, ranging from polar to tropical. Rate processes derived in this way show a temperature dependency such that each 10°C temperature rise results in a doubling to tripling of the rate (i.e. a Q_{10} value of 2–3). These relationships were designed for large-scale (e.g. equator versus pole) comparisons, but fixed Q_{10} values are often used erroneously to describe the temperature response of a particular species.

In contrast, each component species has a dome-shaped temperature relationship. Above their optimal temperatures for growth, respiration costs increase to the point when anaerobic metabolism may be required (Pörtner and Farrell, 2008). In polar environments the ectotherms are characteristically stenothermic, with a narrow window of temperature tolerance. Consequently, loss of aerobic scope has been found at temperatures above as little as 2°C (Peck et al., 2004). For post-larval *E. superba* the temperature optimum for growth was found to be 0.5–1°C, with the scope for growth severely curtailed when temperatures exceeded 3°C (Atkinson et al., 2006). The growth of *E. superba* based on their food, body, length, temperature and time of year can be predicted to an some extent (Ross et al., 2000; Kawaguchi et al., 2006; Atkinson et al., 2006; Tarling et al., 2006) and such empirical models have been used to predict their response to climatic change scenarios (Wiedenmann et al., 2008). More work on temperature responses of other polar ectotherms is needed, because the global literature syntheses were not designed to examine the effects of temperature change on specific species or ecosystems.

Using so-called ‘constant’ terms in the energy budget for inter-conversions

Trophic models often need to budget energy or C between ingestion, growth, respiration or excretion and assimilation. For *E. superba*, *T. gaudichaudii*, *S. thompsoni* and large copepods and possibly *O. similis*, there is now some information on parts of the energy budget. For others, fixed conversion values are often used to roughly estimate one term in the energy budget from another.

One such conversion is the gross growth efficiency, defined as growth divided by ingestion within the same time period, in C or N units. Based on a literature compilation, Straile (1997) found values for copepods typically of 20–30%, but this disguises great variability in the individual component data. While this reflects the difficulty in measuring each of its two components, it also probably reflects great variability in food quantity and quality which dictate how much of the absorbed food can be allocated to growth.

An analogous situation applies to absorption (assimilation) efficiency (AE). Models often treat AE as a fixed value, typically around 60–80%. However, just like every term in the energy budget it is a variable, depending both on the nutrient (Mayor et al., 2011) and the feeding rate (Thor and Wendt, 2010). High feeding rates depress AE, due to the process of ‘superfluous feeding’ which, contrary to its wasteful-sounding name, maximises absolute rates of nutrient absorption. This process has been found for *E. superba*, whose AE varies between specific fatty acids and leads to pellets varying 30-fold in their C and N content, as a proportion of pellet dry mass (Atkinson et al., 2012). Likewise, great variability has been found in AEs of SO copepods (Schnack, 1985), and this variability needs to be incorporated into the energy budget using equations such as those presented in Thor and Wendt (2010).

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Table A1: Selection of studies providing mesozooplankton biomass or total abundance within the Southern Ocean. Databases containing mesozooplankton data are described under 'Data sources' on page 180.

Region	Study area	First author	Study month
Wide geographic area	Circumpolar	Foxton, 1956	all
	75–160°W PFZ, AAZ	Hopkins, 1971	year-round
	from SAZ into Ross Sea	Biggs, 1982	summer
	New Zealand–Ant, 44–64°S	Flint and Timonin, 1982	Jan–Feb
	Croker Passage	Hopkins, 1985a	Mar–Apr
	115°E line and 150°E line 45–65°S	Kawamura, 1986	Dec–Jan
	63–64°S, 43–44°W	Kawamura, 1987	Dec
	Lazarev Sea, 66–68°S, 5–15°E	Pakhomov et al., 1993	Jan–Feb
	15–60°W, 52–72°S	Voronina et al., 1994	Feb–Apr
	PFZ well north of South Georgia	Atkinson, 1996; Atkinson et al., 1996b	Feb
	Cape Town–Sanae and New Zealand to Ross Sea	Pakhomov and McQuaid, 1996	Dec 1979–Jan 1980, Jan–Feb 1981
	Atl sector from 30°E to 85°W, all lats	Rudjakov, 1996	year-round
	6°W, same as Franz and Gonzalez study	Dubischar and Bathmann, 1997	Oct–Nov
	6°W, 47–59°S	Franz and Gonzalez, 1997	Oct–Nov
	1°E to 2°W, 67–69°S	Froneman et al., 1997	Dec–Jan
	Subtropical Convergence area near New Zealand	Bradford-Grieve et al., 1998	Jun and Oct
	Cape Town – Sanae (0°)	Pakhomov et al., 2000	Jan–Feb
	Entrance of Ross Sea, Balleny Islands	Sertorio et al., 2000	Dec–Jan
	90–160°E, PFZ, AAZ and CCC	Chiba et al., 2001	Mar
	170–175°E, 53–66°S	Urban-Rich et al., 2001	Dec 1997, Feb–Mar 1998
	140°E, 61°S	Zeldis, 2001	Feb
	43–46°S 63–64°E (most N of SAF)	Labat et al., 2002	Jan–Feb
	49–58°S, 62°E (SW of Kerguelen)	Mayzaud et al., 2002a, 2002b	Oct–Nov
	49–58°S, 62°E (SW of Kerguelen)	Mayzaud et al., 2002a, 2002b	Feb–Mar (1994), Jan–Feb (1999)
	South of Tasmania SR3 transect	Hunt and Hosie, 2003	Nov–Dec
	South of Tasmania SR3 transect	Hunt and Hosie, 2005	Feb–Mar
	South of Tasmania SR3 transect	Hunt and Hosie, 2006a, 2006b	Nov–Mar
30–80°E, 62°S to the coast	Swadling et al., 2010	Jan–Feb	
25–100°E, 48–62°S	Takahashi et al., 2010a	Jan (2005–2009)	
Almost circumpolar south of SAF, mostly 0–180°E	Hosie et al., 2003	All year, most Sept–Apr	
Lazarev Sea, 68°S, 0.5–1°E, 12 d drogue study	Pakhomov et al., 2002b	Dec–Jan	

(continued)

Table A1 (continued)

Region	Study area	First author	Study month
Wide geographic area (continued)	SAZ and Subtropical frontal Zone east of New Zealand 6°E and 48–65°S	Zeldis et al., 2002	Oct–Nov 1997 and Aug 1998
	PFZ at 28–36°E, 48–52°S (MOEVS 2, 4 and 5 cruises)	Pakhomov and Froneman, 2004a, 2004b Bernard and Froneman, 2009; Bernard, 2006	Dec–Jan Apr
Antarctic Peninsula area	Bransfield and S Drake Passage	Schnack et al., 1985	Dec
	Bellingshausen transect out of ice	Atkinson and Shreeve, 1995	Oct–Dec
	Tip of Ant Pen, including Weddell and Drake Passage	Alcaraz et al., 1998	Jan
	Bransfield Strait	Hernandez-Leon et al., 1999	9 Dec (to 2 Jan 1992)
	Bransfield Strait	Hernandez-Leon et al., 2000	Jan
	Bransfield Strait, Drake passage	Cabal et al., 2002	Dec 1995–Feb 1996
	Marguerite Bay area	Ashjian et al., 2004	Apr–Jun and Jul–Aug 2001
	Bransfield Strait (transect across it)	Catalán et al., 2008	Jan–Feb
	Drake Passage	Takahashi et al., 2010b	Feb
	Right down the W side of the Weddell Sea	El-Sayed and Taguchi, 1981	Feb–Mar
Weddell Sea area	Near ice edge, W. Weddell	Hopkins and Torres, 1988	Mar
	N and E fringes of Weddell Sea	Boysen-Ennen et al., 1991	Feb–Mar
Inner Ross Sea area	McMurdo, through ice	Foster, 1987	Nov–Dec
	McMurdo Sound, Ross Sea	Hopkins, 1987	Feb
	Terra Nova Bay, Ross Sea	Pane et al., 2004	Jan–Feb
	Cumberland Bay	Ward, 1989	Summer and winter
South Georgia and its bloom area	South Georgia shelf and oceanic sites	Ward et al., 1995	Jan
	South Georgia shelf site	Atkinson et al., 1996a	Jan
	South Georgia shelf/slope	Pakhomov et al., 1997b	Feb–Mar
	Oceanic zone (>2 000 m) around South Georgia	Atkinson and Peck, 1988	Nov–Dec 1981, Jul–Aug 1983
	Transect from APF to W end of South Georgia	Atkinson et al., 1999	Dec–Feb
	South Georgia shelf and oceanic sites	Ward and Shreeve, 1999	Oct–Nov
	South Georgia, East and West Core Boxes	Atkinson and Whitehouse, 2001	Dec–Jan
	South Georgia shelf and oceanic sites	Ward et al., 2006b	Mar–Apr

(continued)

Table A1 (continued)

Region	Study area	First author	Study month
Marion/Prince Edward Islands area	Prince Edward Islands	Grindley and Lane, 1979	Mar and Nov
	Prince Edward Islands	Boden, 1986	May
	Prince Edward Islands	Boden, 1988	May
	Close to Prince Edward Islands	Perissinotto, 1992	Apr 1985 and Apr–May 1989
	44.5–47°S upstream of Marion Is and between islands	Froneman and Pakhomov, 1998	April–May
	Prince Edward Islands, 45.5–48°S, 35.5–40.5°E	Ansorge et al., 1999	Apr–May
	Around PEIs, 45–47.5°S, 36.5–41.5°E	Froneman et al., 1999	Apr–May
	Marion Island: upstream and inter-island	Hunt et al., 2001	Apr–May
	Close to Prince Edward Islands, but on-and off-shelf	Froneman et al., 2002	Apr–May
	Upstream, inter-island and downstream of Marion Island	Hunt and Pakhomov, 2003	Apr–May
Crozet/Kerguelen area	Kerguelen, Kerfix and Biostation station	Razouls et al., 1998	year-round
	Crozet	Fielding et al., 2007	Nov 2004–Jan 2005
	Kerguelen plateau and Kerfix site	Carlotti et al., 2008	Jan–Feb
Inshore, high Antarctic	KEOPS area SE of Kerguelen	Sarthou et al., 2008	Jan–Feb
	Under sea-ice, Syowa Station	Fukuchi et al., 1985	May to Dec
	Coastal site near Davis	Swadling et al., 1997	Dec–Feb

Table A2: Selection of studies providing data on macroplankton biomass based on various large nets (see final column). This does not include acoustic methods or krill-specific surveys, described in Atkinson et al. (this volume). Databases containing macrozooplankton data are described in the 'Data sources' section on page 180.

Region	Study area	First author	Study month	Net type
Wide oceanic area, large latitudinal or longitudinal range	Prydz Bay Region, 60–68°S, 60–80°E	Pakhomov, 1989	Feb–Mar 1985, Dec 1985–Jan 1986, Feb–Mar 1986	Isaacs-Kidd Trawl
	Prydz Bay Region, 60–68°S, 60–80°E	Pakhomov et al., 1993	Feb–Mar 1987, Dec 1987–Mar 1988	Isaacs-Kidd Trawl
	Prydz Bay region 50–95°E	Hosie, 1994	Sep–Mar	RMT8
	Prydz Bay region 67–78°E	Hosie and Cochran, 1994	Jan–Feb	RMT8
	STC, APF, Atlantic sector 135–145°E, 62–65.5°S 36–42°E, 45–48°S (PFZ, AAZ)	Pakhomov et al., 1994 Chiba et al., 1998 Pakhomov and Froneman, 2000	Jan–Feb and Jun–Jul 1993 Jan–Feb May	RMT-8 ORI net, 1.6 m mouth diam RMT8
Antarctic Peninsula area	80–150°E	Hosie et al., 2000	Jan–Mar	RMT8
	Circumpolar	Atkinson et al., 2004	Nov–Mar	Multiple
	Cosmonaut Sea, 60–70°S, 30–60°E	Hunt et al., 2007	Jan–Feb	Bongo, Melnikov Net
	Croker Passage, W Antractic Peninsula	Lancraft et al., 2004	Mar–Apr	Tucker trawl
	Bransfield Strait (transect across it)	Catalan et al., 2008	Jan–Feb	BIONESS 1 m ² frame
Weddell Sea area	N and E fringes of Weddell Sea	Boysen-Ennen et al., 1991	Feb–March	RMT1+8
	Scotia Weddell	Lancraft et al., 1989	?	Tucker trawl
	NW Weddell Sea, ice-covered stn 62°S, 42°W	Kaufmann et al., 1995	Sept–Oct	Tucker trawl, 9 m ² mouth area
	NW Weddell sea, 62–64°S, 44–50°W	Fisher et al., 2004	Sept–Oct 1995, Apr–May 1996, Nov–Dec 1996	10 m ² area MOCNESS trawl
Marion/Prince Edward Islands area	Prince Edward Islands	Miller, 1982	May–Jun	RMT8
	Marion Island 37–38.5°E, 45–47°S	Pakhomov and Froneman, 1999b	Apr–May	RMT8
Inshore, high Antarctic	Kerguelen Islands	Pakhomov, 1995	Feb–Mar	Melnikov Net