Chapter 5
Feeding and Food Processing in Antarctic Krill (*Euphausia superba* Dana)

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Abstract *Euphausia superba* is exceptional among euphausiids for the large filtering surface of the feeding basket and its fine mesh size (2–3 μm), which remain into adulthood. This enables them to feed efficiently on nano- and microplankton, and to reach substantial growth rates with food concentrations as low as 0.5 μg Chlorophyll *a* L^{-1}. Even though phytoplankton – in particular diatoms – are their staple food, protozoans and small copepods are ingested simultaneously and represent an important supplementary food source year-round. However, krill feeding behaviour is more complex than just filter-feeding in the water column, it includes raptorial capture of larger zooplankton, handling of 'giant' diatoms, scraping algae from beneath sea ice and lifting detritus from the seabed. High mobility and physiological robustness enable krill to explore three feeding grounds – the water column, the sea ice and the benthos. Variability in access and productivity of these feeding grounds leads to fundamental differences in krill overwintering across their habitats. Gut passage time, absorption efficiency and fecal pellet density vary with food concentration and nutritional needs. Therefore krill fecal pellets have a dual role; some promote the export of carbon and nutrients while others facilitate the recycling of material in the upper water column. Krill grazing can suppress phytoplankton blooms, but this tends to be a localised phenomenon where krill abundances are exceptionally high. Conversely, krill appear to have major conditioning effects due to nutrient supply (e.g. ammonium, iron), although their role in Southern Ocean biogeochemical cycles is only starting to be discovered.

Keywords Diet • Ingestion rates • Stable isotopes • Polyunsaturated fatty acids • Fecal pellets

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5.1 Introduction

Nutrition provides the building blocks of all organisms and fuels the dynamic interactions between them (Simpson and Raubenheimer 2012). Most aspects of the biology of *Euphausia superba* indeed hinge in some way around feeding or avoiding being eaten. For example the amount and quality of food sets the ingestion rate, gut retention time and absorption efficiency. Those in turn affect the rest of the krill physiology, including excretion, respiration, mobility, growth and gonad production (Ikeda and Dixon 1984; Ross et al. 2000; Pond et al. 2005). Finding food requires aggregation in the water column, or visits to sea ice or the seabed according to region, season and life stage, with specialised feeding mechanisms on each substrate. Conceptual models of distribution, from the circumpolar scales to that of an individual within a school, involve food acquisition and predator avoidance as well as ocean physics. Feeding is therefore a central thread of krill biology.

Studies of krill feeding have a long history and the slowness in progress reflects the great difficulty in obtaining real-world data on how they feed, what they eat and how much. On one hand, krill are large and well suited for laboratory maintenance and experimentation (Ross and Quetin 2003). On the other hand, their complex foraging behaviour in association with schooling and extensive vertical and horizontal migration make it difficult to recreate natural conditions in the laboratory.

Early studies of krill nutrition examined their gut contents (Barkley 1940) and mouthpart morphology (Kils 1983; Suh and Nemoto 1988; Hamner and Hamner 1988) and established that the species is well adapted to feeding on phytoplankton. This earlier work contains the most thorough observations of the mouthpart morphology and feeding mechanisms made to date. It is surprising that the great improvements in filming technology in the last 30 years have not been applied to krill feeding.

In the 1980s, research on krill rapidly expanded with new studies covering all aspects of their ecology. Many of the early krill incubation experiments used small (<10 L) containers and derived daily rations that were only a few percent of the total body carbon per day (see Perissinotto et al. 1997; Pakhomov et al. 2002). With the increase in incubation volume, the application of through-flow systems and the use of new, more in-situ related approaches, krill clearance- and ingestion rates started to reflect those of micronekton (Clarke et al. 1988). Nevertheless, it was still not properly known what they eat and where they feed. Three breakthrough findings followed, however. (1) Both larval and postlarval krill were filmed feeding on the underside of sea ice (Stretch et al. 1988; Marschall 1988; Hamner et al. 1989), (2) they were found to readily eat copepods (Price et al. 1988), and (3) they were seen in aggregations at the seabed (Gutt and Siegel 1994), providing yet another potential food source. It is only now, three decades later, that we are starting to quantify the relative roles of these food substrates.

The 1990s and 2000s were perhaps a less glamorous time to study krill feeding. These marked a period of infilling the above breakthroughs to provide solid quantitative information. To do this the methods needed to be used carefully and in combination (see Sect. 5.4). For instance the application of isotopic- and fatty acid trophic markers increased, and gut fluorescence and fecal pellet egestion estimates were used alongside traditional feeding incubations and gut content analysis.

The last 5 years have made us realise that some of the previous controversies about krill feeding have in fact reflected real differences, either in terms of region, season or krill ontogeny. For instance the feeding on copepods is very region-specific and so are overwintering strategies (Schmidt et al. 2014), and the reliance on ice algae decreases with ontogeny (Quetin et al. 1994; Meyer 2012). There has also been a resurgence of studies that examine the biogeochemical ramifications of krill feeding, for instance in carbon export via their fecal pellets (Atkinson et al. 2012; Manno et al. 2015), or in controlling phytoplankton blooms and regenerating nutrients (Tovar-Sanchez et al. 2007; Schmidt et al. 2011; Whitehouse et al. 2011).

The sections below review these developments in krill feeding. The topic has been incorporated previously by Clarke and Morris (1983), Miller and Hampton (1989), Knox (1994), and Quetin et al. (1994) in their wider-ranging reviews of krill ecology. This chapter highlights the key developments in the study of krill feeding, namely how they feed, what they feed on and at what rates, before putting krill feeding into a wider context. This context includes the energy budget of krill, the comparison with other Southern Ocean euphausiids, their role in the food web and in biogeochemical cycling. While we describe larval feeding, most emphasis is on post-larvae, given the separate chapter dedicated to larval krill biology (see Chap. 6, Kawaguchi 2016).

5.2 Feeding Apparatus

In euphausiids, feeding involves the integrated action of externally located thoracopods and mouthparts and the internally placed armature of the stomach wall (Hamner and Hamner 1988; Suh and Nemoto 1988). The thoracopods gather the food, the mouthparts handle it and the mandibles pierce, cut and grind the items before they are swallowed. The internal armature of the stomach breaks the food into even smaller pieces until they are fine enough to enter the digestive gland for final digestion and absorption (Suh 1996). The principal filtering apparatus of *Euphausia* species is a feeding basket collectively formed by six pairs of thoracopods (Barkley 1940; Kils 1983; McClatchie and Boyd 1983). The fine structure of this basket is a three-dimensional filter of primary, secondary and tertiary setae (Suh and Nemoto 1987). Primary setae are present on the ischium and merus of the thoracopods. Along the primary setae, there are two rows of secondary setae inserted at an angle of 90° and again a single row of tertiary setae along the secondary setae (Suh and Nemoto 1987). The terminal segments of the thoracopods bear comb setae with a comb-like device at their ends. The filter area and the intersetal distance determine the filtering efficiency of the feeding basket, which can differ between species and size classes (Boyd et al. 1984; Suh and Nemoto 1987).

In *E. superba*, the filtering area of the basket increases from ~70 mm^2 in juveniles (20 mm body length) to ~277 mm^2 in adults (50 mm body length), while the minimum spacing between tertiary setae remains small (2–3 μm, Suh and Nemoto 1987). In other Southern Ocean euphausiids, the filter area of the basket is only 20–30 % of that of *E. superba* with the same body length, the minimum spacing between tertiary setae is larger (>8 μm) and the maximum spacing between primary setae is similar or slightly larger (see Sect. 5.12). McClatchie (1985) compared the filtering area of *E. superba* with that of Northern krill, *Meganyctiphanes norvegica*, and suggested that if the two species apply their feeding baskets in the same way and at the same rate, 22–39 mm long *E. superba* would have a three-times higher clearance rate than *M. norvegica* of similar size (McClatchie 1985). This indicates that the feeding basket of *E. superba* is exceptional among euphausiids for its large filter area, the fine mesh sizes and the nearly consistent minimum spacing between tertiary setae from juvenile to adult.

Once the food is enclosed in the feeding basket, various mouthparts (mandibular palps, maxillules and maxillae) are involved in passing it on to the oral cavity built by the upper lip (labrum), mandibles and lower lip (labia). The mandibles are hard and have strong cusps, the *pars incisive*, in the ventral region and grinding surfaces, the *pars molaris*, in the dorsal region. Large grinding areas of the mandible are associated with a phytophagous tendency, whereas a pronounced cutting region indicates carnivorous feeding (Nemoto 1967; Mauchline 1989). Although the large grinding region of the *E. superba* mandible is characteristic of an herbivorous euphausiid (Nemoto 1967), the marginal teeth are spine-like as in omnivorous-carnivorous species (McClatchie and Boyd 1983). These spines may facilitate piercing of animal prey, functioning as an adjunct to the *pars incisive* (McClatchie and Boyd 1983). The grinding region is differentiated into very rugged cusped transitional areas and a broad plate-like region, which indicates specialization for fracturing hard tests and for finer grinding of particles (McClatchie and Boyd 1983). Ridges on the plate-like region are spaced at ~5-μm intervals, suggesting that particles smaller than 10 μm can be ground up efficiently (McClatchie and Boyd 1983). After crushing and grinding by the mandibles, the stomach is an additional organ for the maceration of food particles (Suh 1996). The gastric mill is the main grinding region within the stomach. *E. superba* have a well-developed gastric mill with strong cuticular structures, lateral teeth and cluster spines, which act in crushing hard food items such as diatom frustules (Suh and Nemoto 1988; Ullrich et al. 1991). A complex system of muscles enables movements of the stomach wall, which compress the food between the armoured areas.

In summary, *E. superba* is equipped to feed on a wide range of food items. Two different types of filter nets are formed by the setal arrangements of their feeding basket. First, a very fine net of secondary and tertiary setae, which allows *E. superba* to filter nanoflagellates and small resuspended particles, and second, a coarse net formed by primary and comb setae suitable to retain larger items such as diatoms. Other Southern Ocean euphausiids are not equipped to feed efficiently on items as small as 2–3 μm, which gives *E. superba* a considerable competitive advantage (Suh and Nemoto 1987). The elaborated *pars molaris* and the well-developed gastric mill enable *E. superba* to break and macerate strongly-silicified diatoms. Handling of larger animal prey is supported by spine-like marginal teeth on their mandibles.

5.3 Feeding Mechanisms

5.3.1 Filter Feeding

Euphausiids are able to sense odours of phytoplankton along a diffusion gradient (Price 1989; Hamner and Hamner 2000). In a positive response, the scent trail is tracked; filtration rates increase and the krill try to remain within the area of highest phytoplankton concentration (Price 1989; Hamner and Hamner 2000). Negative responses to chemoreception include the rejection and avoidance of particles in the water. Surprisingly few studies examined the actual mechanism of food- and water flow through the feeding appendages in close-up detail. Of these, the study by Kils (1983) stands out since it details quite different ways of moving the feeding appendages that could explain some of the contrasting results on food size selection (see Sect. 5.9).

Euphausia superba has a chamber-like food basket which acts as a pressure-pumping mechanism (Hamner et al. 1983). Kils (1983) suggested from observations of wild and captive krill that the most common movement of these feeding appendages was in compression filtration (he also termed this mode “pump filtration” although subsequent authors have described these as if they were separate modes). This energy-intensive opening and closing of the filtering basket is synchronised with the pleopod swimming beat to maintain steady forwards motion. To open the basket, the paired thoracic legs move downward and outward in a metachronal rhythm which creates a pressure gradient that sucks water and particles into the basket from the front (McClatchie and Boyd 1983; Hamner and Hamner 1988). Food collects inside the basket while the euphausiid expels water laterally through the setae by rapidly compressing the thoracopods. The filter setae are then scraped and cleaned by a second set of comb setae and the particles passed forward to the mouth (Hamner and Hamner 1988). The metachronal rhythm of the thoracic legs during expansion and contraction of the basket enables the passage of food from posterior to anterior legs (Mauchline 1989). After the mouthparts gather a food bolus the feeding bouts cease, the mandibular palps press the bolus against the mandibles and ingestion ensues (Hamner et al. 1983).

The distribution of intersetal distances in the feeding basket determines the minimum size of particles retained. When the thoracopods are closed and pressed to the ventral side of the body, water is rapidly compressed within the feeding basket. This increases water velocity and Reynolds number, and decreases the width of the boundary layer around the setules, so that water is forced through the very finely spaced (2–3 μm) tertiary setae, termed microsetules (McClatchie and Boyd 1983). A fundamental difference between the relatively small maxillary filter of copepods and the large thoracic filter of krill is that only in the latter the filtering area is great enough for the water volume to be passed through the meshes (McClatchie and Boyd 1983).

5.3.2 *Feeding on Ice Algae*

Krill's ability to feed on ice algae was initially encountered in the laboratory (Hamner et al. 1983), but has subsequently also been observed in situ (Spiridonov et al. 1985; O'Brien 1987; Stretch et al. 1988; Marschall 1988). Stretch et al. (1988) found that krill foraging near ice floes exhibits two distinct behaviour patterns. When stimulated by algae released from melting ice they show area-intensive foraging. This behaviour is characterised by high speed swimming and rapid turning, accompanied by fast opening and closing of the feeding basket. Thereafter krill often orientate themselves with the ventral side towards the under surface of the ice and scrape algae with the tip of their fully-extend thoracopods. The terminal segments of their thoracopods (dactylopodites) are well-suited for this behaviour as they have rake-like structures which are much stronger and thicker than normal setae (Kils 1983). Observations by Marschall (1988) using a remotely operated vehicle showed that krill were rare under smooth-bottomed ice, but reached high densities under rugged ice. Individuals close to the ice had often dark green digestive glands due to the intensive uptake of chlorophyll pigments.

5.3.3 *Feeding at the Seabed*

While krill were previously known to associate with the seabed (Gutt and Siegel 1994; Ligowski 2000), it was only in summer 2006/2007 that adult krill were for the first time observed feeding at the benthos. This was off the western Antarctic Peninsula in water depths ranging from 500 to 3500 m (Clarke and Tyler 2008). Typically, the krill would dive head first into the sediment from a height of <1 m above the seabed. This would raise a small volume of sediment into the water column, and the krill would then swim rapidly upward and filter the resuspended material with characteristic movements of their feeding baskets. It seemed that krill were resuspending sediment to extract phytodetritus or other food material (Clarke and Tyler 2008). To date, there are more than 30 studies that bring evidence of krill-seabed-interactions. These comprise direct observations of krill at the seabed, their entrapment in epibenthic sampling equipment, their presence in the stomachs of benthic predators or the encounter of seabed material in their own stomachs. This shows that feeding at the seabed may be a common behaviour of this species across Southern Ocean habitats, with major implications for the food web and the vertical transport of nutrients (Schmidt et al. 2011).

5.3.4 Feeding on Copepods

In situ, krill feed on a range of copepod species and size classes (prosome length: 0.1–2.2 mm; modal prosome length: 0.27 mm; Schmidt et al. 2014). The following taxa were identified in the stomach content of freshly caught krill: *Oithona* spp., *Ctenocalanus citer*, *Drepanopus forcipatus*, *Stephos longipes*, *Microcalanus pygmaeus*, *Metridia* spp., *Calanoides acutus* and *Calanus propinquus* (Hopkins and Torres 1989; Lancraft et al. 1991; Schmidt et al. 2014). It has been suggested that small copepods such as *Oithona* spp. are passively caught when euphausiids filter-feed on phytoplankton, since they are unable to withstand the negative pressure caused by the feeding beats (Barange et al. 1991; Gibbons et al. 1991; Schmidt 2010). In contrast, raptorial feeding on larger copepods entails the complex succession of detection, attack, capture and finally ingestion. Euphausiids can use vision, mechanoreception and chemoreception to detect prey (Hamner et al. 1983; Torgersen 2001; Abrahamsen et al. 2010). So far, raptorial feeding mechanisms have not been described for *Euphausia superba*. However, it has been suggested that northern krill, *Meganyctiphanes norvegica* use mechanoreception, not vision, as the main sensory mode in near-field prey detection (Browman 2005; Abrahamsen et al. 2010). Browman (2005) clarified that the morphology of the *M. norvegica* eye does not enable sufficient spatial resolution to detect small objects at close range. However, additional clues such as movements, changes in light intensity or bioluminescence may enable krill vision to pick up clusters of prey at a distance. The process of copepod capture by *M. norvegica* has been described as follows: Attack responses are initiated well before the copepod reaches the feeding appendances. During an attack, antennae move towards the target, followed by propulsion and opening of the feeding basket (Abrahamsen et al. 2010). If successful, the copepod is sucked into the basket with the inward flow of water. Once the copepod is captured, the cusps of the mandibles and the spines of the maxillules can pierce the integument (Mauchline and Fisher 1969). It has been reported that some euphausiid species only extract the soft internal tissue of the copepods and discard the remains (Beyer 1992, and references therein). *E. superba* seem to ingest copepods completely (Atkinson, personal observations), although it is not yet known whether the mechanisms of copepod capture are the same as those described above for *M. norvegica*.

5.4 Methods to Study Krill Feeding

Like no other aspect of animal biology, diet and feeding have provoked the development of a large array of study methods. For krill at least 13 different approaches have been applied, covering various aspects of ‘feeding’ from morphological adaptations and feeding mechanisms to diet, trophic level, food selectivity and feeding rates. Each of the approaches has its strengths and limitations, but in their sum, they have supplied a large amount of information on krill feeding (Table 5.1). Many of the early studies were carried out in the laboratory, keeping krill in confinement. Even though these studies show what krill are doing under specific conditions, the results may not reflect their in situ behaviour. For instance, krill's preference and high intake of animal food in the laboratory (McWhinnie and Denys 1978; Boyd et al. 1984; Price et al. 1988; Nordhausen et al. 1992; Granéli et al. 1993; Kawaguchi and Takahashi 1996; Atkinson and Snÿder 1997) is not confirmed by trophic level estimates or stomach content analysis on freshly caught krill (Table 5.1). The latter has shown that krill can feed on a range of copepod species and size classes (see Sect. 5.4), but the number of copepod mandibles found in their stomachs is low (mean: 1 ± 2, max: 18 mandibles stomach^{-1}, Schmidt et al. 2014) compared to the more carnivorous euphausiid *Meganyctiphanes norvegic a* (mean: 48 ± 41, max: 151 mandibles stomach^{-1}, Schmidt 2010; see also Båmstedt and Karlson 1998). Therefore krill ingestion rates of over 700 copepods d^{-1} (Nordhausen et al. 1992) seem to be a laboratory artefact. Likewise, even though krill feed readily on moults, euphausiid ommatidia have not been found in their stomachs (Hopkins et al. 1993b; Schmidt et al. 2006), suggesting that cannibalism (McWhinnie and Denys 1978) is not a common feeding strategy. Finally, in the field, the likelihood of predator-prey-interactions between krill and larger copepods or salps is reduced as the latter divert into deeper water to avoid vertical overlap with krill swarms (Atkinson et al. 1999; Pakhomov et al. 2002).

Krill feeding is a complex interaction between nutritional requirements, swimming, swarming, and vertical and horizontal migration, which cannot easily be recreated in the laboratory. Therefore, laboratory experiments may be suitable to study specific aspects of feeding (e.g. the mechanics of food capture), while for diet studies the use of in situ-based approaches is recommended. Here, three in situ approaches are highlighted:

1. *Direct observations in the field*. Krill feeding underneath ice and at the seabed are aspects that require better regional coverage and more detailed understanding. While the initial studies have suggested that this behaviour is stimulated by the available food such as seabed phytodetritus (Clarke and Tyler 2008) or abundant ice algae (Marschall 1988), we still do not know what percentage of the local population is involved in this behaviour and what krill are gaining from this diet. Therefore it would be useful to extend the in situ observations over longer time-scales and different regions, and to collect krill directly from these surfaces (e.g. by pump suction or with epibenthic sledges) to examine their diet and body stores in comparison to krill concurrently sampled in the open water away from sea ice or the seabed.
2. *Evaluating krillfeeding activityin relation to surface chlorophyll a concentrations and krill swarm characteristics*. Most juvenile and adult krill live in the open ocean (Atkinson et al. 2008) with reduced access to a food-rich seabed or ice habitat. Therefore the diet of these krill may differ from those living over shelf-areas and needs separate consideration. As krill spend a large part of their

Table 5.1A Overview of methods to study krill feeding behaviour and diet

Method	Principle	Studied aspect	Uses	Limitations
Functional morphology studies	Cross-species comparison of the morphology of feeding-related structures (e.g. feeding basket, mandibles, gastric mill).	Lower size limit of food items. Existence of structures to fracture and grind diatoms, or pierce copepods.	Indicates ontogenetic- and species-specific differences in diet or food-size spectrum	Mandibles and gastric mill are similar for herbivorous and omnivorous species as the feeding on hard-shelled food items imposes a high demand on their mechanical capabilities
Direct in situ observations	Observing krill in their natural environment by remotely operated vehicles, moored cameras or scuba divers.	Feeding behaviour	Helps to realise the full range of krill feeding behaviour under natural conditions.	Does not give information about ‘how typical’ this behaviour is for the population. Observations may be specific to certain locations.
Assessing the fullness of the krill stomach and gut	Freshly caught krill are scored for the fullness of their stomach/gut as an index of their feeding activity	Feeding activity	If temporal or spatial coverage is high, feeding activities can be related to e.g. time of the day, season or sampling depth.	A sufficient number of krill needs to be scored from each station. Gives no information on ingestion rates.
Assessing the colouration of the digestive gland	Freshly caught krill are scored for the ‘greenness’ of their digestive gland, as a measure of ingested phytoplankton pigment.	Feeding on phytoplankton	If temporal or spatial coverage is high, feeding activities can be related to in situ phytoplankton abundance, size-class structure or taxonomic composition.	This is only a crude indication of carbon intake, as pigment-to- carbon ratios are variable. A sufficient number of krill needs to be scored from each station. Gives no information on ingestion rates.
Gut fluorescence analysis	In situ ingestion rates can be estimated from phytoplankton pigment content in freshly-caught krill, gut passage time and pigment-to-carbon ratio.	Feeding activity and phytoplankton ingestion rates	Insights into short-term variability in feeding activity (i.e. gut fullness). Phytoplankton ingestion rates and overall krill grazing impact can be estimated.	Calculations of ingestion rates have to account for pigment destruction during gut passage, changes in gut passage time with no/or alternative food, and variable pigment-to-carbon ratios.

(continued)

Table 5.1A (continued)

Method	Principle	Studied aspect	Uses	Limitations
Fecal pellet egestion rates	Freshly-caught krill are incubated onboard ship to measure their egestion rates.	Carbon egestion rates (with possible extrapolation to ingestion rates)	Reflects in situ feeding activity. Measurement of carbon egestion, fecal pellet density and sinking rates give insights into food processing and potential fate of pellets.	Conversion to ingestion rates requires knowledge of the carbon absorption efficiency (literature values vary from 42 to 94 % for krill).
Visual identification of the stomach content	Items in the stomach of freshly-caught krill are identified and measured under the microscope	Krill diet (restricted to food with solid remains; e.g. diatoms, thecate dinoflagellates, tintinnids, foraminifera, copepods, cnidaria, lithogenic particles)	Size-measurements of food items and subsequent volume calculations allow a crude estimation of the relative importance of main food categories (diatoms, thecate protozoans, copepods) in the krill diet.	No information on soft-shelled or very small food items (e.g. athecate protozoans, bacteria). Partial digestion and maceration of solid items can hinder identification to species level.
Molecular identification of the stomach content	Items in the stomach of freshly-caught krill are identified via their DNA using polymerase chain reaction (PCR)	Krill diet	Soft- and very small food items can be targeted. Theoretically, all items can be identified to species-level.	Relies on complete nucleotide databases or the ability to develop species-specific primers. No information on size of items. Fast DNA-digestion limits quantitative estimates
Immuno-chemical analysis of stomach content	Stomach extracts from freshly-caught krill are tested for anti-serum activity to a specific target species with an enzyme-linked immuno-sorbent assay (ELISA)	Krill diet	Gives unambiguous information about the ingestion of items of particular interest under natural conditions, e.g. krill feeding on *Phaeocystis* spp.	Requires additional laboratory experiments to calibrate anti-serum responses against known proportions of the target species in the stomach extract
Fatty acid (FA) biomarkers	Some organisms produce unique FA that can be traced in their consumers, e.g. in their stomach content (recent diet) or tissue (integrated diet).	Krill diet (restricted to food sources with indicative FA, e.g. diatoms, flagellates, bacteria, wax-ester-rich copepods)	Certain food sources can be compared for their relative importance in the krill diet, e.g. diatoms-*vs*-flagellates, or diatoms-*vs*-copepods.	Dietary effects can be obscured by different total lipid content of krill, as storage lipids (triacylglycerol) contain generally more saturated FA and

				structure lipids (phospholipids) more unsaturated FA.
Bulk stable isotopes	Naturally occurring isotopes of nitrogen ($^{15}N/^{14}N$) show an enrichment of ~3.4‰ from prey to consumer. The trophic level of krill can be calculated as $TL_{krill} = [(\delta^{15}N_{krill}-\delta^{15}N_{primary\ producer})/3.4]+1$.	Trophic level (TL)	Stable isotope measurements can be carried out in a similar manner across the whole food web; so the TL of krill can directly be compared to that of other species.	The interpretation of small-scale differences between stations may be hindered if krill feed in multiple habitats and $\delta^{15}N$ values in krill and their food reflect different integration periods.
Compound-specific stable isotopes	Some amino acids are strongly fractionated when passing through the food web (e.g. Glu), while others remain unchanged (e.g. Phe). This gives an internal index of trophic position: $\Delta\delta^{15}N_{Glu\text{-}Phe}$: + 7‰ per trophic level	Trophic level	Small-scale differences in trophic level can be assessed.	Heterotrophic food sources (protozoans, copepods) remain unidentified. Some studies suggest that microbes fractionate nitrogen in a similar manner to metazoan, while others found that feeding on protozoans is isotopically invisible.
Incubation experiments	Krill are incubated in laboratory containers, and food is offered in a range of concentrations or mixtures. The removal of food is assessed.	Krill diet, food selectivity, feeding rates	Suitable to study selective feeding on phytoplankton assemblages and seasonal differences in feeding activity.	In confinement, krill and their prey may divert from their natural behaviour due to wall effects, lack of turbulence, hindered vertical migration and swarming, lack of escape options for prey.

Table 5.1B Key findings revealed by each of the methods in Table 5.1A

Method	Important findings
Functional morphology studies	Suh and Nemoto (1987): The lower size limit of filterable particles is 2–3 μm for juvenile and adult *E.s.* Compared to other SO euphausiids, the feeding basket of *E.s.* has the largest filtering area and smallest mesh sizes. *E.s.* are the most efficient filter feeder on small items.
	McClatchie and Boyd (1983): Among euphausiids, the mandibles of *E.s.* have the largest *pars molaris* (= grinding region), indicating herbivory. But in common with omnivorous-carnivorous species, *E.s.* mandibles have spine-like marginal 'teeth', facilitating a piercing of animal prey.
	Ullrich et al. (1991): The gastric mill of *E.s.* has strong cuticular lateral teeth and numerous cluster spines, which are suitable to crush hard-shelled food items, e.g. diatom frustules.
Direct in situ observations	Hamner et al. (1983): When krill orientate in schools and swim rapidly, their feeding basket remains closed (i. e. schooling and intensive feeding are incompatible).
	Marschall (1988): Krill aggregate under rugged sea ice with high algal growth and feed by continuously scraping the ice surface with the tips of their thoracopods while opening and closing their feeding basket.
	Clarke and Tyler (2008): Krill swim or sink to the seabed as deep as 3500 m and feed on phytodetritus by nose-diving into the sediment and filtering the resuspended material.
Assessing the fullness of the krill stomach and gut	Morris and Ricketts (1984): There are more krill with full stomachs during or immediately after the hours of darkness, probably reflecting an increased level of feeding activity at night.
	Schmidt et al. (2014): Krill show regional differences in their feeding activity during winter. Individuals with empty stomachs are common in the Lazarev Sea (~80 %), but rare at South Georgia and in the Bransfield Strait (20 %).
Assessing the colouration of the digestive gland	Kawaguchi et al. (1999): There is in situ evidence that krill are feeding on micro- (>10 μm) and nanophytoplankton (2–10 μm), but not on picophytoplankton (<2 μm).
Gut fluorescence analysis	Priddle et al. (1990): Differences in the gut fullness of 3264 krill from 38 swarms reflect the patchiness of phytoplankton, while intrinsic properties (i.e. krill body length, sex-and-maturity stage), swarm characteristics (i.e. packing density, cross-sectional area), sampling time and depth are of minor importance.
	Perissinotto et al. (1997): Krill ingest ~13 % body carbon day^{-1} in a dense phytoplankton bloom. Gut passage times are 3–4.5 h for juveniles and 6–10 h for adults. Krill populations can consume 0.1–51 % of the local primary production day^{-1}.

Fecal pellet egestion rates	Clarke et al. (1988): High fecal production rates and high C content in pellets (5–14 % of dry mass) suggests that krill energy intake may be 17–28 % body carbon day^{-1}, far exceeding estimates with other methods.
	Atkinson et al. (2012): At high food concentrations, krill feed ‘superfluously’, which facilitates maximum rates of nutrient uptake – i.e. high feeding rates and fast gut passage ensure a constantly high substrate concentration in the gut and therefore a high rate of nutrient gain. This can lead to low absorption efficiencies and therefore high carbon content in krill fecal pellets (up to 30 % of dry mass).
Visual identification of the stomach content	Barkley (1940): During the summer months, stomachs of *E.s.* contain a large amount of diatoms. Species belong mainly to the following groups: Fragilariopsis, Coscinodiscus, Actinocyclus, Asteromphalus and Biddulphia.
	Hopkins and Torres (1989), Hopkins et al. (1993a, b): Protozoa (dinoflagellates, tintinnids, foraminifera, radiolaria, heliozoa) and metazoa (copepods, cnidaria) are regularly found in krill stomachs in autumn, winter and spring.
	Schmidt et al. (2014): Across 92 stations, algae comprised 71 ± 29 %, protozoans 17 ± 21 % and metazoans 12 ± 25 % of the identifiable food volume in krill stomachs. Copepods and protozoans supplement the krill diet year-round and can occasionally be the dominant food source. The relative importance of copepods is highest in ice covered regions during autumn and winter.
Molecular identification of the stomach content	Martin et al. (2006): Krill ingest a broad diversity of taxa, including diatoms, dinoflagellates, cryptomonads, prasinophytes, ciliates, cercozoans, choanoflagellates, turbellarians and sponge larvae. Diatoms are the most prevalent group.
Immuno-chemical analysis of stomach content	Haberman et al. (2002): Krill from the western Antarctic Peninsula feed on the prymnesiophyte *Phaeocystis antarctica*, especially in nearshore areas. However, overall *P. antarctica* comprises a small proportion of the phytoplankton intake by krill.
Fatty acid (FA) biomarkers	Pond et al. (2005): In the vicinity of South Georgia, high growth rates of krill co-occur with intensive feeding on diatoms.
	Schmidt et al. (2006): In a non-bloom, flagellate-dominated system krill are able to sustain moderate growth rates when feeding on athecate dinoflagellates.
	Schmidt et al. (2014): During winter, krill larvae contain variable but sometimes very high proportions of diatom-markers and moderate proportions of copepod-markers in their tissues. In postlarval krill, the role of diatoms and flagellates decreases, and the role of copepods increases with body length.

(continued)

Table 5.1B (continued)

Method	Important findings
Bulk stable isotopes	Stowasser et al. (2012): In the pelagic food web of the Scotia Sea, the TL of *E.s.* is higher than that of salps, similar or lower than that of common pelagic copepods, and lower than that of other euphausiids. In total the system has 4 TL, with krill occupying level 2.5 (i.e. omnivorous).
	Polito et al. (2013): Adult krill (both males and females) have a broader dietary niche and occupy a higher TL than juveniles. While phytoplankton remains life-long an important food source, krill feed on average more carnivorously as their body size increases.
Compound-specific stable isotopes	Schmidt et al. (2006): During spring-summer, krill occupied a higher TL at South Georgia (TL 2.8) and in an ice edge bloom (TL 2.7), than in non-bloom regions of the Scotia Sea (TL 2.5).
Incubation experiments	Haberman et al. (2003): Krill grazing is negligible in cryptophyte-dominated assemblages. In phytoplankton mixture, krill select diatoms over prymnesiophytes (*Phaeocystes*) even when both are of similar size.
	Wickham and Berninger (2007): Krill furcilia larvae can feed on a range of ciliates and on the small copepod *Oithona similis*. In natural autumn assemblages, ciliates are preferential ingested over phytoplankton.
	Meyer et al. (2009), Meyer (2012): Krill ingestion rates show a positive linear response to the available food concentration. However, while for furcilia larvae this functional response has a similar slope year-round (i.e. no seasonal change in feeding activity), adult krill from the Lazarev Sea show a steep slope during summer but gentle slopes in autumn and winter (i.e. seasonal reduction in feeding activity).

lives within swarms, feeding and swarming are necessarily interlinked (see Chap. 8, Tarling and Fielding 2016). High travelling speed and large swarm size may enhance the likelihood of finding patchy food; on the other hand, krill in large dense swarms may be more prone to starvation if food is scarce. Therefore it would be instructive to relate the average krill feeding activity in different swarms to in situ food availability and swarm characteristics such as speed, size, shape and density (Priddle et al. 1990). With indices of feeding activity such as gut fluorescence, stomach/gut fullness or colour of the digestive gland a large number of animals can be assessed in relatively short time and therefore a sufficient temporal-spatial coverage can be achieved. Combined data from different regions and seasons can give an overview about the in situ frequency of 'high', 'moderate' and 'low' feeding activity. This may show that even during summer 'high' feeding activities are relatively rare in the open Southern Ocean.

3. *Relating krill diet to performance indices*. To date there is no study which has quantified all major food items in the krill diet. Visual stomach content analysis gives only information about food sources with digestion-resistant remains and therefore misses out on the numerous soft items such as naked flagellates, athecate ciliates and some metazoa. Ratios of fatty acid trophic markers can indicate changes in the relative importance of food sources (e.g. diatoms vs. flagellates, or diatoms vs. copepods), but conversion to carbon intake is difficult. Newly emerging molecular approaches may offer a way forward (see Sect. 5.14), however, rapid or differential digestion of prey DNA remains an obstacle (Troedsson et al. 2009; see Chap. 7, Jarman and Deagle 2016). The estimation of feeding rates is likewise problematic. Gut fluorescence and fecal pellet egestion of freshly-caught krill are considered to reflect in situ feeding rates but both approaches have severe limitations (Table 5.1). Therefore valuable insights into the effects of food quantity and quality may arise when krill diet is related to performance indices such as egg production rate, lipid content or instantaneous growth rate (Ross et al. 2000; Schmidt et al. 2006; see also Chap. 3, Reiss 2016 and Chap. 4, Meyer and Teschke 2016). In this way the net benefit of a certain feeding environment can be established.

5.5 Ontogenetic Changes in Feeding Activity and Diet

Female krill spawn during summer (November–March) and their offspring develop through a succession of larval stages until they become juveniles the following spring (see Chap. 6, Kawaguchi 2016). After one whole season of growth as juveniles, krill reach adulthood at the beginning of their second year. During this period the body length increases from ~0.6 to ~30 mm and the facility to resist starvation increases. Thus, juvenile and adult krill deposit large amounts of lipid before the winter (~40 % of dry mass, Hagen et al. 2001) and can survive over 200 days without food (Ikeda and Dixon 1982). In contrast, larvae contain small lipid stores (6–25 % of dry mass, Hagen et al. 2001; Meyer et al. 2002a) and require regular food intake (Meyer and Oettl 2005).

The ontogenetic differences in body size and food requirements are reflected in the feeding activity and diet of juvenile and adult krill: First, younger krill have overall a higher feeding activity than adults due to higher metabolic rates and lower lipid stores (Fig. 5.1a). Second, adult krill are stronger swimmers (Huntley and Zhou 2004), which allows them to explore a wider range of habitats (water column, sea ice, seabed) and increases the ability to capture motile prey. Consequently, adult krill have a wider dietary niche than juveniles and are on average more carnivorous (Fig. 5.1b, Polito et al. 2013; Schmidt et al. 2014). Finally, during winter, larval krill are more closely associated with sea ice than adults. This spatial segregation most likely reflects the different balance between the need to feed (high in larvae, lower in adults) and the risk of predation under the ice (low in larvae, high in adults; Quetin et al. 1994). Therefore, larvae krill feed on ice algae and associated heterotrophs during winter, while adults are more likely to starve or occasionally catch larger copepods (Fig. 5.1c, Többe et al. 2010; Schmidt et al. 2014).

Gravid male and female krill differ in their energy expenses and lipid metabolism (Clarke and Morris 1983; Pond et al. 1995; Virtue et al. 1996); however, it seems that their overall food intake and diet remain similar (Priddle et al. 1990; Schmidt et al. 2004, 2006; Polito et al. 2013). Nevertheless, concurrent stable isotope- and fatty acid measurements on individuals from the same swarm indicate the existence of dietary ‘preferences’ (Schmidt et al. 2006). Neighbouring krill can differ by 1–2 ‰ in their δ^{15}N values (~0.5 trophic level) unrelated to sex, maturity stage or body length (Schmidt et al. 2006, Polito, personal communication). This may reduce within-swarm competition for food, but also indicates the complexity of krill feeding behaviour.

5.6 Seasonality of Feeding

It has often been suggested that krill feed on phytoplankton during summer, and when it becomes scarce in autumn and winter they switch to heterotrophic food, benthic material or ice algae, or they cease feeding completely. Now we know that this view is too simplistic. Benthic feeding can occur year-round (Ligowski 2000; Clarke and Tyler 2008; Schmidt et al. 2011). Heterotrophic food such as copepods and protozoans are often abundant within phytoplankton blooms (Leakey et al. 1994) and therefore supplement the diet even in spring and summer (Hopkins et al. 1993a; Schmidt et al. 2006). Depending on the latitude, phytoplankton may be available in winter (Morris and Priddle 1984) and ice algae may be available in summer (Brierley et al. 2002). The krill habitat is highly variable in terms of day-length, ice cover, ocean productivity, water depth, convolution of the coastline and seabed, and therefore seasonal aspects in krill feeding are specific to the region they are living in (see Sect. 5.7). In essence, krill encounter two broadly-defined periods in a seasonal cycle – one where the phytoplankton abundance is sufficient to

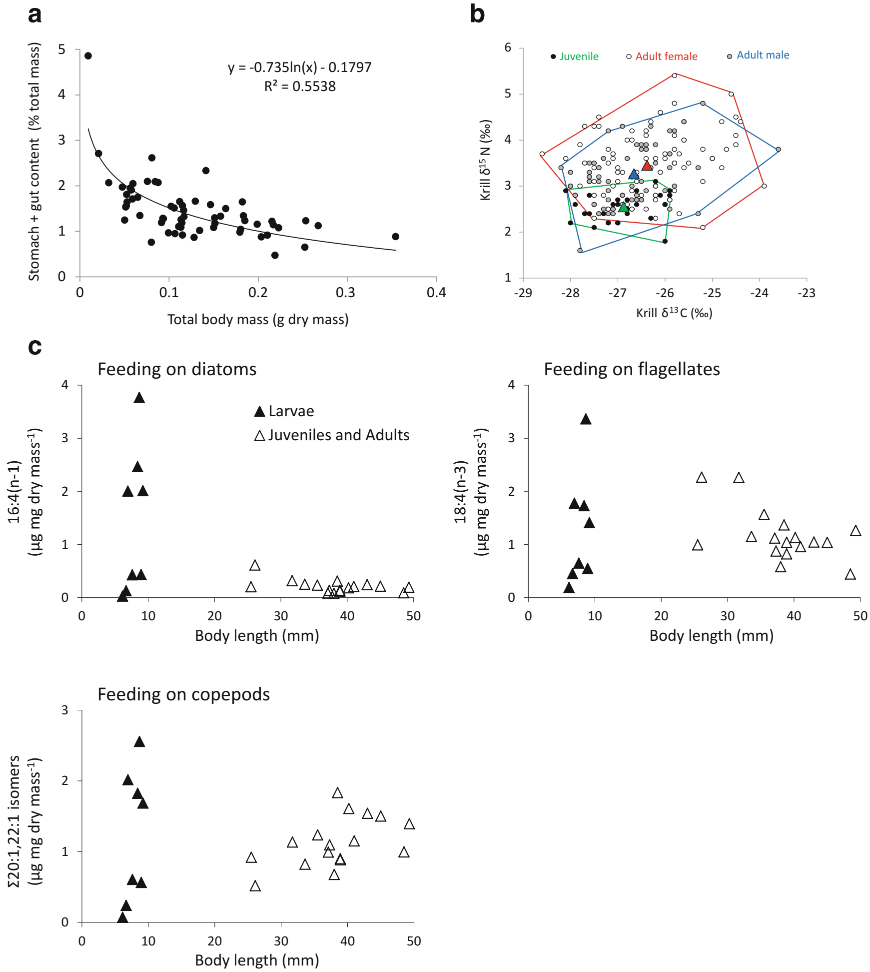


Fig. 5.1 Ontogenetic changes in feeding activity and diet. (**a**) The relative mass of the stomach- and gut content as a function of the total body mass. The panel indicates that a swarm of small krill (0.1 g dry mass) contains on average about twice as much total ingested food than a swarm of large krill (0.3 g dry mass) with the same biomass. Each of the symbols represents a pooled sample of 10 krill with the same body length. The data derived from two summer cruises in the Scotia Sea and at South Georgia (Schmidt, unpublished). (**b**) Trophic level differences between juvenile and adult krill. The plot indicates individual krill (circles); mean values for juveniles (green triangle), adult females (red triangle) and adult males (blue triangle) and the total isotopic niche area for each of them (solid line convex hulls). The data derived from two summer cruises near the South Shetland Islands and the northern Antarctic Peninsula (Polito et al. 2013). (**c**) The amount of fatty acid trophic marker in larval and postlarval krill during a winter cruise in the Lazarev Sea. The data show that feeding conditions for larvae were highly variable, but at some stations superior to postlarval krill. In postlarval krill, ingestion of diatoms and flagellates decreased with body length, while the ingestion of copepods increased. Each of the symbols represents a pooled sample of 10 krill with the same body length (Modified after Schmidt et al. 2014)

grow and spawn (chlorophyll *a*: ≥ 1 µg L^{-1}, Ross et al. 2000; Atkinson et al. 2006), and one where it is not sufficient. The length of the favourable period varies from several months at South Georgia to a few weeks at Bouvet Island or East Antarctica (see Sect. 5.7).

To fulfil their life-cycle, krill have firstly to make maximal use of the phytoplankton blooms to fuel growth, reproduction and the build-up of body reserves. Secondly they need to avoid excessive loss of body condition during non-bloom periods. The first is most likely facilitated by their ability to ingest and process diatoms and co-occurring heterotrophs efficiently (see Sect. 5.11, Pond et al. 2005; Schmidt et al. 2012). They achieve the second by a combination of using lipid stores and feeding on alternative food sources (flagellates, copepods, seabed material, see Sect. 5.7). The seabed for instance can act as a 'food bank', where seasonally high fluxes of phytoplankton and fecal pellets arrive, become buried and degrade only slowly (Smith et al. 2006). Studies on benthic deposit feeders have shown that high-quality organic matter can be available at the seabed even in winter (Smith and DeMaster 2008).

It has also been suggested that krill enter a stage of inactivity (quiescence) during winter, where they reduce their metabolic rates to save energy (Quetin and Ross 1991; Torres et al. 1994; Meyer et al. 2002b; Meyer 2012). This change in behaviour may be mediated by photoperiod (Teschke et al. 2007). However, an alternative explanation is possible. Rather than being an 'overwintering strategy', lower respiration rates during winter may simply reflect lower food intake. Respiration rates of adult krill are on average ~3 times lower in winter compared to summer (Meyer 2012), well within the >fourfold differences seen between fed and non-fed copepods in the laboratory (Kiørboe et al. 1985). Feeding is associated with energy-demanding processes such as absorption of food and biosynthesis of new tissue, which explains the causal link between starvation and reduced respiration rates (Kiørboe et al. 1985). Longer-term starvation may have additional side-effects such as a reduction of the gut surface area and a drop in the activity of digestive enzymes, which will affect subsequent ingestion rates (Kreibich et al. 2008; Wirtz 2013). This may explain why winter krill do not respond to excess food in the laboratory in the same manner as well-fed summer krill (Meyer 2012). There is evidence that krill feeding activity during winter differs between regions of similar latitude (e.g. Lazarev Sea vs. Bransfield Strait, Schmidt et al. 2014) and therefore seasonal feeding behaviour may not be triggered solely by photoperiod.

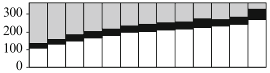
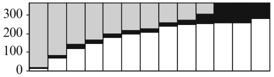
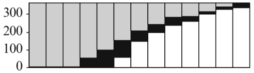
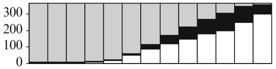
5.7 Regional Differences in Krill Feeding

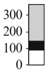
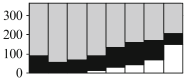
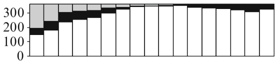
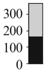
The circumpolar habitat of Antarctic krill spans about 19 million km^2, with the islands of South Georgia and Bouvet as the northern limit (~53°S) and the pack ice zone of the southeastern Weddell Sea as the southern limit (~75°S) (see Chap. 2, Siegel and Watkins 2016). Environmental conditions clearly differ across these regions (Table 5.2). South Georgia, for instance, has an extended shelf habitat with summer surface temperatures of up to 5 °C. Here, the phytoplankton bloom lasts for several months and the area is ice-free even in winter. The Lazarev Sea is another extreme: deep-oceanic, ice covered for 4–9 months year^{-1}, temperatures rarely exceed ~0 °C and the phytoplankton bloom is as short as ~1 month year^{-1}.

These regional differences are reflected in krill feeding activity and diet. At South Georgia, most krill engage in feeding even during winter, they ingest high amounts of lithogenic particles year-round due to both feeding at the seabed and by uptake of glacial flour in the water column. Copepods and protozoans are an important supplementary food source in summer, autumn and winter (Fig. 5.2a, Morris and Priddle 1984; Schmidt et al. 2014). In the Lazarev Sea, feeding during winter seems less common for postlarval krill (Schmidt et al. 2014). However, the occasional consumption of copepods represents a considerable food intake (Fig. 5.2a). During both autumn and winter, copepods contribute substantially to the diet of adult krill in the Lazarev Sea (Fig. 5.2a, b). This is in contrast to the Scotia Sea and Bransfield Strait, where krill feeding on copepods was rarely found, neither when using visual stomach content analysis nor fatty acid trophic markers (Fig. 5.2a, b). At South Georgia, krill feed mainly on small copepods such as *Oithona* spp., whereas in the Lazarev Sea the large winter-active *Calanus propinquus* is a common prey (Schmidt et al. 2014). While *Oithona* spp. is most likely caught when krill are filter-feeding on suspended material, the capture of *C. propinquus* may require directed raptorial behaviour. The relative importance of diatoms vs. flagellates in the krill diet also differs between regions. At South Georgia krill feed mainly on diatoms, but proportions are shifted towards flagellates in the Scotia Sea, Bransfield Strait and Lazarev Sea, especially during summer and autumn (Fig. 5.2b). Long-lasting diatom blooms at South Georgia are favoured by high nutrient supply from the island and shelf area.

The comparison between South Georgia and the Lazarev Sea suggests that in productive shelf areas postlarvae krill are likely to supplement their diet with seabed material, while in the deep ice-covered ocean they feed more carnivorously. Additional, more subtle factors may also play a role, such as the local copepod abundance and species composition (Rudjakov 1996; Atkinson and Sinclair 2000), the type and 'age' of the sea ice (Marschall 1988), the overall productivity of the area and the seabed morphology (Wakefield et al. 2012). To resolve such issues, more cross-regional studies are required. Therefore it is important that krill feeding is examined in a consistent manner, i.e. using the same study method or set of methods. Table 5.2 gives an overview of environmental conditions across the main krill habitats, and available information on krill observations under the ice or at the seabed. This table also indicates that there are regional differences in krill body condition and size structure of the population, which most likely reflect their nutrition. Understanding these regional differences is essential to predict fluctuations in the circumpolar krill stock and to guide a sustainable krill fishery.

Table 5.2 Characteristics of the circumpolar habitats of Antarctic krill

Region	Water depth (m)	Average seasonal length (days) of ice cover (white), phytoplankton bloom (black) and non-bloom (grey)	Krill onshore-offshore distribution	Max. krill body length (mm, 95 % percentile)	Autumn/Winter lipid content (% dry mass)	Krill observed under sea ice	Krill-seabed interactions
Lazarev Sea 57–70°S; 5°W-5°E	3000–5000		Mainly oceanic	52	47	Sp, S, A, W	
Cosmonaut Sea 57–70°S; 30–50°E	1000–5000		Shelf break and off-shelf	51		Sp, S, W	S, A, W
Cooperation Sea, Prydz Bay 57–70°S; 70–80°E	1000–3000		Shelf break and off-shelf	55			S, A
Mawson Sea 57–66°S; 95–120°E	1000–4000		Shelf break and off-shelf	50		Sp	
Somov Sea 58–71°S; 160–170°E	1000–3000		Shelf break	51		S	S
Western Antarctic Peninsula 57–70°S; 65–75°W	500–3000		Inner shelf	56	20	Sp, S, A, W	S, A, W

Bransfield Strait 62–64°S; 58–61°W	100–700		Shelf	54	48	W	S, W
Scotia Sea 53–61°S; 40–50°W	500–3000		Oceanic	53		Sp, A, W	Sp, S
Weddell Sea 78°S; 30–60°W	1000–5000		Unknown	unknown	40	Sp, S, A, W	S
South Georgia 53–54.4°S; 36–41°W	200–1000		Mainly shelf	58	36	–	Sp, S, A, W

(1) Annual length of ice cover, phytoplankton bloom and non-bloom as in Schmidt et al. (2014). Histogram bars represent 1° latitudinal steps from the north (left) to the Antarctic continent (right), except for Bransfield Strait and South Georgia where data are integrated across the whole latitudinal range given

(2) Maximum krill body length (i.e. body length that includes 95 % of the $\geq$40 mm population); Schmidt et al. (2014)

(3) Krill winter lipid content; Hagen et al. (2001), Ju and Harvey (2004), and Schmidt et al. (2014)

(4) Krill observed under sea ice; Guzmán (1983), Naito et al. (1986), Kawaguchi et al. (1986), O'Brien (1987), Kottmeier and Sullivan (1987), Marschall (1988), Stretch et al. (1988), Daly (1998), Hamner et al. (1989), Siegel et al. (1990), Daly and Macaulay (1991), Melnikov and Spiridonov (1996), Brierley et al. (2002), O'Brien et al. (2011), and Flores et al. (2012b)

(5) Krill-seabed interactions, Schmidt et al. (2011)

Sp spring, *S* summer, *A* autumn, *W* winter

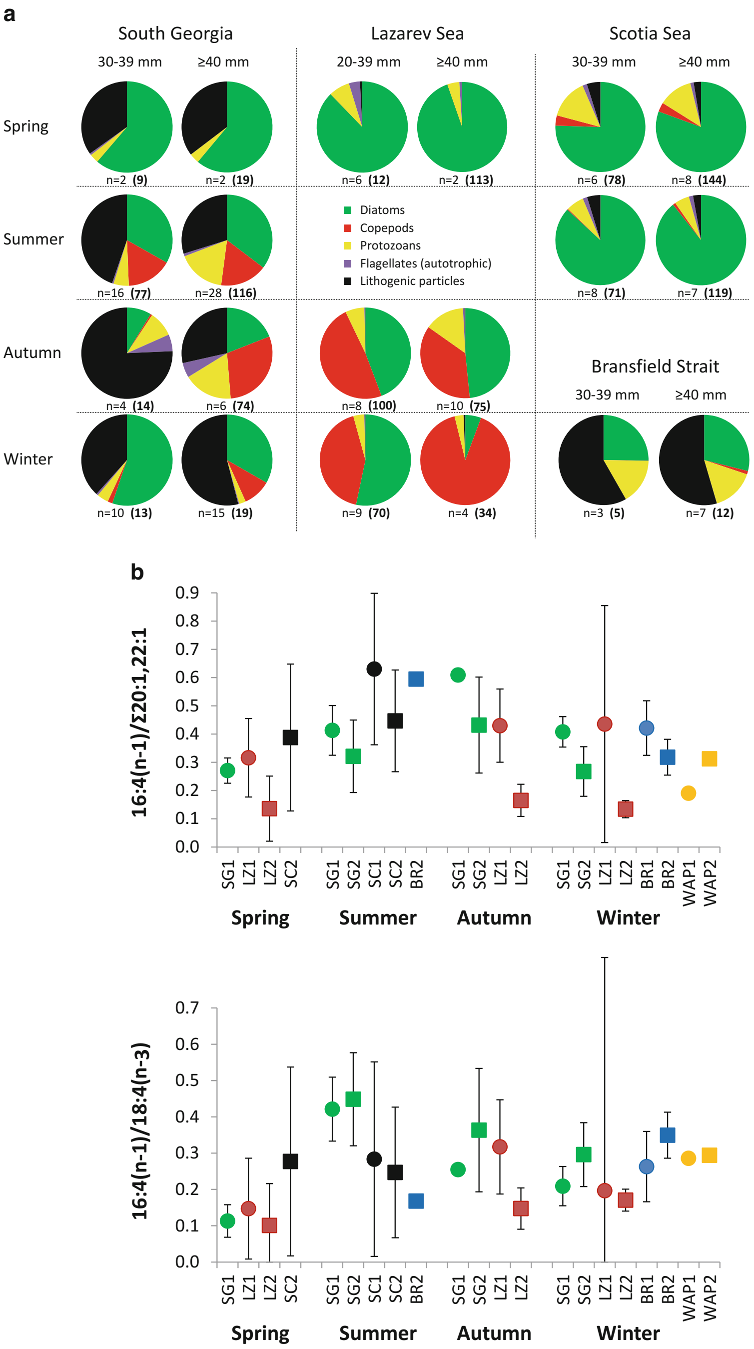


Fig. 5.2 Regional differences in krill diet. (**a**) Krill stomach content at South Georgia (spring, summer, autumn, winter), in the Lazarev Sea (spring, autumn, winter), Scotia Sea (spring, summer) and Bransfield Strait (winter) (Original data in Schmidt et al. 2014). Two size classes of krill were considered, ≥ 40 mm (mainly adults) and < 40 mm (mainly juveniles). n number of

5.8 Ingestion Rates and Functional Response

5.8.1 Ingestion Rates

A previous review of krill energetics (Quetin et al. 1994) concluded that: "We now view *Euphausia superba* as an active organism, perhaps more like a small schooling fish than a scaled-up copepod. *E. superba* has a high energy throughput, perhaps 20 % of body carbon per day or higher, sustained by a high and effective rate of filtration". This radically different view questioned previous approaches whereby feeding rates were derived from incubations in small bottles. However it begs the question of just how to derive real-world feeding rate measurements for krill, and 20 years later this has still not been resolved.

Several authors have compiled daily rations of krill estimated with a wide range of direct and indirect methods (Knox 1994; Perissinotto et al. 1997; Pakhomov et al. 2002). These values range from a few percent to ~28 % with little consensus on what the maximum daily ration might realistically be. In Table 5.3, we compile a series of measurements that may represent maximum ingestion rates of larvae and postlarvae. These values were all derived in bloom conditions in summer, based either on bottle incubations (larvae), gut fluorescence (juveniles) or faecal egestion (adults). With the latter method exceptionally high values were estimated, 17–28 % body C d^{-1}. Here ingestion rates were calculated from fecal pellet egestion rates assuming a carbon absorption efficiency of 70–85 % (Clarke et al. 1988).

However daily rations much greater than 20 % may be unrealistically high for postlarval krill for three reasons: Firstly, krill are known to feed "superfluously" in high food concentrations with fast gut throughput and high egestion rates, which leads to low absorption efficiencies and carbon-rich fecal pellets (Atkinson et al. 2012; Schmidt et al. 2012). Thus, some of the high ingestion rates calculated from carbon egestion and literature values on absorption efficiency may have been overestimates, with the real carbon absorption efficiency being lower. Secondly, maximum in situ growth rates of postlarval krill are equivalent to ~5 % of body C d^{-1} (Clarke and Morris 1983; Atkinson et al. 2006). Such growth rates require a daily ration of no more than 16–19 % when assuming a gross growth efficiency of 0.26–0.32 (Lasker 1960, 1966). The third reason is that, in line with allometric scaling expectations, the mass of the krill stomach content as a percentage of the total

Fig. 5.2 (continued) stations. The number in brackets is the total volume of items identified in the stomach (× 10^6 μm^3) for individuals that had been feeding. (**b**) The ratio of fatty acid trophic markers in krill tissue from South Georgia (SG, green), the Lazarev Sea (LZ, brown), Scotia Sea (SC, black), Bransfield Strait (BR, blue) and the western Antarctic Peninsula (WAP, yellow) during different seasons. Juveniles (1, circles) and adults (2, squares) are presented separately. The following marker fatty acids were used 16:4(n−1) for diatoms, Σ20:1, 22:1 isomers for copepods and 18:4(n−3) for flagellates. The plots are based on data presented in Cripps and Atkinson (2000), Atkinson et al. (2002), Ju and Harvey (2004), Pond et al. (2005), Schmidt et al. (2014), and Reiss et al. (2015)

Table 5.3 Compilation of studies conducted during summer bloom periods in which high (possibly near maximum) daily rations of krill life stages have been determined

Stage	Maximum daily ration (% body C d^{-1})	References
Calyptopis III	25.9	Meyer et al. (2003)
Calyptopis III – Furcilia I	17.8	Huntley and Brinton (1991)
Furcilia I	26.2	Meyer et al. (2003)
Furcilia I–II	8.5	Huntley and Brinton (1991)
Furcilia II	14.6	Meyer et al. (2003)
Juvenile	13	Perissinotto et al. (1997)
Adult	17–28	Clarke et al. (1988)

body mass declines with increasing krill size (Fig. 5.1a). This suggests that on average daily rations of adults are lower than those of larvae (see Table 5.3).

In Fig. 5.3, these maximum daily ration estimates are plotted against a compilation of maximum ingestion rates of pelagic invertebrates ranging from nanoflagellates to fish (Kiørboe and Hirst 2014). For all life-cycle stages of krill the maximum rates exceed those predicted from the regression line, being particularly evident for the postlarvae. Clearly there are caveats with any such attempt to put krill feeding rates into wider context, for example the values have all been adjusted to a temperature of 15 °C using the same Q_{10} value of 2.8 (Kiørboe and Hirst 2014). Nevertheless, even when based on the lower rations for postlarvae of 13–17 % (Table 5.3) and notwithstanding uncertainty over temperature conversions, *E. superba* postlarvae seem to achieve exceptionally high food intake for their size (see Fig. 5.3). In summary, while it seems unlikely that maximum daily rations of postlarvae greatly exceed 20 %, krill are clearly a species with high energy throughput.

5.8.2 Functional Response

Functional responses of *Euphausia superba* feeding rates have been measured in the laboratory both for adults and larvae. A common finding is that feeding rates do not saturate even at high food concentrations (Price et al. 1988; Atkinson and Snÿder 1997; Ross et al. 1998; Meyer 2012; see Chap. 4, Meyer and Teschke 2016). This is in contrast to results of growth studies using the instantaneous growth rate (IGR) method, where modest half saturation concentrations of 0.33 μg Chl *a* L^{-3} (Atkinson et al. 2006) and 0.50 μg Chl *a* L^{-3} (Ross et al. 2000) have been determined.

Several factors may contribute to this finding. First, it may represent "superfluous" feeding (Schmidt et al. 2012) whereby at high food concentrations, feeding rates increase and gut transit time and absorption efficiency decrease, allowing increased total absorption rates of essential molecules. This has been established for

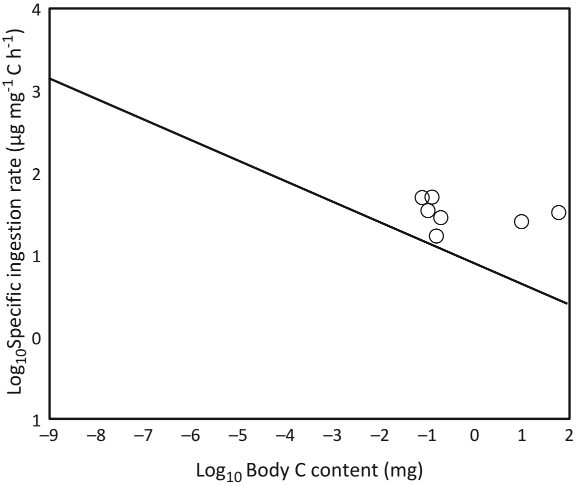


Fig. 5.3 Ingestion rates and functional response. Comparison of high (likely maximum) specific ingestion rates of ontogentic stages of krill derived in summer bloom conditions (Table 5.3) with a literature best-fit regression (Kiørboe and Hirst 2014) across a wide range of pelagic organisms, denoted by the solid line. Krill source data were from the publications in Table 5.3, adjusted to a common reference temperature of 15 °C using a Q_{10} of 2.8 in common with Kiørboe and Hirst (2014). A conservative value for the maximum adult ration (17 %) is plotted for reasons presented in the text. The regression line (slope −0.25) derived from a meta-analyses of 327 maximum ingestion rates for protozoans, flagellates, ciliates, copepods, other crustaceans, euphausiids, amphipods, chaetognaths, cnidarians, ctenophores, tunicates and fish (Kiørboe and Hirst 2014)

copepods (Thor and Wendt 2010) where maximum ingestion rates are controlled by food processing in the gut rather than by food concentration or the ability to feed rapidly (Wirtz 2013). For krill, fast gut throughput rates (Clarke et al. 1988; Pond et al. 1995) and high carbon- and fatty acid concentrations in rapidly egested pellets support the notion of ‘superfluous’ feeding (Atkinson et al. 2012; Schmidt et al. 2012). Secondly, functional response experiments are seldom run for a full 24 h-period, so longer experiments would be needed to test whether the high ingestion rates, measured for instance over 12 h, sustain commensurately high daily ration values. Finally, the low saturation concentration for growth may reflect only the growth in length (mm d^{-1}) measured by the IGR technique; while additional capacity for growth may be channelled into the build-up of gametes or lipid reserves (Hagen et al. 2001). In any case, the discrepancy between functional responses for somatic growth and feeding requires consideration when quantifying the energy budget of krill.

5.9 Effects of Temperature, $p\mathrm{CO_2}$ and Food Size

In future climate scenarios, increased water temperature, reduced pH, increased freshwater run-off and increased abundance of small cryptophytes relative to diatoms are commonly cited combinations of conditions (Flores et al. 2012a;

Kawaguchi et al. 2013; Ducklow et al. 2013; Constable et al. 2014). Even though several of these apply only to part of the krill habitat (e.g. Western Antarctic Peninsula) this section examines the effects of these potential stressors on feeding.

To our knowledge, the direct effect of increased temperature on krill feeding rates has not been measured, probably because it is hard to do so in a laboratory setting due to artefacts associated with containment and temperature acclimation. The only experiment to date examining direct effects of $p\mathrm{CO}_2$ on krill metabolism is by Saba et al. (2012). At $p\mathrm{CO}_2$ concentrations of ~700 ppm, a stress-type response of elevated feeding-, respiration- and excretion rates was found when compared to rates at ambient $p\mathrm{CO}_2$ concentrations.

The notion that krill feed inefficiently on nano-sized particles while salps benefit from decreased food sizes is mentioned increasingly in the context of climate change stressors (see Sailley et al. 2013; Constable et al. 2014). This concept may be based on the observation of low krill feeding rates when a cryptophyte-dominated diet was offered in the laboratory (Haberman et al. 2003). However, it counters other studies which suggest that krill can feed efficiently on small items and have a large predator-prey size ratio (Kils 1983; Suh and Nemoto 1987; Kawaguchi et al. 1999). In Fig. 5.4, available experimental and in-situ studies are combined to derive their food-size spectrum. A major drawback of such studies is that they invariably test only a minor component of the full food spectrum. When offered just one or a few food sources in the laboratory, feeding behaviour can differ substantially from that in natural mixtures in the sea (Wirtz 2014). Nevertheless, these studies document krill's ability to ingest cells as small as 3–4 μm as well as copepods as large as ~3 mm.

While the potential food size ranges across three orders of magnitude, the preferred size is still not clear. Some studies suggest it to be ~20–30 μm (Boyd et al. 1984), or >40 μm (Quetin and Ross 1985), while a laboratory study with a mixture of copepods, algae and protozoans suggested maximal clearance rates were on copepods of ~1 mm (Atkinson and Snÿder 1997). Subsequent field studies, however, suggest that this latter result (and indeed several others in which laboratory-held krill ingested copepods in preference to algae) are laboratory artefacts. Analysing the gut content of krill from a variety of regions and seasons, the modal copepod prosome length based on mandible widths was only 267 μm (Schmidt et al. 2014). This supports the concept that *E. superba* are mainly a filter feeding species that only occasionally catches some larger metazoans.

The optimum prey size for krill is likely somewhere within the range 40–300 μm, and their predator-prey size ratios are not unusually high, compared to other suspension feeders of equivalent size. Krill have perhaps been described as having an exceptionally high predator-prey size ratio because they are often compared with copepods, whose ratios are mainly in the range 10–50 (Hansen et al. 1994). Figure 5.5 illustrates the fact that, among microplankton feeders, predator-prey size ratios tend to increase strongly with grazer size. This brings the optimum predator-prey size ratio for krill to ~1000, in line with other large microphages such as salps and planktivorous fish.

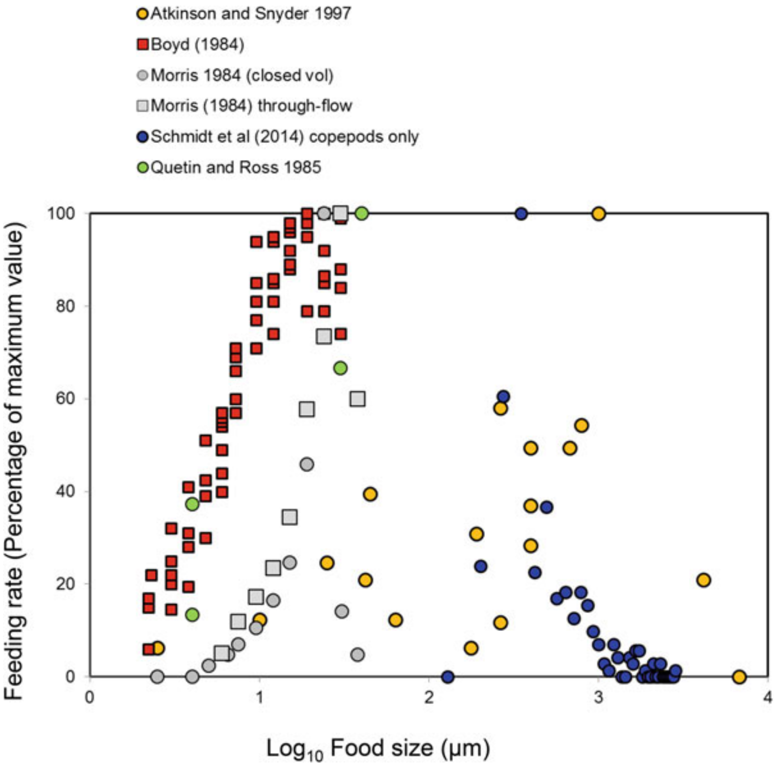


Fig. 5.4 Effects of food size. Compilation of studies that examine *E. superba* feeding rates across a spectrum of food sizes. Results are normalised by expressing them as percentages of the maximum value obtained in each study. For Schmidt et al. (2014) the results are from multiple regions and seasons (see Fig. 5.2a), with copepod prosome lengths calculated from mandible width using Karlson and Båmstedt (1994) and converted to total body length assuming this is 1.3× prosome length (a total of 253 mandibles were recorded and measured). Values in each size category are expressed as percentages of the maximum value, which is 71 mandibles recorded within the category of 350 μm copepod total length. Other values pertain to clearance or ingestion rates (for mixed assemblages of phyto- and zooplankton in Atkinson and Snÿder 1997, and solely phytoplankton in the remaining studies). Food size (x-axis) refers to the maximum linear dimension

In addition to the large predator-prey size ratio, another important trait of krill is their wide range in potential predator-prey size ratios (roughly 20–20,000, by body length). Figure 5.5 shows that *E. superba* can access food items spanning about three orders of magnitude in equivalent spherical diameter. While salps and sardines also display this ability to a lesser extent, the range of available food sizes is far smaller in many copepods (Fig. 5.5). Therefore, in a given volume of water, krill encounter a larger amount of suitable food items than copepods. Based on Southern Ocean biomass spectra there are similar amounts of plankton biomass within equal logarithmic intervals of mass (Tarling et al. 2012). This would imply that for krill

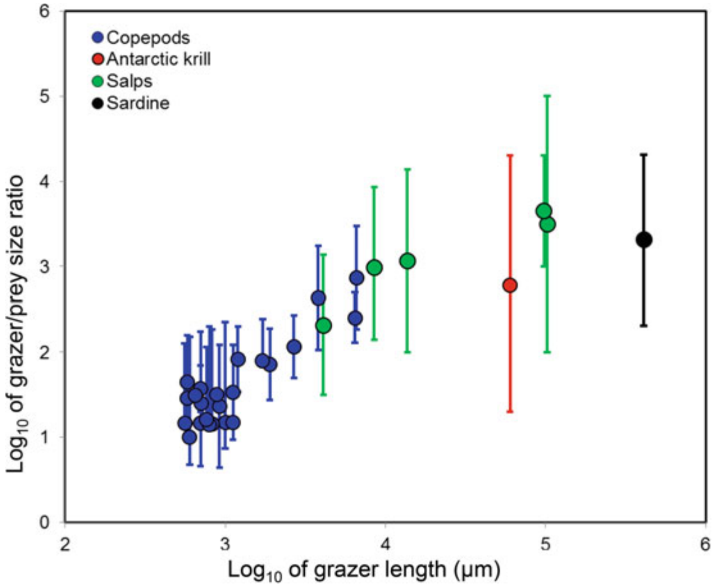


Fig. 5.5 Effects of food size. Compilation of data on optimum and range in predator-prey size ratio (in terms of length or equivalent spherical diameter), plotted against grazer length. Non-krill data are compiled from Hansen et al. (1994), Fuchs and Franks (2010), Wirtz (2012), Saiz et al. (2014), and Nikiloudakis et al. (2012) and references therein. Krill data are derived from Fig. 5.4

with a thousand-fold range in food size the available food concentration could be ~50 % higher than for copepods with a hundred-fold range in food size.

With the rapid warming at the Western Antarctic Peninsula there have been predictions of increased meltwater run-off that may favour the occurrence of cryptophytes over diatoms (Ducklow et al. 2013; Mendes et al. 2013). Diatoms are generally considered of higher food quality for zooplankton than cryptophytes or prymnesiophytes (Ross et al. 2000). Indeed, fast gonad development in krill co-occurs with the spring diatom bloom (Cuzin-Roudy and Labat 1992; Schmidt et al. 2012) and krill are more enriched in polyunsaturated fatty acids (PUFA) when feeding on diatoms rather than copepods (Schmidt et al. 2014). This may imply that the lack of diatoms can have adverse effects on krill development and their nutritional quality for higher predators. However, krill occurrence at the inner shelf is a phenomenon specific to the Western Antarctic Peninsula, while in other regions they have a more oceanic distribution and are therefore less affected by melting glaciers (Atkinson et al. 2008). Moreover, food quality depends on a range of factors such as species composition and status of the bloom. In a study in the Scotia Sea for instance, diatom-dominated diets led to moderate- or high growth rates in krill depending on whether it was a spring bloom near the ice edge or a summer bloom at South Georgia, while a nanoflagellate-dominated diet in the open ocean did likewise support moderate growth rates (Schmidt et al. 2006).

5.10 Feeding Selectivity

Feeding selectivity in krill can occur in several forms. In terms of food size, the mechanical characteristics of the feeding basket will help to set an upper and lower possible size of particles that can be eaten (see Sect. 5.9). Superimposed on that, the feeding basket can be used in different ways (see Sect. 5.3) to achieve different effective mesh sizes depending on food concentration and size (Kils 1983). However, this physics-based selectivity does not explain the finding of Haberman et al. (2003), where laboratory-acclimated krill selected diatoms over *Phaeocystis antarctica* of similar size. Remote chemical detection is a possible selection mechanism employed by copepods (Kiørboe 2011). Alternatively, tasting and post capture rejection may lead to selectivity. However, given the great size of the krill feeding basket compared to the volume of water entrained in a copepod's feeding current, rejection or ingestion of small cells on an individual basis seems unlikely.

In the field, the large behavioural repertoire of krill allows them to switch between food substrates – the water column, the sea ice, the sea bed. Given the mobility of krill, they may be caught in different vertical horizons from where they have been recently feeding. Thus individuals caught from the upper water column can retain tracers of feeding activity either from the overlying sea ice (Meyer et al. 2002a; Stübing et al. 2003) or from the seabed (Ligowski 2000; Schmidt et al. 2014). Such mobility makes it very hard to disentangle the various forms of selectivity that krill may use. With the improvements in filming techniques since the 1980s, further in situ studies may reveal more detail of the actual mechanisms of food selection.

5.11 Food Processing

The stomach and digestive gland are sites of food digestion. In the anterior region of the stomach (cardia) the food is ground and mixed with digestive enzymes. In the posterior part of the stomach (pylorus) the crushed food is filtered and the filtrate is pumped into the digestive gland (Ullrich et al. 1991). The digestive gland is a system of blind-ending tubules consisting of a uni-layer epithelium with special cells for enzyme synthesis and nutrient resorption (Sabarowski and Buchholz 1999). Digestive enzymes are released directly into the lumina of the tubules to act upon the filtered chymus. Coarse food residues are transported into the hindgut, where material is packed into fecal pellets for egestion.

A number of digestive enzymes have been identified from the digestive tract of *E. superba*, including glucanases (e.g. laminarinase, amylase, cellulose, galactosidase), proteases (e.g. trypsin, chymotrypsin) and chitinases (e.g. endo-chitinase, *N*-acetyl-β-D-glucosaminidase) (Mayzaud et al. 1985; Sabarowski and Buchholz 1999; Saborowski 2012). Chitin consists of amino sugar and is therefore of considerable nutritive value. There are various potential sources of chitin in the krill diet, e.g. copepods, diatoms of the genus *Thalassiosira* and moulted cuticles of their fellows. The latter are regularly found in stomachs of freshly-caught krill (Hopkins et al. 1993a, b; Schmidt et al. 2006) and krill have been observed to skilfully handle and ingest moults during laboratory incubations (Hamner et al. 1983). Saborowski (2012) compared the proteolytic activities of *E. superba* with those of *Meganyctiphanes norvegica*, and found more complex digestive properties in *E. superba*, e.g. the expression of four rather than one trypsin isoforms and elevated proteinase activities in the stomach. The author explained these differences with the more herbivorous diet of *E. superba* (Saborowski 2012). Phytoplankton contains less protein than zooplankton, therefore the protein uptake has to be optimised, for example by increasing the digestive enzyme activities and by using multiple endopeptidases, each with slightly different substrate specificities.

Algae are generally considered ‘less digestible’ or ‘low energy’ food, while copepods and athecate protozoans are more ‘easily digestible’ prey. For decapods it has been found that herbivorous larvae adjust to their low energy food with high enzyme activities, rapid gut passage and low absorption efficiency (Le Vay et al. 2001). In contrast, carnivorous larvae show lower levels of enzyme activities but compensate by longer gut retention and higher absorption efficiency (Le Vay et al. 2001). This fits with observations on *E. superba*, where carbon absorption efficiency usually ranges from 72 to 94 % (Kato et al. 1982), although values as low as 42 % have been reported (Schnack 1985a). When feeding on phytoplankton blooms, krill often produce large amounts of relatively carbon-rich, loosely-packed fecal pellets indicating fast gut passage and low absorption efficiency (Atkinson et al. 2012). The benefit of this ‘superfluous’ feeding is that substrate concentrations are constantly high in the stomach, which combined with high digestive enzyme activities leads to high absolute rates of nutrient gain (e.g. mol nutrient absorbed hour^{-1}) (Jumars 2000). Thus, even extensive uptake of ‘indigestible’ lithogenic particles (Schmidt et al. 2011) does not necessarily indicate inefficient feeding, because high enzyme activities and fast gut passage can ensure that significant amounts of the associated organic matter are extracted.

For adult krill, estimates of gut passage time vary from 47 min to ~10 h (Pond et al. 1995; Clarke et al. 1988; Pakhomov et al. 1997; Perissinotto et al. 1997), reflecting differences in food quantity and quality (Pond et al. 1995; Perissinotto and Pakhomov 1996). To evaluate the relative absorption efficiency for specific food components, their ratios can be compared in the diet and the fecal pellets. During a multi-seasonal study in the Scotia Sea, the C:N mass ratio of krill fecal pellets ranged from 4.9 to 13.2 (median 7.8), which was higher than values in krill tissue (3.9) or their food (5.4), pointing to preferential uptake of nitrogen over carbon (Atkinson et al. 2012). There is also evidence that krill can vary the absorption efficiency for individual fatty acids according to their nutritional needs (Schmidt et al. 2012). At an initial stage after the winter, fatty acid absorption was most efficient for the essential PUFAs 20:5(n−3) and 22:6(n−3), while during vitellogenesis when oocysts are supplied with lipidic yolk and grow in size, the uptake of 14:0 and 16:1(n−7) was favoured (Schmidt et al. 2012). The preferential absorption of PUFAs and 16:1(n−7) was also found in laboratory feeding experiments with postlarval krill (Stübing et al. 2003).

5.12 Trophic Overlap with Other Southern Ocean Euphausiids

Seven species of euphausiids occur in the Southern Ocean and the region just north of the Polar Front, with their habitats spanning different latitudes (John 1936; Everson 2000; Mackey et al. 2012). *Euphausia crystallorophias* prefers neritic waters and is the most common euphausiid on the Antarctic continental shelf. It is the only species that prevails in the permanent pack ice zone. *E. superba* and *Thysanoessa macrura* are found from the seasonal pack ice zone to the Antarctic Polar Front. *Euphausia triacantha* and *E. frigida* are distributed from north of the continental shelf break to the Antarctic Polar Front, *Thysanoessa vicina* is dominant in a narrow band on both sides of the Polar Front and *E. vallentini* occurs north of it. While *E. superba* often occupies the upper ~100 m water column, the populations of other species spread from the subsurface down to variable, but usually much greater water depths (Lancraft et al. 1991; Haraldsson and Siegel 2014).

There are only a few studies which have compared the diet of these species using the same methodological approach (Table 4.4). Examinations of the feeding apparatus have shown that the basket of *E. superba* has a larger filtering area and finer mesh sizes than that of the other euphausiids. The feeding baskets of *E. vallentini*, *E. crystallorophias* and *E. frigida* have medium-size meshes, and that of *E. triacantha* has coarse meshes. Therefore, *E. superba* seems better adapted to filter-feed on small particles than the other euphausiids. In agreement with this morphology, *E. superba* contained more diatom indicating fatty acids in their tissues and occupied a lower trophic level when analysed together with other species (Table 4.4). According to their fatty acid composition, *E. triacantha* and *T. macrura* are the most carnivorous species. However, *E. crystallorophias* has also been described to feed on metazoans, including polychaetes, pteropods and coelenterates (Hopkins 1987). At the same time, relatively high proportions of the fatty acids 16:1(n – 7) and 18:4(n – 3) indicate that *E. crystallorophias* also graze on phytoplankton (Kattner and Hagen 1998). Despite living in the pack-ice region, *E. crystallorophias* seems not to inhabit ice crevices or to scrape algae from beneath the ice (O’Brien 1987; Nordhausen 1994), unlike *E. superba*. However, *E. crystallorophias* have been caught and filmed at the seabed (Atkinson, unpublished observations) and benthic diatoms were found in their stomachs (Kittel and Ligowski 1980). Given the overlapping habitats of the Southern Ocean euphausiids, further comparative studies of their diet and food processing would be valuable.

5.13 Ecosystem Implications of Krill Feeding

5.13.1 *Grazing Impact on Phytoplankton*

Primary production in the Southern Ocean may be limited by three factors: nutrients, light and grazing (Venables and Moore 2010). During a scientific cruise in the Scotia-Weddell Sea it was observed that a krill swarm grazed down a diatom dominated bloom within a few hours (Smetacek and Veth 1989). This is not surprising because large krill swarms may contain up to 10,000–30,000 individuals m^{-3} (Hamner et al. 1983), each capable of clearing several litres per hour (Quetin et al. 1994). However, since swarms are local phenomena it is not to be expected that krill can graze down phytoplankton across large areas (Atkinson et al. 2014). Thus, krill grazing impact is highly variable, even within the same region and season (*see* Pakhomov et al. 2002, their Table 5.4). High rates (40–420 % of daily primary production) have been observed near the South Shetland Islands (Holm-Hansen and Huntley 1984), in the Lazarev Sea (Perissinotto et al. 1997), in the Bransfield Strait (von Bodungen 1986), at the western Antarctic Peninsula (Ross et al. 1998), in the Prydz Bay Region (Samyshev 1991) and at South Georgia (Pakhomov et al. 1997).

At the eastern side of South Georgia, a negative relationship was found between krill density and phytoplankton abundance (Whitehouse et al. 2009). Calculations confirmed that krill grazing rates exceeded the phytoplankton growth rates in this area (Whitehouse et al. 2009). Further downstream, along the island, ample supply of micro- and macronutrients promoted higher primary production rates, while lower krill densities had less grazing impact. Here the relationship between krill- and phytoplankton abundance was positive (Whitehouse et al. 2009). Both high krill densities and low chlorophyll *a* concentrations are a recurring phenomenon at the eastern side of South Georgia (Fig. 5.6), which indicates that in this region phytoplankton is often under ‘top-down’ control by krill.

In addition to reducing phytoplankton stocks, krill can also modify its species composition. Near the Antarctic Peninsula, Kopczynska (1992) found strong evidence that both deep mixing and krill grazing act to suppress diatom blooms and cause flagellates to dominate. Likewise, Jacques and Panouse (1991) found in the Weddell/Scotia Confluence area a rapid change from a high biomass netplankton community to a nanoplankton system and interpreted this as an effect of krill grazing. Larval krill may also be important phytoplankton grazers as a study in the Bellingshausen Sea has shown (Pakhomov et al. 2004).

5.13.2 *Nutrient Recycling and Mobilisation*

Traditionally, microheterotrophs are considered the main agents in nutrient recycling. However, Antarctic krill play a crucial role in some parts of the Southern Ocean due to their large biomass, intensive feeding and access to food sources

Table 5.4 Dietary differences between *E. superba* and other Southern Ocean euphausiids

Feeding indicator	Characteristics	E. s.	T. m.	E. c.	E. f.	E. t.	E. v.	References
Body length (mm)		60	37	41				
Morphology of the feeding basket (adults)	Lower limit of filterable particle sizes (μm)	2–3		16–23	15–19	27–39	8–11	1
	Filter area (mm^2)	277		45	15	45	28	1
Fatty acid trophic marker (autumn)	Diatoms – 16:4(n−1) (% of total FA)	0.7	0.2		0.3	0.3		2, 3
	Flagellates – 18:4 (n-3) (% of total FA)	2.0	1.0/ 1.6	3.4	0.9	1.1		2–4
	Copepods – 20:1 (n-9) (% of total FA)	1.1	1.1/2.3	1.3	1.4	2.1		2–4
Trophic level based on $\delta^{15}N$ values		2.5	3.1	3.2	3.0	3.3		5
Stomach content	Spring	Phytoplankton, protozoans	Phytoplankton, invertebrate eggs		Phytoplankton, invertebrate eggs			6
	Summer		Metazoans, phytoplankton, protozoans	Metazoans, phytoplankton, protozoans				7

(continued)

Table 5.4 (continued)

Feeding indicator	Characteristics	E. s.	T. m.	E. c.	E. f.	E. t.	E. v.	References
	Autumn	Phytoplankton, protozoans, metazoans	Metazoans, phytoplankton, protozoans					8, 9
	Winter	Phytoplankton, protozoans, metazoans						10

E. s. *Euphausia superba*, T. m. *Thysanoessa macrura*, E. c. *Euphausia crystallorophias*, E. f. *Euphausia frigida*, E. t. *Euphausia triacantha*, E. v. *Euphausia vallentini*

(1) Suh and Nemoto (1987), (2) Stübing and Hagen (2003), (3) Kattner and Hagen (1998), (4) Hagen and Kattner (1998), (5) Stowasser et al. (2012) and Stowasser unpublished, (6) Hopkins et al. (1993a), (7) Hopkins (1987), (8) Hopkins (1985), (9) Hopkins and Torres (1989), (10) Hopkins et al. (1993b)

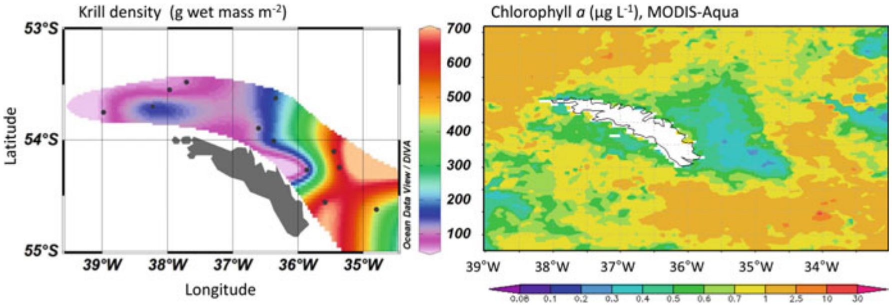


Fig. 5.6 Krill grazing impact on phytoplankton. Spatial overlap between the region of high krill density (left) and low chlorophyll a concentrations (right) at the eastern side of South Georgia. Here the phenomenon is illustrated with data from summer 2010/2011 (Fielding and Schmidt, unpublished), but has also been encountered during other seasons (e.g. Whitehouse et al. 2009)

which are less efficiently used by microbes, e.g. lithogenic particles or large, silicified diatoms (Hamm et al. 2003). While krill grazing reduces phytoplankton stocks, their simultaneous regeneration of nutrients promotes new growth. One example is their excretion of ammonium. Many phytoplankton species prefer the uptake of ammonium over nitrate for energetic reasons (Dortch 1990), and the amount of ammonium released by krill covers a significant part of the primary producers requirements at South Georgia (Atkinson and Whitehouse 2001; Whitehouse et al. 2011) and at the Western Antarctic Peninsula (Lehette et al. 2012).

Another example is the mobilisation of iron by krill, which is often a limiting nutrient in the Southern Ocean. Krill not only recycle iron when grazing on phytoplankton (Tovar-Sanchez et al. 2007), they also introduce new iron into the foodweb when feeding on lithogenic particles from the seabed or glacial outlets (Schmidt et al. 2011). Acidic digestion and mechanical impact during gut passage mobilise some of the iron attached to the lithogenic particles (Lewis and Syvitski 1980). Dissolved iron released by krill can cover >30 % of the iron demand during a phytoplankton bloom on the north-western shelf of South Georgia (Schmidt et al. unpublished data).

Krill feeding is also a major source of dissolved organic carbon in the Southern Ocean, which stimulates microbial activity and bacteria-mediated nutrient recycling (Ortega-Retuerta et al. 2009; Ruiz-Halpern et al. 2011; Arístegui et al. 2014). In common with releases of ammonium and iron, DOC excretions can lead to higher primary production rates. These examples illustrate that ocean productivity is a complex phenomenon, initially set by physical and geochemical nutrient supply, but enhanced in intensity and duration by biological processes which facilitate the mobilisation and recycling of these nutrients.

5.13.3 Repackaging of Material into Fecal Pellets

During krill gut passage, undigested components are packaged into fecal pellets. Depending on diet and food processing, these fecal pellets are highly variable in size, carbon content, density and therefore sinking rate (Atkinson et al. 2012). The carbon content of krill fecal pellets varies from 0.8 to 29 % of dry mass (median ~10 %) and the sinking rates from 16 to 1218 m d^{-1} (McDonnell and Buesseler 2010; Atkinson et al. 2012).

The fate of these pellets depends on a number of factors, including the depth of release, water column mixing, structure and abundance of the mesopelagic community. Broadly, there are three scenarios: Some pellets are eaten and remineralised within the surface layer (Cadée et al. 1992; Gonzalez 1992). Others sink out of the mixed layer and provide nutrient-rich food to bacteria, protozoans, copepods and other scavengers in the ocean's twilight zone (von Bodungen 1986; Steinberg et al. 2008; Manno et al. 2015). The remainder reach the deep ocean or seabed and contribute to the long-term sequestration of atmospheric carbon (Wefer et al. 1988; Manno et al. 2015).

Paradoxically, it is krill pellets that are mostly found in sediment traps even though salps can be just as numerous in the Southern Ocean and their pellets tend to sink even faster (Pakhomov et al. 2006). One suggested mechanism is that krill occur in swarms and produce a 'rain' of pellets which can exceed the repackaging abilities of scavengers. Significant particle export via krill fecal pellets has been reported from sediment trap studies at the Western Antarctic Peninsula (McDonnell and Buesseler 2010; Gleiber et al. 2012), Bransfield Strait (von Bodungen 1986; Wefer et al. 1988), near the South Shetland Islands (Schnack 1985b), Weddell-Scotia area (Cadée et al. 1992; Gonzalez 1992), Weddell Sea (Bathmann et al. 1991; Gonzalez et al. 1994), Prydz Bay (Whiteley 2003), Davis Sea (Suzuki et al. 2003) and near South Georgia (Priddle et al. 1995; Manno et al. 2015). Further studies are required to clarify the dual role of krill fecal pellets promoting either the recycling of carbon and nutrients in surface waters or their export to depth.

5.13.4 Krill as a Food Source

The high abundance, relatively large body size (4–6 cm), and appearance as dispersed individuals as well as dense swarms makes krill a favourable food source for a range of predators, including squid, fish, benthic fauna, sea birds, penguins, seals and whales (see Chap. 9, Trathan and Hill 2016). Krill are considered a high quality lipid and protein source, with unique abundance of the oxmega-3 polyunsaturated fatty acids (PUFA) eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) (Gigliotti et al. 2011). The latter are attributed to krill consuming marine micro-algae (Kolakowska et al. 1994), with most of the EPA deriving from diatoms and DHA from dinoflagellates (Dalsgaard et al. 2003).

Both lipid- and PUFA content in krill vary with season, region, body size and large-scale climatic conditions (Hagen et al. 2001; Ruck et al. 2014; Schmidt et al. 2014; Reiss et al. 2015). High krill lipid content coincides with ice cover and low temperatures (Ruck et al. 2014), while high PUFA levels are associated with a diatom diet (Schmidt et al. 2014). Differences can be considerable, for instance, a 20 % reduction in lipid content co-occurred with a 1–2° increase in temperature (Ruck et al. 2014), and the PUFA content was ~50 % lower in krill feeding on copepods rather than diatoms (Fig. 5.7). Therefore, rising water temperatures and the replacement of diatoms by other species, as predicted for Southern Ocean climate change scenarios (Vaughan et al. 2003; Mendes et al. 2013) may lead to significant reductions in krill lipid- and PUFA content. This has implications both for krill and their dependant predators, as lipids form energy stores for overwintering, and PUFA have key structural and regulatory roles in organisms (Dalsgaard et al. 2003; Trumble and Kanatous 2012).

High fluoride levels in Antarctic krill have attracted attention because they are toxic to many terrestrial vertebrates. Thus, to allow consumption by domestic animals or humans, fluoride has to be removed and those expenses adversely affected the economics of krill exploitation in the past. Natural predators of krill seem to be immune to these toxic effects, and build up exceptionally high fluorine concentrations in their bones (Schneppenheim 1980). In turn, this has led to the application of fluorine as a biotracer of krill in penguin diets (Thomas et al. 2013). High fluoride levels are not restricted to *E. superba* but are found in several Southern Ocean euphausiids and across a range of other Antarctic invertebrate taxa (Sands et al. 1998). There appears to be a process of active fluorine uptake but the mechanisms and reasons for this remain elusive. One possible explanation is that fluoride is taken up as an exoskeleton hardener. This is supported by Sands

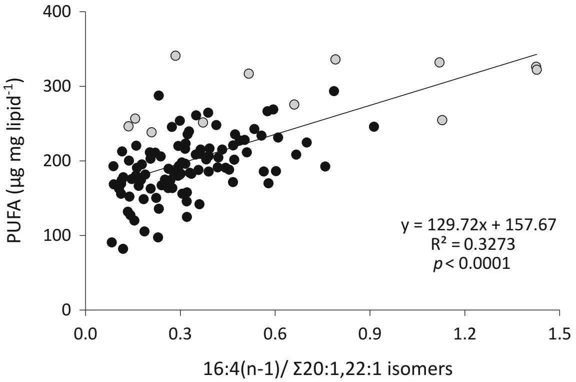


Fig. 5.7 Krill as a food source. Krill PUFA content as a function of their feeding on diatoms vs. copepods. The fatty acid 16:4(n−1) is used as a marker for diatoms and the Σ20:1, 22:1 isomers as marker for copepods. *Grey dots* indicate larval krill and *black dots* postlarval krill. Each of the *symbols* represents a pooled sample of 10 krill with the same body length (Modified after Schmidt et al. 2014)

et al. (1998) who found the highest fluoride concentrations in krill mouthparts, which need strengthening to handle large, heavily silicified diatoms (Hamm et al. 2003).

5.14 Future Prospects

The process of feeding and nutrition shapes almost all aspects of krill biology in some way or other. However, this chapter has shown that the topic of feeding is so hard to study without artefacts that progress has been slow over the last century. So what major knowledge gaps remain, which methods have told us most in the past, and are there any promising new techniques on the horizon?

Krill nutrition is included either directly or indirectly in many conceptual and numerical models of Southern Ocean food webs and biogeochemical cycles. Probably the major single challenge is to encapsulate, in a numerical way, the enormous flexibility of krill feeding behaviour. For instance the interaction of ice type, water depth and water column food levels might dictate the time budgets for krill life stages between ice, seabed and water column. A further facet to this is the great regional variability in the biology of *Euphausia superba* around Antarctica. For example their basic onshelf-offshelf distribution differs radically between the Western Antarctic Peninsula, the Scotia Sea and the Indian sector (Atkinson et al. 2008) and this is corresponds with fundamental regional differences in feeding and overwintering strategy (Schmidt et al. 2014). Clearly we should not generalise about krill from studies in just one place, but rather understand what is causing these differences. Do they represent highly flexible behaviour of a single population or specific subpopulation-level responses?

Looking back at the observations relating to krill feeding over the last century, most progress has been made, in our opinion, by in-situ – based approaches. While laboratory incubations of krill are suitable to study certain aspects of their behaviour and the processing of food, other topics such as food selectivity on mobile prey or feeding rates are certainly affected by the confinement and pre-conditioning of krill. The "natural" approach includes the breakthrough photographic observations of Marschall (1988), Hamner and Hamner (2000), and Clarke and Tyler (2008) which have changed the way we think about krill, even though they are not always accompanied by a weight of numerical data. Authors have repeatedly stressed that a social species like krill needs to be studied in situ, within its natural schooling element (Ritz et al. 2011). However, this in no way restricts us to acoustic-, photographic- or diver observations. Many of the references cited in this chapter in fact entail "in-situ" based approaches. Their authors have caught krill from a multitude of distinct schools and then either instantly frozen them for biochemical or microscopical analyses, or immediately incubated them to determine excretion, egestion or moulting rates that still reflect the in situ feeding conditions.

Several new opportunities and technologies may help us to progress our understanding of krill feeding and nutrition. High-throughput molecular techniques are advancing, and Next Generation Sequencing (NGS) is starting to allow us to read thousands of recovered gene sequences from plankton samples (Lindeque et al. 2013; see also Chap. 7, Jarman and Deagle 2016). DNA digests rapidly in the stomach (Troedsson et al. 2009) and differential digestion of prey is a potential bias. However this approach is not limited to prey with identifiable hard parts and unlike some of the targeted Polymerase Chain Reaction (PCR) approaches (Töbe et al. 2010), the detectable suite of prey items are not restricted to those previously selected for amplification (Pinol et al. 2014). This ability of NGS to cover the diversity of potential prey items is a great advantage, notwithstanding the fact that many of these sequences may not yet be in any molecular reference database (Lindeque et al. 2013). NGS methods can be standardised to make them transferable between laboratories, which would allow a large scale study of krill feeding behaviour that is so valuable.

A message emerging from this chapter is that no single diet method is suitable on its own, and combining multiple methods in a standardised manner across multiple years, seasons or regions is needed. NGS is only just starting to be used to examine marine invertebrate diets (O'Rorke et al. 2012), and while it will not replace existing methods, it promises to be a highly complementary approach. As an example, fatty acid markers and lipid content of krill are commonly measured, and these would provide time-integrated indices of diet and feeding performance as an ideal complement to NGS-type snapshots of diet. Alongside in-situ indices of performance such as the Instantaneous Growth Rate (IGR) method or morphometric condition indices, it will be possible to make the link between available food, the feeding process and the value of this food for krill.

Another development that may help us to understand krill feeding and nutrition may come from the krill fishery (Kawaguchi and Nicol 2007). The current krill fishery is dominated by Norway, who target high quality products for omega-3 food supplements (Nicol et al. 2012). These vessels are intensive samplers of krill; for example they have supplied frozen krill for diet studies to cover the winter period that is poorly accessible to science cruises (Schmidt et al. 2014). Like krill predators the fishery benefits from specimens with high PUFA-content. As this quality is continuously monitored aboard ship during year-round fishing, this could provide insights into nutrient transfer through the food web.

In summary, krill nutrition and feeding behaviour form the link between the biogeochemical part of the food web and fisheries- or predator-based models (Murphy et al. 2007, 2012; Hill et al. 2012). Even though krill feeding is not parameterised explicitly in some of these models it is still important. For example changing sea ice concentrations can affect krill recruitment, but while this is likely via larval feeding success, the mechanisms are debated (Lowe et al. 2012). Other potential stressors of climate change, such as warming or decreased pH, may mean increased food requirements to compensate for higher metabolic costs (Saba et al. 2012). Likewise, increased glacial meltwater and cryptophytes may have affects through feeding mechanisms or food quality. In turn, krill have been suggested to exert "wasp-waist" control on the rest of the food web, namely top-down on levels below them and bottom up on their predators, although the mechanisms and strengths of these controls are still unclear (Atkinson et al. 2014). Understanding such dynamics, and incorporating them into emerging modelling approaches (Litchman et al. 2013; Murphy et al. 2012) requires new and existing methods to be combined, and applied across larger spatial and temporal domains.

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