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**KRILL MOTION IN THE SOUTHERN OCEAN:
QUANTIFYING IN SITU KRILL MOVEMENT BEHAVIORS AND
ENERGETICS**

**BY
MARY KATHRYN KANE**

**A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
IN
OCEANOGRAPHY**

UNIVERSITY OF RHODE ISLAND

2019

DOCTOR OF PHILOSOPHY DISSERTATION
OF
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2019

ABSTRACT

Krill are a major link in the transfer of carbon between primary production and upper trophic level organisms, like whales and penguins, in the Southern Ocean. However, not much is known about *in situ* individual krill behaviors, and there have been no seasonal comparisons of individual krill motility in the Southern Ocean. To address how individual krill movement behaviors and energetic requirements shift between seasons, we used a novel stereo-camera and environmental sensor system to observe krill in three bays in the Western Antarctic Peninsula in May-June 2013 (i.e., the late austral autumn) and December 2014 (i.e., the late austral spring). Krill abundances and movement behaviors were determined from *in situ* image sequences collected for up to 10 minutes at specific depths throughout the water column, up to 625 m deep; using a semi-automated tracking method, 3345 individual krill tracks were collected. We found that seasonal changes in individual krill behaviors coincided with seasonal shifts in krill vertical distributions. During late spring, net upward swimming direction ($0.9 \pm 2.1^\circ$ from horizontal) and vertical velocity (0.3 ± 0.2 Body Lengths (BL) s^{-1}) resulted in shallower maximum abundances of krill within the water column proximate to near-surface phytoplankton distributions. During late autumn, krill swimming patterns tended downward, including swimming direction ($-5.2 \pm 0.8^\circ$ from horizontal) and vertical velocity (-0.1 ± 0.0 BL s^{-1}), leading to deeper distributions proximate to the benthos. Individual krill motility was greater in spring than autumn, as evidenced by a significant increase in swimming speeds (5.4 ± 0.2 BL s^{-1} vs. 2.8 ± 0.0 BL s^{-1}) and turning rates ($120 \pm 5^\circ s^{-1}$ vs. $106 \pm 2^\circ s^{-1}$); however, krill were capable of swimming just as quickly in late autumn as late spring. Furthermore, we found that krill consumed up to 18% of their

carbon weight (CW) in late spring and up to 11% CW in late autumn, larger than the estimates of carbon requirements currently assumed in most krill models. Despite krill consuming more carbon in late spring than late autumn, krill required 15 - 48% higher concentrations of carbon in the water column in late autumn than late spring to cover energetic costs, likely due to the decrease in prey encounter rates with decreasing swimming speeds. Moreover, modeled diel shifts in krill motility demonstrated how shifts in krill swimming speeds can result in different energetic costs and prey concentration requirements. The most ideal motility pattern for krill to minimize energetic requirements and maximize prey encounter rates was to swim faster when feeding and swim more slowly when not feeding. Additionally, we found that krill motility shifts with changes in krill aggregation density; krill swimming speeds increased by 39% and 42% between solitary krill and krill in aggregations with densities $>10 \text{ krill m}^{-3}$ and $>1 \text{ krill m}^{-3}$ in late autumn and spring, respectively. The relationship between swimming speed and density was particularly strong during light periods, with krill swimming speeds increasing by 34% and 91% between solitary krill and krill in dense aggregations in late autumn and spring, respectively. Modeling of krill energetics suggest that individual krill in dense aggregations may be able to cover their energetic costs at 17 - 19% lower prey concentrations than solitary krill. The results of this thesis show that krill remain important consumers of lower trophic levels throughout the year along the Western Antarctic Peninsula due to their active movement in both late autumn and spring, although krill consume more prey in late spring due to higher energy requirements. Moreover, the results imply that the seasonal shifts in krill vertical distributions are caused by changes in individual krill swimming behaviors; this was

likely driven by the shift in prey resource, with phytoplankton in surface waters being preferred in late spring and the sediment being the primary source of food in the late autumn. These results also suggest that denser krill aggregations will intensify krill contributions to local biogeochemical cycles, food web dynamics, and benthic-pelagic coupling.

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PREFACE

This doctoral dissertation is presented in manuscript format and is subdivided into five chapters. Chapter One is a general introduction describing what is known about krill physics and physiology, behaviors, and aggregations, and the knowledge gaps in krill movement behaviors which I address in this dissertation. Chapter Two is titled “Krill Motion in the Southern Ocean: quantifying *in situ* krill movement behaviors and distributions during the late austral autumn and spring” and was published in the scientific journal Limnology and Oceanography on Sept. 27, 2018. Chapter Three is titled “Seasonal Shifts in Krill Energetic Requirements Due to Changes in Individual Krill Movement Behaviors.” Chapter Four is titled “Shifts in Individual Krill Motility With Changes in Aggregation Density.” Chapter Five serves as a reflection on our findings about krill motility in different seasons and considerations of future work needed to address remaining knowledge gaps.

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CHAPTER 1

GENERAL INTRODUCTION

Introduction

Krill are important in the Southern Ocean carbon cycle as key links between lower trophic organisms, such as phytoplankton and copepods, and upper trophic organisms, like whales and seals (Quetin & Ross 1991; Ballerini *et al.* 2014; Saba *et al.* 2014). They contribute to benthic-pelagic coupling, nutrient recycling, and carbon sequestration in the Southern Ocean (Le Fèvre *et al.* 1998; Tovar-Sanchez *et al.* 2007; Lehet *et al.* 2012). Additionally, the Antarctic krill fishery is the largest fishery by tonnage in the Southern Ocean (Nicol *et al.* 2011; Atkinson *et al.* 2012a). As such, a large emphasis has been placed on researching this keystone taxon in the Southern Ocean.

The largest focus of krill research has been on determining krill abundances and distributions throughout the Southern Ocean (Atkinson *et al.* 2012a). While krill have a circumpolar distribution around Antarctica, the majority of their biomass is concentrated within the Southwest Atlantic sector of the Southern Ocean near the Antarctic Peninsula (Atkinson *et al.* 2008). The Antarctic Peninsula region may be an important overwintering habitat for krill larval stages and is thought to be a region key to repopulating some of the surrounding areas, such as South Georgia (Priddle *et al.* 1988; Witek *et al.* 1988; Siegel 1992; Hofmann *et al.* 1998; Murphy *et al.* 1998). For this reason, a number of studies have focused on modeling krill growth rates and potential migration from the Antarctic Peninsula to South Georgia across the Scotia Sea (Hofmann & Lascara 2000; Fach *et al.* 2002, 2005; Atkinson *et al.* 2006; Richerson *et al.* 2015).

Studies conducted in the last few decades have also found that krill inhabit a larger portion of the vertical water column than previously thought and frequently exploit prey resources at depths up to 3000 m on a regular basis (Kawaguchi *et al.* 1986; Ligowski 2000; Clarke & Tyler 2008; Kawaguchi *et al.* 2011; Schmidt *et al.* 2011, 2014). While large-scale population distributions have received a large amount of attention, studying individual and local aggregation krill behavior has been more complicated and thus less well-studied.

Individual krill behavior has been studied using a variety of methods, including laboratory studies and *in situ* observations from cameras, acoustics, and SCUBA divers (Hamner & Hamner 2000; Nicol & Brierley 2010; Atkinson *et al.* 2012a; Tarling & Fielding 2016). Laboratory studies are used to investigate krill physiology and measure the behaviors of both individual and small groups of krill. These studies further our understanding of how individual krill behave and how various conditions, such as different temperatures and salinities, affect their physiology and metabolism (McWhinnie & Marciniak 1964; George 1984; Price 1989; Aarset & Torres 1989; Ngan *et al.* 1997; Kawaguchi *et al.* 2010; Murphy *et al.* 2011, 2013). *In situ* observations enable descriptions of larger krill aggregations and behaviors, as well as some measurements and descriptions of *in situ* individual krill behavior (Hamner *et al.* 1983; O'Brien 1987; Gutt & Siegel 1994; De Robertis *et al.* 2003; Klevjer & Kaartvedt 2011; Tarling & Fielding 2016). The combination of studies has provided a clearer picture about how krill thrive in the seasonally dynamic and complex Southern Ocean.

Physics and Physiology

Krill are entirely pelagic organisms and must continuously move throughout their

adult life (Kils 1981). To swim, krill beat their pleopods, or swimming appendages, in a metachronal gait pattern, where the five pairs of pleopods move in lag phase motion with one another, with the last pair beginning the pattern (Kils 1981; Murphy *et al.* 2011). The flow generated by this gait is then jetted out below and behind the krill body, which generates lift and propels the krill forward (Kils 1981; Yen *et al.* 2003; Catton *et al.* 2011; Murphy *et al.* 2011). Krill can increase their swimming speeds by: (1) increasing the amplitude of their beats by broadening their strokes; or, (2) increasing the frequency of their beats by moving their pleopods more quickly (Johnson & Tarling 2008; Murphy *et al.* 2011). Krill respiration rates increase with increasing swimming speeds above 3 cm s⁻¹ (Torres & Childress 1983; Swadling *et al.* 2005). At swimming speeds below 3 cm s⁻¹, krill respiration rates remain within routine metabolic rates; thus, there is no apparent increase in respiration until krill swimming speeds reach 3 cm s⁻¹ (Swadling *et al.* 2005).

As negatively-buoyant organisms, krill must continuously swim to produce a flow field in the direction opposite to the gravitational field to maintain their position in the water column (Kils 1981). One method to decrease energetic costs is to adjust their angle to increase drag against a current and direct the force of their flow downward (Kils 1981). Krill are known to spread out their pleopods occasionally when they sink to slow their descent; this behavior, known as hovering, is thought to conserve energy (Kils 1981; Murphy *et al.* 2013). It is estimated this behavior may conserve 40% of the energy required to continuously swim (Kils 1981; Murphy *et al.* 2013). Since krill sink when they hover and must swim to recover their position in the water column, the exact energetic benefits of this behavior are still uncertain (Kils 1981).

The different variations in krill size, sex, and molt stage provide an explanation for some of the large variability in krill swimming capacity and respiration rates. Overall, smaller krill have a lower routine respiration rate than larger krill, although larger krill have a lower respiration rate per gram than smaller krill (Meyer 2012). Smaller krill also have pleopods with smaller surface area, meaning they must beat their pleopods at a greater frequency to achieve the same swimming speeds as to their larger counterparts (Johnson & Tarling 2008; Murphy *et al.* 2011). Sex is known to affect the pleopod beating rates, with adult female krill having faster pleopod beating rates and weaker power strokes than adult male or subadult krill (Johnson & Tarling 2008). Molting stage also affects krill swimming behaviors, with molting and post-molting krill having the lowest swimming capacity compared to pre-molting and intermolt krill, and krill in the intermolt stage having the highest swimming capacity (Johnson & Tarling 2008).

Krill utilize a combination of senses to maintain their position in the water column, communicate with other krill, and follow chemical trails to phytoplankton blooms. Krill lack a statocyst, or gravity-sensing organ, and must thus use other methods to determine and maintain their position in the water column. The primary method is by aligning themselves to light (Land 1980; Grinnell *et al.* 1988; Wiese 1996). However, when light is not present, krill use their antennae and mechanosensory setae to determine their position (Grinnell *et al.* 1988). It is also thought that krill communicate by using a combination of visual and mechanosensory cues, and that krill deliberately place themselves in positions within schools to obtain the most information and take advantage of vortices created by the pleopod beats (Wiese 1996; Yen *et al.* 2003; Patria & Wiese

2004; Catton *et al.* 2011). In addition, krill are able to chemically follow trails, be it to feed on phytoplankton or when finding a mate (Price 1989; Hamner & Hamner 2000; Kawaguchi *et al.* 2011). The interpretations of the combination of visual, mechanosensory, and chemosensory stimuli in the water column influence krill responses to the environment around them.

Krill incur metabolic costs when feeding. Oxygen consumption increases in krill when they catabolize food (Ikeda & Dixon 1984; Atkinson *et al.* 2012b). These costs also change with food sources: higher protein sources, such as copepods, require more energy to metabolize, and carbohydrate-rich phytoplankton are not as energetically-costly to digest (Fach *et al.* 2008). Egestion rates also affect krill metabolism; slower egestion rates enable krill to more thoroughly digest food, especially when food resources are limited, and faster egestion rates mean krill do not break down food as efficiently, which may cost krill additional nutrients at the time (Ikeda 1984; Ikeda & Dixon 1984; Atkinson *et al.* 2012b). However, egestion rates are linked with ingestion rates (i.e., the greater the ingestion rate, the faster the egestion rate), so the trade-off is likely that the energy gained from consuming more food may outweigh the amount of material not utilized when food is plentiful, and vice-versa when food is scarce.

Seasonality has a large influence on adult krill routine metabolic costs (reviewed in Meyer & Teschke 2016). Long-term laboratory studies on krill metabolism have shown large seasonal shifts in krill metabolic rates (Brown *et al.* 2013; Meyer & Teschke 2016). It has been demonstrated that the seasonal shift in krill metabolic rates is greater than changes in metabolic rates based on different temperatures or food sources and could, in fact, be seen in all treatments (Brown *et al.* 2013). Seasonal changes in krill

respiration rates have been linked to changes in light levels, although there is growing evidence of an internal clock in krill that enables them to determine different changes regardless of shifts in light levels (Mazzotta *et al.* 2010; Seear *et al.* 2012; Brown *et al.* 2013; De Pittà *et al.* 2013; Meyer & Teschke 2016). These large shifts in the routine respiration rates of krill over various seasons point to decreases in respiration being critical for adult krill overwinter survival. Young krill and larval stages show very little decrease in metabolism during spring, summer, and autumn; while there was a decrease in oxygen consumptions in larval stages in winter, a similar study also found these oxygen consumption levels were similar to oxygen consumption levels during starvation (Ikeda 1984; Daly & Macauley 1991; Frazer *et al.* 2002; Meyer *et al.* 2002; Meyer *et al.* 2009; Meyer & Teschke 2016). Decreasing metabolic rates seasonally may be an adaptation for older krill which have developed a lipid reserve and are capable of surviving long periods of starvation (Ikeda & Dixon 1982; Hagen *et al.* 2001; Meyer 2012; Meyer & Teschke 2016).

Behaviors

Krill are nekton and capable of swimming vast distances throughout the Southern Ocean. While part of their circumpolar distribution can partially be attributed to advection, particularly at the larval stages when krill are effectively planktonic, adult krill regularly swim across currents and potentially travel long distances (Atkinson *et al.* 2008; Tarling & Thorpe 2014). Krill regularly move offshore in the spring to deeper waters, likely following plankton blooms, and then move onshore during autumn, likely to avoid winter storms and stronger currents (Siegel 1988; Lascara *et al.* 1999; Nicol 2006; Atkinson *et al.* 2008). In the Southwestern Atlantic sector of the Southern Ocean, krill

migrate from the Antarctic Peninsula across the Scotia Sea to South Georgia during the summer (Fach *et al.* 2002, 2006; Richerson *et al.* 2015); this migration is important, as it replenishes the adult population in South Georgia, which is not self-sustaining (Marr 1962; Mackintosh 1972; Siegel 1992; Hofmann *et al.* 1998; Murphy *et al.* 1998). These large horizontal migrations are important in maintaining krill circumpolar distributions.

In addition to the horizontal distances krill swim on a regular basis, krill exhibit diel vertical migration (DVM) behavior, swimming up at the beginning of the night and slowly returning to depth by the beginning of the day. DVM is exhibited throughout the year, although the vertical ambit shifts between seasons. Krill move up and down 50 meters in summer, whereas krill move as much as 150 meters up and down throughout the night in winter (Godlewski 1996; Siegel 2005; Taki *et al.* 2005). While DVM is thought to be primarily triggered by changes in light levels, krill in laboratory conditions have continued to exhibit DVM under total darkness (Velsch & Champalbert 1994; Ringelberg 1995; Gaten *et al.* 2008). This continuation of DVM in the absence of light points to a circadian rhythm driving this behavior. Krill vertical distributions also change between seasons, with krill having shallower distributions in the spring and summer and deeper distributions in autumn and winter (Lascara *et al.* 1999; Siegel 2005; Taki *et al.* 2005; Lawson *et al.* 2008). In addition to DVM and seasonal shifts in vertical distributions, krill regularly travel thousands of meters to the abyssal plains throughout the year, a journey which is thought to take krill several days to traverse (Clarke & Tyler 2008; Schmidt *et al.* 2011). The regular vertical migrations of krill, whether daily DVM, seasonal shifts in vertical distributions, or longer travel distances from the surface to the abyssal plains, demonstrate that krill utilize a wide array of habitats in the Southern

Ocean.

Antarctic krill are omnivorous and feed on a wide variety of organisms. When filter feeding in the water column, krill beat their thoracic appendages to filter the water while moving in loops and increasing their swimming slightly from resting (Hamner *et al.* 1983; Kils 1983; Price *et al.* 1988; Hamner & Hamner 2000). Krill are selective filter feeders and are able to differentiate between different phytoplankton and microzooplankton species in the water column (Haberman *et al.* 2003; Lehetto *et al.* 2012). When feeding on sea ice, krill swim upside down and scrape the ice with their thoracic appendages, which enables them to access the algae in the sea ice (Hamner *et al.* 1983; Stretch *et al.* 1988; Marschall 1988); krill also consume detritus collected inside sea ice formations (Meyer *et al.* 2017). When they feed on sediment off the bottom, krill turn sideways to “scoop” up detritus into the water column and filter out detrital carbon and other food particles within the sediment (Clarke & Tyler 2008). Larger krill (> 18mm) are more carnivorous and feed on heterotrophic organisms, including copepods and even cannibalizing other krill, as evidenced by copepod and krill parts found in krill guts (Boyd *et al.* 1984; Price *et al.* 1988; Haberman *et al.* 2003; Schmidt *et al.* 2014; Schmidt & Atkinson 2016). Individual krill are also known to sink and return to the surface throughout the night while feeding; it is thought that krill sink when they are satiated, as it becomes less important to remain in the upper portion of the water column where prey are and more important to hide from predators by moving deeper (Pearre 2003; Tarling & Johnson 2006; Swadling 2006). It may be that it is also less energetically costly to hover while digesting food and then return to the surface to feed more when the organism is less full than maintaining their position in the water column

(Tarling & Johnson 2006). The various feeding strategies of krill enable them to utilize the pelagic water column, sea ice, and detritus at the sediment layer throughout the year in order to obtain enough calories to survive periods of starvation during the winter (Meyer 2012; Meyer & Teschke 2016; Meyer *et al.* 2017).

To avoid being consumed, krill have three main anti-predatory behaviors (O'Brien 1987). The first anti-predatory behavior is to move to avoid sensed predators, which is generally done when a predator is not within striking distance. However, in field observations, krill perception of danger is better in the horizontal plane of the krill than above or below (Wiese 1996). If a predator comes within striking distance, krill in large enough groups utilize coordinated escape behavior. Krill orient themselves to one another and use coordinated movements to confuse predators; depending on the predator size, a large group may break up into several smaller groups to further confuse predators, or several small groups will coalesce into a larger group to confuse and potentially intimidate the predator. When neither of these two strategies is effective, the third anti-predatory behavior is the individual escape behavior, where krill bend quickly in half to propel themselves backward at very quick speeds in random directions (Kils 1981; O'Brien 1987). Kils (1981) estimated krill could travel as fast as 100 cm per sec using this technique, which is much faster than the estimated maximum speeds of 40 cm per sec of the metachronal gait. The combination of these escape behaviors enable krill to survive in the Southern Ocean.

Aggregations

Antarctic krill are defined as an obligate schooling species, meaning they form and live in groups for the majority of their adult lifespan (Marr 1962; Miller & Hampton

1989; Hamner & Hamner 2000; Tarling & Fielding 2016). Classification of the aggregation types has varied historically, and there is still a level of confusion when explaining the differences between some types of aggregations (Miller & Hampton 1989; Ritz 1994; Tarling & Fielding 2016). For the purpose of this introduction, I will use aggregation to refer to a group of krill. Where specificity is required and available, I will differentiate krill aggregations into 2 types: (1) schools refer to groups of krill in which individuals orient themselves towards one another; and (2) swarms refer to groups of krill with little to no orientation and attraction between individuals.

In most studies, aggregations of krill are distinguished by physical characteristics, primarily by the largest dimension of the aggregation (Tarling & Fielding 2016). In general, the largest dimension of krill aggregations can be on the order of tens of meters to several hundred meters (Miller & Hampton 1989; Tarling *et al.* 2009; Tarling & Fielding 2016). Occasionally, krill have been observed in huge aggregations, sometimes referred to as superswarms, which can span several kilometers (reviewed in Miller & Hampton 1989; Tarling *et al.* 2009; reviewed in Tarling & Fielding 2016). In most krill aggregations, there is generally one dimension which is very narrow, typically less than 3 meters thick; this small dimension enables water to transport waste, oxygen, and nutrients through the swarm and prevents krill in the middle of the swarm from dying (Brierley & Cox 2010).

While there are some common characteristics between aggregations, there is huge variability in the sizes and shapes of aggregations (Tarling *et al.* 2009; Tarling & Thorpe 2014). However, certain types of krill aggregations are more likely to form under specific conditions. Changes in seasons affect the size and density of krill aggregations,

with summer aggregations being smaller, more densely packed, and more numerous than aggregations in winter months (Daly & Macaulay 1991; Lawson *et al.* 2008). Currents affect the formation of aggregations through advection, and while krill are capable of swimming across most currents present in the Southern Ocean, it is less energetically costly to move through regions with slower currents than areas with faster currents; as such, krill aggregations may form in regions of slower currents, including underwater canyons (Flierl *et al.* 1999; Hofmann & Murphy 2004; Zhou & Dorland 2004). Different aggregations also form under different food conditions. In areas with fewer food resources, krill are more likely to actively search for food, form larger groups, and orient towards one another as they forage for phytoplankton patches (Ritz 1994; Grünbaum *et al.* 1998; Hamner & Hamner 2000; Tarling *et al.* 2009; Tarling & Fielding 2016). In regions with higher food concentrations, aggregations in the water column tend to be smaller and less oriented to one another, likely due to krill feeding activities (Price 1989; Strand & Hamner 1990; Grünbaum 1998; Tarling *et al.* 2009; Tarling & Fielding 2016).

Schooling behaviors in general are thought to have evolved primarily as an anti-predatory strategy (Ritz *et al.* 2011). Krill within a school are of similar size, sex, and maturity, preventing predators from being able to visually pinpoint a single individual (O'Brien 1987; Miller & Hampton 1989; Hamner & Hamner 2000); if a single krill encounters a school of krill that are not of similar size, sex, and maturity, it will not stay within that school (Hamner & Hamner 2000). However, it has also been shown that schooling may not be an effective anti-predatory behavior for all sizes of krill (Alonzo & Mangel 2001; Tarling & Fielding 2016). It has been hypothesized that anti-predatory benefits are more likely to occur for krill of an intermediate size; smaller krill, which are

more planktonic, form schools through advection and may not be able to maintain these aggregations, while larger krill may not be able to hide as easily in schools (Alonzo & Mangel 2001; Tarling & Fielding 2016).

In addition to being an anti-predatory strategy, schooling krill may have several advantages over solitary krill. One advantage is that schooling krill may be able to find food more consistently. Krill within schools are able to work together to detect and forage on phytoplankton patches more consistently and successfully than solitary krill (Grünbaum 1998; Flierl *et al.* 1999; Hamner & Hamner 2000). A second hypothesis for the importance of maintaining krill schools may be that krill schooling decreases their swimming energetic costs. Ritz (2000) found that the energetic costs in schooling mysids decreased sevenfold when they schooled and proposed the same energetic savings might occur in krill. The physics of krill swimming may support this: the jet flow created by krill swimming produces upward vortices, and individual krill may be able to position themselves to take advantage of this flow (Wiese 1996; Yen *et al.* 2003; Catton *et al.* 2011). Krill inside of a school have an energetic advantage, as they have a buffer against ocean currents created by krill on the outer edge of the school (Flierl *et al.* 1999); however, as there is less oxygen and food available within the school compared to on the edge, krill within a school do rotate positions (Flierl *et al.* 1999; Brierley & Cox 2010).

Similar to schooling, krill swarms can be formed for a number of reasons. One reason swarms form is when schooling krill encounter a phytoplankton patch and feed. Once a school of krill finds a phytoplankton patch, individual krill engage in feeding behavior, where their speeds slightly increase, their thoracic appendages form feeding baskets and beat to move water through them, and they increase their turning rates to

filter as much water as possible, changing their orientations and no longer orienting to one another (Hamner *et al.* 1983; Price 1989). While krill may initially compete for food when a patch is found, it is too energetically costly for krill to continue feeding throughout the night (Boyd *et al.* 1984). Instead, krill sink when they are satiated, then swim back up to continue feeding after having digested some of the food in their guts (Pearce 2003; Tarling & Johnson 2006). The feeding behaviors enable the same aggregation of krill to remain near a phytoplankton patch without all individual krill competing for food simultaneously.

A second reason krill swarms form is when several different schools encounter one another. Schools of krill are very likely to be similar to one another in terms of size, sex, and maturity (Hamner & Hamner 2000; Tarling *et al.* 2009). As such, krill schools must intermingle with one another for krill to maximize mate finding. Schools of krill located near one another but in different orientations may create the appearance of a krill swarm when detected by acoustic methods (Hamner & Hamner 2000; Tarling *et al.* 2009; Krafft *et al.* 2012; Tarling & Thorpe 2014). Groups of schools coalescing together are more likely to form in regions with high phytoplankton abundance, slower currents, and advection into certain regions.

Knowledge Gaps:

There are discrepancies between individual krill behavior under laboratory conditions and krill behavior in the ocean. In particular, krill in laboratory conditions are known to behave more sluggishly than in the ocean. Studies have shown freshly-caught krill have a higher metabolic rate than krill which have been held in laboratory conditions for several hours (McWhinnie & Marciniak 1964; Lehet *et al.* 2012). Krill in

laboratory conditions may also consume less food than in the ocean; Boyd *et al.* (1984) calculated krill consumption rates as being up to 10% of the krill carbon weight (CW) per day in a laboratory study, but field studies have found krill can consume up to 28% CW (Clarke *et al.* 1988; Schmidt & Atkinson 2016). Additionally, laboratory studies make it difficult to ascertain large-scale behaviors, such as diel vertical migrations and swarming (Strand & Hamner 1990; Swadling *et al.* 2005; Gaten *et al.* 2008; Kawaguchi *et al.* 2010; Tarling & Fielding 2016); the biggest contributing factor is probably the limited size of tanks, which are exponentially smaller than the Southern Ocean (Siegel 2005; Taki *et al.* 2005). Moreover, krill behavior can be influenced by the size and shape of the containers they are kept in, and krill in smaller containers may be reacting in ways that constitute fight-or-flight behaviors rather than relaxed behaviors (McWhinnie & Martinacek 1964; Ngan *et al.* 1997; Lehet *et al.* 2012). As such, it is very difficult to compare krill behavior in a laboratory setting to krill behavior in the water column.

Quantifying individual krill movement behaviors throughout the water column in different seasons will provide more realistic estimates of krill motility energetic requirements in the Southern Ocean. Most studies of individual krill movement behaviors have been limited to the upper 200 m of the water column or at the seafloor, largely due to a lack of appropriate technologies (Kils 1981; Gutt & Siegel 1994; De Robertis *et al.* 2003; Nicol & Brierley 2010; Kawaguchi *et al.* 2011; Klevjer & Kaartvedt 2011; Atkinson *et al.* 2012a; Kubišius *et al.* 2015). Studies of individual krill motility have primarily been conducted using acoustics, which limits the depth range individual krill movement behaviors can be studied (De Robertis *et al.* 2003; Klevjer & Kaartvedt 2003, 2011). Other studies of krill swimming behaviors have averaged acoustic

measurements of krill aggregations, limiting the amount of variation in individual behaviors observable (Zhou & Huntley 1996; Zhou & Dorland 2004; Tarling *et al.* 2009; Tarling & Thorpe 2014). To our knowledge, there have been no prior studies on individual krill movement behavior throughout the water column in opposing seasons in the Southern Ocean. Understanding these seasonal shifts in krill movement behaviors in the water column will provide more realistic estimates of variations in krill carbon requirements due to shifts in krill motility and insights into how krill impacts on food webs on biogeochemical cycles differ throughout the year.

Additionally, while there has been a large focus on krill behaviors within aggregations, there has been no effort to determine how aggregations affect individual krill behaviors. The primary focus on krill aggregations has been on classifying them and determining when aggregations are most likely to form (Tarling *et al.* 2009; Krafft *et al.* 2012; Tarling & Thorpe 2014). Studies on individuals within aggregations have been on nearest neighbor distances and average swimming speeds of krill in the aggregations (Hamner & Hamner 2000; Zhou & Dorland 2004; Kubišius *et al.* 2015). Studies of other aggregating organisms have revealed very complex interactions between individuals, including changes in aggregation shapes, organization, and how organisms track neighbors (Ballerini *et al.* 2008; Katz *et al.* 2011; Vicsek & Zafeiris 2012; Shelton *et al.* 2015). However, there have been no studies focused on how variations in krill aggregation density influence individual krill movement behaviors.

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CHAPTER TWO

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Krill motion in the Southern Ocean:

**quantifying *in situ* krill movement behaviors and distributions during the late
austral autumn and spring**

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swimming behaviors; *in situ* observations

Abstract:

Krill movement behaviors and vertical distributions were measured in spring and autumn using a profiling stereo-camera and environmental sensor system to quantify seasonal changes in the role of krill in Southern Ocean food webs. Krill were observed in May-June 2013 and December 2014 in 3 bays in the Western Antarctic Peninsula. Krill abundances and movement behaviors were determined from *in situ* image sequences collected for up to 10 minutes throughout the water column, up to 625 m deep; 3,345 individual krill tracks were collected. Seasonal changes in individual krill behaviors coincided with seasonal shifts in krill vertical distributions. During late spring, net upward swimming direction ($0.9 \pm 2.1^\circ$ from horizontal) and vertical velocity (0.3 ± 0.2 Body Lengths (BL) s^{-1}) resulted in shallower maximum abundances of krill within the water column proximate to near-surface phytoplankton distributions. During late autumn, krill swimming patterns tended downward, including swimming direction ($-5.2 \pm 0.8^\circ$ from horizontal) and vertical velocity (-0.1 ± 0.0 BL s^{-1}), leading to deeper distributions proximate to the benthos. Individual krill motility was greater in spring than autumn, as evidenced by an increase in swimming speeds (5.4 ± 0.2 BL s^{-1} vs. 2.8 ± 0.0 BL s^{-1}) and turning rates ($120 \pm 5^\circ s^{-1}$ vs. $106 \pm 2^\circ s^{-1}$). Remarkably, krill in autumn were capable of swimming as quickly as krill in spring. These results suggest seasonal shifts in krill movement behaviors have direct ramifications for krill distributions, proximity to food sources, and impacts on biogeochemical cycling in coastal Antarctic waters.

Introduction:

Krill are a crucial link between primary production and upper trophic levels in the Southern Ocean food web (Quetin & Ross 1991; Nicol & Brierley 2010; Atkinson *et al.* 2012b; Ballerini *et al.* 2014; Saba *et al.* 2014). In addition to serving as key prey to some of the largest animals on Earth, krill constitute the largest fishery by tonnage in the Southern Ocean (Nicol 2006; Brierley 2008; Atkinson *et al.* 2009; Atkinson *et al.* 2012b; Nicol *et al.* 2012; Nicol & Foster 2016). Krill are critical conduits of biogeochemical processes in the marine food web, including nutrient recycling, benthic-pelagic coupling, and carbon sequestration in the Southern Ocean (Le Fèvre *et al.* 1998; Schnack-Schiel & Isla 2005; Tovar-Sanchez *et al.* 2007; Schmidt *et al.* 2011; Lehet *et al.* 2012). The lack of data on krill behavior, distribution, and abundance throughout seasonal cycles hinders accurate assessments of krill energetic requirements, the role of krill in the Southern Ocean food web, and ultimately biogeochemical cycling.

It has been traditionally assumed krill live in the upper portion of the water column (shallower than 400 m depth) (Atkinson *et al.* 2012b, references therein). As such, there have been many studies of krill abundance and distribution in the upper 400 m of the Southern Ocean using hull-mounted echosounders, acoustic Doppler current profilers (ADCPs), and net trawls, such as the Multiple Opening/Closing Nets and Environmental Sensing Systems (MOCNESS) and Tucker trawls (Wiebe *et al.* 1976, 1985; Zhou & Dorland 2004; Atkinson *et al.* 2012b, references therein). However, Clarke and Tyler (2008) documented krill interacting with the benthos at depths up to 3500 m, depths far below where krill were thought to thrive. Furthermore, Schmidt *et al.* (2011) concluded krill likely occupy the full extent of the water column and suggested up

to 20% of krill biomass may be found at depths greater than 200 m during the summer. Consistent interactions with the benthos throughout the year, and thus consistently deeper vertical distributions of krill, suggest a necessary revision of the importance of potential food sources sustaining krill populations and the possible modification of krill mediated elemental cycling involving the benthos.

Compounding the lack of information on krill vertical distributions at depth, the majority of krill profiling studies have been conducted in late austral spring, summer, and early autumn (Lascara *et al.* 1999; Zhou & Dorland 2004; Nicol 2006; Nicol & Brierley 2010; Atkinson *et al.* 2012b). The few late autumn and winter studies show the majority of krill biomass reside in deeper water (> 100 m) away from the ice during winter, potentially at depths below where ship-based sonar sampling would be effective (Lascara *et al.* 1999; Lawson *et al.* 2004, 2008; Marrari *et al.* 2011; Wiebe *et al.* 2011). Thus, krill behaviors and distributions outside the late austral spring to early autumn, particularly on the shelf, are poorly known.

Along with distributions and abundance, quantifying individual krill movement behavior will better define the function of krill in the ecosystem. To our knowledge, studies of krill movement behaviors in the water column are rare and are mostly confined to the upper 200 m of the water column or at the seafloor; this paucity of observations is largely due to the lack of appropriate technologies (Kils 1981; Gutt & Siegel 1994; De Robertis *et al.* 2003; Nicol & Brierley 2010; Kawaguchi *et al.* 2011; Klevjer & Kaartvedt 2011; Kubišius *et al.* 2015). Much of what is known about krill movement behaviors has been observed under laboratory conditions, including the physics and physiology of krill movement, chemical and mechanosensory triggers for krill behaviors, and correlations

between krill swimming speeds and respiration (Kils 1981; Hamner *et al.* 1983; Price 1989; Strand & Hamner 1990; Hamner & Hamner 2000; Swadling *et al.* 2005; Murphy *et al.* 2011, 2013). *In situ* studies investigating individual krill movements which used acoustics were made at limited spatial and temporal resolutions and low abundances (De Robertis *et al.* 2003; Klevjer & Kaartvedt 2003, 2011). Other studies investigating krill swimming speeds were based on acoustic measurements of large swarms and provided average velocities but little information on variations in individual swimming (Zhou & Huntley 1996; Zhou & Dorland 2004; Tarling & Thorpe 2014). There have been no comparisons of *in situ* whole water column krill swimming behaviors in contrasting seasons in the Southern Ocean, which are essential for determining krill energetic requirements throughout the year.

Studying seasonal changes in krill behavior and distributions *in situ* will provide insights into how krill impacts on food webs and biogeochemical cycles change throughout the year. While krill are thought to preferentially select phytoplankton as their main prey, krill are known to feed on other sources when phytoplankton abundances are low, including microzooplankton and copepods, detritus, and other krill (Boyd *et al.* 1984; Kawaguchi *et al.* 1986; Ligowski 2000; Haberman *et al.* 2003; Schmidt *et al.* 2011; Atkinson *et al.* 2012b). Whether krill feed on lower trophic levels, detritus, or starve is dependent on several factors, including availability of prey, location, life stage, and season (Quetin & Ross 1991; Ligowski 2000; Atkinson *et al.* 2002; Meyer *et al.* 2010; Flores *et al.* 2012; Schmidt *et al.* 2014). Furthermore, there is growing evidence krill have an endogenous rhythm which exhibits seasonal metabolic changes during the year, with lower metabolic rates in the late autumn and winter relative to spring and summer

(reviewed in Meyer & Teschke 2016). Measurements of krill movement behaviors and distributions in seasons with contrasting levels of productivity will further elucidate the links between krill and the Southern Ocean food web and biogeochemical cycles throughout the year.

In the last few decades, camera observations and tracking of organisms in the water column, such as jellyfish and fish, with remotely-operated vehicles have become more prevalent and create viable methods for *in situ* observations (Rife & Rock 2001; Kubišius *et al.* 2015). Here, we report krill movement behaviors and vertical distributions as a function of season, location, and co-occurring environmental conditions collected with a newly developed stereoscopic camera system deployed in three bays of the Western Antarctic Peninsula (WAP) during the late autumn of 2013 and the late spring of 2014. We document seasonal shifts in individual movement behaviors of krill that are directly linked to shifts in the depth distribution of krill populations.

Methods:

Krill camera observations

Camera system deployments were conducted during two cruises on the *R.V.I.B. Nathaniel B. Palmer* in the WAP in Wilhelmina, Andvord, and Flandres Bays (Figure 2.1). Late austral autumn camera deployments were conducted between 19 May 2013 and 6 June 2013 and austral spring camera deployments between 6 and 23 December 2014 (Table 2.1). Krill were observed in 18 of 19 analyzed deployments in late autumn and 11 of 18 deployments in late spring (Table 2.1). Deployments were made both during the day and night and from the surface to within 3 m of the bottom, which ranged between 270 and 625 m depth.

The camera system consisted of two Allied Vision Manta G-145B NIR cameras with Fuji HF9HA-1B lenses placed in 2000 m rated flat port pressure housings (Figure 2.2). The camera optical axes were mounted parallel, and the calibrated distance between image centers was 104 mm with a calibrated focal depth range from 0.2 to 2.0 m in late autumn and 0.3 to 1.0 m in spring. During both cruises, the field of view was approximately 1.2 m wide by 1.0 m at the maximum focal distance. The camera's field of view was illuminated by three 70 W red (760 nm wavelength) light-emitting diodes (LEDs) except for one deployment during the late autumn, when the camera field was lit by two 90 W full spectrum white LEDs (447 nm and 560 nm wavelengths) (Deployment 39, Table 2.1). All five LEDs were Deep Sea Power and Light SLS 5000 series SeaLite Spheres with an output of approximately 6000 Lm each.

To concurrently measure environmental conditions, a SeaBird SBE 49 FastCAT conductivity, temperature and depth (CTD) sensor and 1200 kHz ADCP (Teledyne

Navigator) were mounted on the camera system. The camera system was connected to the ship via a steel standard armored fiber-optic cable that enabled real time streaming of images. Images were taken at a rate of 10 frames per second with an image resolution of 1038 by 1388 pixels.

During both cruises, the camera system was deployed while the ship held station to profile the water column and was stopped for a minimum of 30 s at predetermined depths, hereafter horizons, during the downcast. During the austral autumn, horizons were spaced every 50 m in the water column. In the austral spring, because krill were expected to be shallower in the water column, the camera was stopped every 10 – 20 m in the upper 100 m, then every 25 m for the next 100 m, and then every 50 m until the camera reached the bottom. In both seasons, when sampling time permitted, the camera system was stopped during upcasts at depths where krill had been seen during the descent to obtain more individual movement behavior observations. In the late autumn, only horizons observed during downcasts were used to determine krill vertical distributions. In late spring, due to the scarcity of krill seen, horizons from the up- and downcasts were combined to determine krill vertical distributions.

Environmental conditions

Depth, salinity, and temperature data from the Seabird 49 were used to describe characteristics of the water column concurrent with filming. CTD measurements at the surface were discarded for two deployments during late autumn where unusually low salinity values (< 33.5 ppt) suggested water had frozen in the plumbing before the camera system was deployed.

Surface photosynthetically available radiation (PAR) data were collected by the

shipboard light sensors (Biospherical Licor Chelsea Sensor, Serial No. 4721) and used to determine daylight intensity and duration. Due to high frequency fluctuations in light intensity, the highest 10% PAR values recorded during camera deployments were averaged, here termed the average maximum irradiance, and used to determine if deployments occurred during light or dark periods. During the late austral autumn, deployments were characterized as “dark” when average maximum irradiance was $\leq 3 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. During the late austral spring, deployments were characterized as “dark” when average maximum irradiance was $\leq 100 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, as PAR values were rarely below $10 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ and a light intensity of $100 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ corresponded to civil sunrise and sunset.

Organism abundances

During late autumn, the majority of organisms observed in the images were krill. Other visible organisms, such as amphipods and ctenophores, amounted to $\ll 1\%$ of organisms observed. Based on MOCNESS and ring net tows conducted during the same cruise, the krill observed in the images were most likely *Euphausia superba* (Cleary *et al.* 2016).

During late spring, there was an increase in the diversity and quantity of other taxa observed, including an increase in the number of amphipods, chaetognaths, and various medusae. There were also an order of magnitude fewer krill observed. Based on krill identified in the video, the vast majority of krill ($\gg 99\%$) observed in the water column during the late spring were also likely *Euphausia superba*.

Image processing

Images were processed to enable semi-automated detection of krill. Because

organisms aside from krill were observed very infrequently ($<< 1\%$) in the late autumn, the primary objective of the automated detection method was to separate krill from marine snow. Raw images were preprocessed to compensate for unevenness in the lighting. Several different image processing methods were tested and the most accurate approach identified using Model II regression of human versus automated counts from videos representing different depths, particle and krill abundances, locations, and times of day. Accuracy was determined by the regression characteristics of the greatest r^2 -value ($r^2 = 0.72$), lowest error, and a slope estimate which indicated that the automated method undersampled the abundance of krill (slope = 0.56). Thus, the algorithm used here provides a conservative estimate of krill abundances. Because overall particle density might affect algorithm efficacy, we tested the krill yield of the image processing method as a function of particle density and found no relationship between the number of krill detected and the overall number of detected objects in the images (Model II regression, $r^2 = 0.01$). Thus, our estimates of krill abundances were not biased by the density of non-krill particles.

The method used to generate the data presented here utilizes the built-in MATLAB function *stretchlim* (The MathWorks Inc., ver. 2013b) to increase the contrast and saturate the lower 60% and upper 1% of pixel values before utilizing *imadjust*, which shifted the range of pixel intensity values such that 1% of the pixels were at the upper and lower saturation limits. A Gaussian high-pass filter was then used to remove background lighting and retain visible krill. The grayscale images were then converted to binary using a threshold generated from the MATLAB function *graythresh*, which uses Otsu's method to minimize the intraclass variance of the set of object pixels and the set of

background pixels (Otsu 1979).

After determining the basic image processing method, the aspect ratio and area values used to identify krill were adjusted in a similar, iterative sensitivity analysis to optimize the number of krill found and minimize the number of particles incorrectly identified as krill. The aspect ratios and areas of the resulting objects in the binary images were used to distinguish krill from non-krill particles, as krill in lateral view have a more elliptical shape and were larger than marine snow particles. Combinations of larger minimum aspect ratio and area values resulted in higher accuracies but yielded lower abundances, while combinations that obtained higher krill abundances were less accurate. To balance needs of data yield with the proper identification of krill, a minimum aspect ratio of 4 and a minimum area of 400 pixels were deemed to be sufficient to distinguish krill from non-krill particles, although this did eliminate krill swimming directly towards or away from the camera. Ultimately, the algorithm identified 68% of the total krill identified by a human with a 31% false positive rate.

Other taxa were more diverse during the spring cruise, so we examined the applicability of the late austral autumn analysis methods to the spring data. The late austral spring images were processed in an identical manner to the autumn images except that a high-pass Gaussian filter with a minimum threshold value of 0.1 was used rather than increasing the contrast in the image before converting the images from grayscale to binary. This slightly modified detection method yielded a significant relationship between human and automated counts in the late spring images (Model II regression,

slope = 0.38, $r^2 = 0.64$).

In situ abundances of krill

In the late autumn, krill abundances at all horizons were determined by averaging the number of krill detected per image across all images in the video, thus yielding an average and variance estimate for krill abundance at each horizon. In the late spring, however, due to the scarcity of krill seen in the images, averaging the number of krill seen per image at each horizon did not produce accurate abundance estimates. Instead, abundances were determined by manually reviewing horizon footage, then counting and averaging the number of krill seen over the 30 s of footage with the greatest abundance of krill at the horizon. In both seasons, only horizons where at least 300 sequential images (30 s) were obtained were included in the analysis.

To account for potential camera avoidance or attraction by krill, the autocovariance of krill abundances in subsequent images at each horizon was determined by treating the per image abundance as a time series. The first time point at which krill abundances in subsequent images were no longer correlated, that is, when the autocovariance was equal to 0, represented the time when the abundances in the images were independent of the initial krill abundance. This time was used as the starting image for determining the abundance of krill at a particular horizon. In both seasons, decorrelation of krill abundances was reached within 30 seconds for 75% of horizons, within 60 seconds for 95% of horizons, and within 120 seconds for 99% of horizons.

To determine the total volume sampled by the camera system, a random set of 1500 individual krill were matched between left and right stereo images and placed in a 3D coordinate system relative to the cameras. This enabled the determination of the total

sample volume in which krill were successfully identified. The majority of krill were identified 0.5 m to 1 m from the camera, with some krill identified as far as 2 m from the camera; the total volume of water sampled was approximately 2.4 m³.

Due to the range of bottom depths of different deployments (Figure 2.3), relative depth, expressed as percent of total water column depth, was also calculated to enable cross-deployment comparison of krill abundances. Krill abundances at each horizon were matched with recorded environmental data from the system-mounted CTD to support analyses of environmental correlates of krill distribution patterns. A Kruskal-Wallis test was used to determine differences between krill abundances at each horizon within each deployment. A Kolmogorov-Smirnov test was used to determine whether krill abundances using both absolute and relative depths, salinity profiles, or temperature profiles differed from each other. Differences were deemed statistically significant at $p < 0.05$.

Krill swimming behaviors

For both seasons, krill movements were quantified using a two-dimensional multi-object semi-automated tracking algorithm developed in MATLAB similar to the approach described in Menden-Deuer and Grünbaum (2006). The tracking algorithm was tested using 4200 images representing a range of krill abundances, from one krill per frame to in excess of 50 krill per frame. The algorithm was successful in tracking krill in images with fewer than 30 krill present, with an overall accuracy of 85% success in correctly tracking a single krill. The minimum length of tracks included in the analysis was 10 frames (= 1 s of footage), yielding a mean track length of 2.5 s in the late autumn and 1.7 s in the late spring, with the longest observations of 22.7 s in the late autumn and

14.7 s in the late spring.

Krill movement behaviors, including swimming speeds, vertical velocities, directionality, and turning rates, were calculated from the resulting 2D paths. Swimming speeds were determined by measuring the distance krill traveled over the number of frames; the distance traveled was determined in apparent body lengths (BL), to account for the varying distances of krill from the camera system. Vertical velocities were determined by taking only the vertical component of the swimming speed. Negative vertical velocities indicate downward swimming, while positive vertical velocities indicate upward swimming. Directionality of movement tracks was measured by comparing the swimming direction of the krill relative to horizontal. Turning rates were measured as changes in swimming directionality over time (e.g., Harvey & Menden-Deuer 2011). Krill lengths were measured from krill collected by the MOCNESS tows of the late austral autumn and ranged between 9 mm and 51 mm, with an average of 29 mm (Cleary *et al.* 2016). These lengths can be used to convert swimming speeds and vertical velocities from apparent body lengths per second (BL s^{-1}) to centimeters per second (cm s^{-1}); for example, a swimming speed of 2 BL s^{-1} would result in a swimming speed range of 1.8 to 10.2 cm s^{-1} , with an average swimming speed of 5.8 cm s^{-1} .

Associations between krill swimming behaviors and location, season, time of day or environmental conditions were examined statistically by binning tracks into different categories (e.g., time of day). A Kolmogorov-Smirnov Test was used to determine significant differences between binned swimming behaviors.

Results:

Late autumn environmental conditions

For all deployments, salinity increased from 33.9 ± 0.3 ppt at the surface to 34.5 ± 0.1 ppt at depths greater than 200 m, and surface waters were colder than waters at depth. In Wilhelmina and Andvord Bay, temperature increased from surface values of $-0.8 \pm 0.4^\circ\text{C}$ to $0.1 \pm 0.2^\circ\text{C}$ around 150 m before decreasing to $-0.1 \pm 0.2^\circ\text{C}$ at the bottom of the water column. In Flandres Bay, the temperature increased from $-0.9 \pm 0.2^\circ\text{C}$ at the surface to about $0.8 \pm 0.2^\circ\text{C}$ at depth, with the vast majority of temperature increase occurring in the upper 100 m. Seawater density followed a similar trend to salinity and increased from $1027.1 \pm 0.2 \text{ kg m}^{-3}$ at the surface to $1027.6 \pm 0.1 \text{ kg m}^{-3}$ at depths greater than 200 m.

Surface PAR values ranged from as low as $2 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ at night, likely from indirect irradiance from the ship, to as high as $600 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ during the day. The average maximum irradiance during camera deployments ranged from 2 to 297 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. The time between civil sunrise and sunset decreased over the course of the late autumn cruise from 6 h 16 min to 3 h 52 min.

Late spring environmental conditions

Salinity for all deployments in late spring followed a similar pattern to salinity in late autumn and increased from 33.5 ± 0.3 ppt at the surface to 34.6 ± 0.1 ppt at depths greater than 200 m. There were two general temperature profiles. In Wilhelmina and Andvord Bay, the temperature decreased from surface values of $0.5 \pm 0.3^\circ\text{C}$ to $-0.7 \pm 0.2^\circ\text{C}$ at the bottom of the water column, with the fastest decrease occurring in the upper 100 m. In Flandres Bay, the temperature decreased in the upper 20 m from $0.8 \pm 0.4^\circ\text{C}$ to

$-0.1 \pm 0.1^{\circ}\text{C}$ before increasing to $0.9 \pm 0.1^{\circ}\text{C}$ at the bottom, with the greatest increase occurring in the upper 300 m. Similar to the late autumn, seawater density in the late spring followed a trend similar to salinity and increased from $1026.4 \pm 0.2 \text{ kg m}^{-3}$ at the surface to $1027.7 \pm 0.1 \text{ kg m}^{-3}$ at depths greater than 200 m.

Surface PAR values range from as low as $3 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ at night to as high as $2333 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ during the day. The average maximum irradiance during camera deployments ranged from 6 to $1800 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$. The time between civil sunrise and sunset increased over the course of the cruise from 20 h 57 min to 21 h 45 min.

Krill vertical distributions

Krill vertical distributions in the three bays along the WAP showed large variability in both seasons. In late autumn, krill abundances differed significantly both with depth (maximum p-value < 0.001) and among locations (maximum p-value = 0.033); three deployments were statistically indistinguishable, as the greatest krill abundance in these profiles was observed at the bottom. Krill were not observed shallower than 50 m, and the greatest abundances of krill in the vertical profiles consistently occurred at or below 200 m. In the late spring, krill abundances were highly variable and differed significantly among locations (maximum p-value < 0.001). Krill were observed throughout the water column; however, the greatest abundances of krill occurred either in the upper 100 m of the water column or near the sediment.

Krill vertical distributions could be separated into two general profile types in the late autumn (Figure 2.4A and B) and three general types in the late spring (Figure 2.4C, D, and E). Midwater profiles were characterized by high abundances of krill in the

middle of the water column, between 40% and 80% of the total depth, which corresponds to depths between 200 and 350 m in late autumn (Figure 2.4A) and depths of 200 to 300 m in the late spring (Figure 2.4D). Benthic profiles were characterized by peak abundances of krill found in the lowest 20% of the water column, equivalent to depths between 200 and 350 m in late autumn (Figure 2.4B) and depths between 300 and 500 m in late spring (Figure 2.4E). Surface profiles occurred only in late spring and were characterized by high abundances of krill between 0% and 40% of the total water column depth, equivalent to depths of 0 to 150 m (Figure 2.4C). In both seasons, deployments with $< 1 \text{ krill m}^{-3}$ or no krill present occurred in all bays

No significant relationship was found between krill abundances and salinity, temperature, or seawater density in either season. However, there was an association between profile type and average maximum irradiance in both seasons. In late autumn, all of the midwater profiles occurred in the dark, while all but one of the benthic profiles occurred during daylight (Figure 2.5A). In the late spring, five of the six surface profiles occurred in the dark, with the shallowest krill abundances occurring at night (Figure 2.5B). Deployments in which $< 1 \text{ krill m}^{-3}$ were observed occurred during both light and dark hours in both seasons.

During three repeat deployments in late autumn over a 13-hour period starting before sunrise, krill peak abundances were observed to shift downward from 200 to 350 m during daylight hours and return to 250 m depth after sunset (Figure 2.6).

Krill swimming behaviors – overall seasonal averages

A total of ~3000 krill were tracked in late autumn and 366 were tracked in late spring (Table 2.2). In late autumn, swimming speeds were $2.8 \pm 0.0 \text{ BL s}^{-1}$ (Figure

2.7A). Krill swimming speeds increased nearly 2-fold in late spring, averaging 5.3 ± 0.2 BL s^{-1} (Figure 2.7A). The average of the top 10% of swimming speeds doubled between seasons and were 6.6 ± 0.1 BL s^{-1} and 12.8 ± 0.5 BL s^{-1} in late autumn and spring, respectively.

Krill vertical velocities tended downward on average in the late autumn and upward in the late spring, with a mean vertical velocity of -0.1 ± 0.0 BL s^{-1} in autumn and 0.3 ± 0.2 BL s^{-1} in spring (Figure 2.7B). Interestingly, there was an increase in the magnitude of the vertical velocities between seasons, where the average maximum 10% of upward vertical velocities for krill in the late autumn was 4.3 ± 0.1 BL s^{-1} and average 10% of maximum downward vertical velocities was -4.3 ± 0.1 BL s^{-1} , while the average for the maximum 10% upward vertical velocities of krill in the late spring was 7.5 ± 0.5 BL s^{-1} and the average for the 10% maximum downward vertical velocities was -6.8 ± 0.7 BL s^{-1} .

Krill turning rates were lower in the late autumn ($107 \pm 2^\circ s^{-1}$) than in the late spring ($120 \pm 5^\circ s^{-1}$) (Figure 2.7C). The average for the fastest 10% turning rates were similar between autumn and spring (315 ± 5 and $314 \pm 23^\circ s^{-1}$, respectively).

In both seasons, krill swam in all directions, although krill swimming directions tended to be more downward in the late autumn (Figure 2.8A) and averaged $-5.2 \pm 0.8^\circ$ from horizontal. In late spring, krill swimming direction tended upward and averaged $0.9 \pm 2.1^\circ$ from horizontal (Figure 2.8B). However, there was large variance in swimming directions in both seasons, with krill swimming in all directions.

Krill swimming behaviors – light dependency

In the late autumn, krill swam significantly faster during the day than at night (3.0

$\pm 0.0 \text{ BL s}^{-1}$ and $2.6 \pm 0.1 \text{ BL s}^{-1}$, respectively; $p\text{-value} < 0.001$) (Figure 2.9A), although the range of swimming speeds was similar. In the late spring, both the average and the range of swimming speeds were similar between day and night (5.1 ± 0.3 and $5.5 \pm 0.2 \text{ BL s}^{-1}$, respectively; $p\text{-value} = 0.61$) (Figure 2.9D).

In the late autumn, the average vertical velocity during the day was half the vertical velocity at night (-0.06 ± 0.06 and $-0.14 \pm 0.06 \text{ BL s}^{-1}$, respectively; $p\text{-value} < 0.001$). The range and variability of vertical velocities was larger during the day than at night (Figure 2.9B). In the late spring, vertical velocities were relatively similar between day and night, with krill on average swimming slightly, but not significantly, more upward during the day (0.35 ± 0.30 and $0.32 \pm 0.30 \text{ BL s}^{-1}$, respectively; $p\text{-value} = 0.35$). However, while the average vertical velocities were similar, the range, and thus variability, of vertical velocities was 31.8% lower during the day compared to the night (Figure 2.9E). Interestingly, krill vertical velocities measured during light periods in both seasons did not statistically differ from one another; the ranges were also similar between the seasons.

In the late autumn, krill turning rates significantly increased between day and night (100 ± 2 and $114 \pm 3^\circ \text{ s}^{-1}$, respectively; $p\text{-value} < 0.001$) (Figure 2.9C). The range of the turning rates was similar between day and night. In the late spring, turning rates were similar between day and night (114 ± 8 and $123 \pm 6^\circ \text{ s}^{-1}$, respectively; $p\text{-value} = 0.43$). The range of turning rates increased between day and night (Figure 2.9F).

In the late autumn, swimming directions were pointed downward throughout the 24-hour period but less so during the day than at night (-1.9 ± 1.1 and $-9.2 \pm 1.1^\circ$ from horizontal, respectively; $p\text{-value} < 0.001$) (Figure 2.10A and B). In the late spring, krill

swimming directions were upward during the day and near horizontal at night (3.0 ± 3.3 and $-0.2 \pm 2.7^\circ$ from horizontal, respectively; p-value = 0.20) (Figure 2.10C and D).

Discussion:

It has proved technically difficult to examine whole water column distributions and movement behaviors of Antarctic krill, which has hindered advances of our understanding of the Southern Ocean food web (Nicol 2006; Brierley 2008; Atkinson *et al.* 2012b, references therein). Here, we report the results of, to our knowledge, the first study to simultaneously quantify individual movement behaviors and whole water column vertical distributions of krill in different seasons. In late spring, krill abundances were greatest in the upper portion of the water column, whereas in late autumn, krill abundances peaked near the bottom. In both seasons, we observed significant light-dependent shifts in where krill abundance maxima were located, with greater krill abundances found at shallower depths at night (i.e., midwater in late autumn and near the surface in late spring) and deeper in the water column during the day (i.e., the benthos in late autumn and deeper overall in late spring). Although krill motility was more vigorous in late spring, krill actively swam and reached similar maximum speeds in both late autumn and spring. Our observations indicate changes in krill vertical distributions were linked to shifts in individual movement behaviors, with shallower vertical distributions in late spring driven by upward motility of krill and deeper distributions in late autumn driven by krill swimming downward. Furthermore, these data suggest krill were actively moving in both seasons, and their role as key predators of lower trophic levels in the Antarctic food web was not restricted to spring and summer.

Compared to the shallower vertical distributions in late spring, krill were rarely seen above 100 m in late autumn, with the greatest abundances found near the seafloor. Previously, post-larval krill were thought to overwinter directly under sea ice in

anticipation of spring ice algal blooms (Hamner *et al.* 1983; Marschall 1988; Nicol 2006). However, biomass studies have found that there is not nearly enough surface area immediately under sea ice to support the total krill biomass found in summer (Lascara *et al.* 1999). It is now thought that overwintering directly under sea ice is more important for larval stages and juveniles in the region of the WAP (Flores *et al.* 2012; Saba *et al.* 2014). Recent studies also suggest adult Antarctic krill may utilize the full water column rather than only the upper 400 m and travel to the seafloor regularly (Clarke & Tyler 2008; Schmidt *et al.* 2011; Atkinson *et al.* 2012b). The majority of krill biomass along the continental shelf of the WAP can be found deeper than 100 m in the open water column during winter and may be deeper than can be effectively detected using ship-based acoustic sampling techniques (Lascara *et al.* 1999; Lawson *et al.* 2004; Lawson *et al.* 2008). Our findings support that krill are found at depth in late autumn, with the highest abundances near the benthos. Moreover, our results suggest krill utilize the benthos throughout the year, as we observed high abundances of krill near the sediment in both late spring and autumn.

Although there was a relative decrease in krill motility between late spring and late autumn, krill were actively swimming in late autumn. The observed decrease in krill motility between late spring and autumn were likely influenced by changes in krill metabolic rates as studies have shown that krill routine metabolic rates in the autumn and winter are approximately 50% and 30%, respectively, of those in the spring and summer (Meyer 2012; Brown *et al.* 2013; Meyer & Teschke 2016). However, the estimated swimming speeds in late autumn were similar to acoustically-estimated 2-3 BL s⁻¹ cruising speeds of krill observed during other seasons (Lochhead 1961; Kils 1981, 1983;

Torres 1984; Zhou & Dorland 2004), which indicates that krill in the Gerlache Strait region were still active. Furthermore, despite the decrease in routine metabolic rates, Meyer (2012) suggested that krill must still actively feed during winter to cover metabolic costs. Since the caloric demands of krill motility have to be supported energetically, these findings may imply but do not prove that krill continue to feed in late autumn.

The seasonal shift in krill vertical distributions in late spring and late autumn was driven by changes in individual krill movement behavior (Figure 2.11); in late spring, krill generally swam more vigorously and mostly upward, whereas in late autumn, krill motility was reduced and directed downward. These seasonal differences could be related to a shift in krill primary food sources between these seasons. As phytoplankton were present in the upper portion of the water column during late spring, evidenced by chlorophyll *a* (*chl a*) concentrations of 3-18 mg m⁻³ (Morison & Menden-Deuer 2018), krill were likely moving upwards in the water column to feed on phytoplankton. This suggestion is well supported by prior observations of krill preferentially feeding on phytoplankton and the presence of diatom prey in the stomach contents of krill collected during the spring in general (Godlewska 1996; Kawaguchi *et al.* 1999; Hamner & Hamner 2000; Ichii 2000; Haberman *et al.* 2003) and during our specific cruise (Cleary *et al.* 2018). Furthermore, we observed increased average swimming speeds and turning rates in spring when *chl a* concentrations were higher, consistent with similar observations made when krill feed on phytoplankton (Hamner *et al.* 1983; Price 1989; Hamner & Hamner 2000; Kawaguchi *et al.* 2010). We also observed increased variance in the vertical velocities of krill at night, consistent with the concept of krill actively

changing depths due to level of fullness (Pearre 2003; Swadling 2006; Tarling & Johnson 2006). In late autumn, phytoplankton prey were scarce, as shown in *chl a* concentrations of maximally 0.4 mg m^{-3} (Morison & Menden-Deuer 2018); additionally, there were very few zooplankton present in the water column, leaving detritus in the sediment as one of the only food sources available to krill. In late autumn, krill may have been moving towards the benthos to feed on detritus, which krill are known to consume (Kawaguchi *et al.* 1986; Ligowski 2000; Clarke & Tyler 2008; Schmidt *et al.* 2011, 2014). Ultimately, our observations strongly suggest that seasonal changes in individual krill swimming behaviors provide the underpinning for seasonal shifts in krill vertical distributions and may be driven by the change in location of primary food sources.

In addition to the seasonal shift, we also observed daily shifts in krill distributions and movement behaviors. In particular, we noted vertical distribution patterns akin to diel vertical migration (DVM) in both seasons, with maximum abundances of krill found shallower at night than during the day; in late autumn, we also observed evidence of DVM at one station monitored over 13 h. Krill in the Southern Ocean exhibit DVM throughout the year, although DVM is highly variable and in some studies not detected (Godlewska 1996; Siegel 2005; Siegel & Watkins 2016; Tarling & Fielding 2016). Remarkably, while we observed shifts in vertical distributions in the late autumn associated with changes in light, krill were found at depths generally considered beyond krill eye sensory capacity for light perception (Hiller-Adams & Case 1984). Zooplankton are known to continue exhibiting DVM in the absence of light (Haney 1988; Velsch & Champalbert 1994; Gaten *et al.* 2008). Additionally, there is a growing body of evidence that krill have an endogenous rhythm (Mazzotta *et al.* 2010; Meyer 2012; Seear *et al.*

2012; Brown *et al.* 2013; De Pittà *et al.* 2013; Meyer & Teschke 2016). Thus, our observations of diel changes in krill behavior and vertical distribution, particularly in the late autumn when krill were generally too deep to sense changes in surface light intensity, suggest that these krill behaviors may be influenced by such an endogenous, light-independent rhythm.

While the described camera system has enabled unprecedented observations of krill *in situ* without limitation to depth or season, we have identified several limitations. One such constraint is the effective field of view which was limited to a few thousand liters of water due to the rapid absorption of red light (760 nm) used to illuminate the water column. Thus, we were unable to observe an entire krill swarm, as krill swarms can be very large and can range from tens of meters to several kilometers long (Tarling *et al.* 2009; Cox *et al.* 2010). The limited sampling volume is also reflected in the fact that while low abundances of krill were observed in shallow waters through the MOCNESS tows and the ADCP (Cleary *et al.* 2016), no krill were observed in the upper 50 m in the late autumn with the cameras. Clearly, the smaller sampling volume of the camera system relative to the orders of magnitude larger volume captured by net tows and ADCP limited our capacity to quantify the relatively low density of krill in shallow waters in late autumn.

While the sampling volume of the camera system was limited, the system was relatively non-invasive and provided a means to observe krill in the water column at high resolution and without disturbing their behavior (Letessier *et al.* 2013), ultimately enabling concurrent observations of movements and distributions. Another advantage of the camera system was that it could be deployed to within 3 m of the bottom and

provided detailed observations close to the seafloor otherwise unattainable by traditional methods (Atkinson *et al.* 2012b, references therein). These near-benthos observations are important given the emerging understanding that the benthos may be an important foraging habitat for krill (Clarke & Tyler 2008; Schmidt *et al.* 2011; Cleary *et al.* 2012). The utilization of this camera system also allowed unprecedented detail in observing krill swimming behaviors on a smaller scale, which enabled us to quantify highly dynamic and variable swimming behaviors between night and day and between the late autumn and spring.

Seasonal shifts in krill behaviors and vertical distributions have implications for seasonal contributions of krill to the food web, nutrient cycling, and carbon sequestration in the WAP. Observations of actively moving krill in both late spring and autumn support the hypothesis that krill remain significant consumers of lower trophic levels and are important in the transfer of energy and matter in the WAP food web throughout the year. These data also reveal seasonal vertical distribution shifts, with krill moving towards the euphotic zone in spring to feed on phytoplankton (Haberman *et al.* 2003; Cleary *et al.* 2018), resulting in shallower distributions, and krill swimming downward in late autumn to likely feed on the benthos, resulting in deeper distributions (Kawaguchi *et al.* 1986; Schmidt *et al.* 2011, 2014). Such seasonal shifts in krill vertical distributions could have a large impact on krill contributions to nutrient and carbon cycling. Studies have shown that krill fecal pellet production is important to carbon sequestration and nutrient recycling when krill are in the upper portion of the water column (Le Fèvre *et al.* 1998; Schnack-Schiel & Isla 2005; Tovar-Sanchez *et al.* 2007; Atkinson *et al.* 2012a; Lehette *et al.* 2012). The late spring measurements indicate krill utilize the whole water

column, including the benthos; as such, they may be an important vector for nutrients such as iron to be reintroduced into surface waters (Schmidt *et al.* 2011). Meanwhile, the observations in late autumn indicate that krill rarely interact with the upper water column, which would decrease the direct contributions of krill to nutrient recycling and carbon sequestration from the euphotic zone. However, the carbon and trace metals krill scavenged at depth may be reintroduced to the surface through predation and consequent defecation by air-breathing diving predators or by krill returning to the euphotic zone in subsequent seasons.

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Tables:

Table 2.1. Specifics of camera deployments with Deployment Number, Date, Time

(local, UTC – 3 h), Location and Depth (m) of camera deployments. Type indicates the location of peak krill abundance in the water column (surface (S), midwater (M), and benthic (B)) with absence of krill = 0. Bold font shows deployments classified as dark.

Three late autumn deployments over a 24-hour period (15 - 17) were used to measure short term changes in krill distribution and are marked with a +. Deployments which were used to quantify krill movement behaviors are marked with an asterisk.

Depl. Num.	Date	Time	Lat.	Long.	Bay	Depth	Type
3*	20-May-13	9:12	64°40.944 S	62°13.877 W	Wilhelmina	500	0
4*	20-May-13	18:54	64°40.844 S	62°13.954 W	Wilhelmina	300	N/A
5*	21-May-13	14:03	64°32.097 S	62°14.062 W	Wilhelmina	600	0
6*	21-May-13	17:00	64°32.097 S	62°14.063 W	Wilhelmina	600	0
9*	23-May-13	15:20	64°50.790 S	62°36.844 W	Andvord	277	B
11*	24-May-13	13:39	64°48.257 S	62°43.340 W	Andvord	300	B
14*	25-May-13	1:19	64°48.788 S	62°42.107 W	Andvord	374	0
15+*	25-May-13	6:53	64°48.501 S	62°43.023 W	Andvord	341	M
16+*	25-May-13	13:19	64°48.629 S	62°43.048 W	Andvord	352	B
17+*	25-May-13	19:11	64°48.698 S	62°42.271 W	Andvord	343	M
18*	26-May-13	16:32	64°48.594 S	62°43.009 W	Andvord	344	0
20*	27-May-13	10:54	64°48.596 S	62°43.003 W	Andvord	347	B
24*	29-May-13	13:43	65°02.956 S	63°18.757 W	Flandres	243	B
25*	29-May-13	14:56	65°02.955 S	63°18.758 W	Flandres	200	B
26*	29-May-13	16:34	65°02.992 S	63°18.886 W	Flandres	269	B
29*	30-May-13	12:38	65°01.264 S	63°15.527 W	Flandres	510	0
31	30-May-13	19:53	65°01.262 S	63°15.512 W	Flandres	517	0
38*	4-Jun-13	18:22	64°37.113 S	62°14.317 W	Wilhelmina	499	M
39*	4-Jun-13	20:11	64°37.096 S	62°14.301 W	Wilhelmina	497	M
103 *	8-Dec-14	1:04	64°40.944 S	62°15.818 W	Wilhelmina	547	S
104 *	8-Dec-14	10:12	64°41.494 S	62°15.101 W	Wilhelmina	529	B
105	8-Dec-14	14:04	64°41.478 S	62°15.049 W	Wilhelmina	533	0
106	8-Dec-14	23:03	64°41.743 S	62°14.831 W	Wilhelmina	534	0
107	9-Dec-14	1:41	64°41.734 S	62°14.838 W	Wilhelmina	536	0
108	9-Dec-14	5:27	64°41.728 S	62°14.809 W	Wilhelmina	517	0
109 *	10-Dec-14	12:12	64°49.329 S	62°39.625 W	Andvord	428	S
112 *	10-Dec-14	22:02	64°50.574 S	62°39.376 W	Andvord	353	S
113 *	12-Dec-14	1:19	65°03.373 S	63°12.057 W	Flandres	327	S
114 *	12-Dec-14	9:47	65°03.323 S	63°19.363 W	Flandres	328	B
115	14-Dec-14	13:47	66°54.375 S	66°50.858 W	Grandidier	484	0
117	14-Dec-14	22:24	66°55.652 S	66°52.117 W	Grandidier	583	0
118	17-Dec-14	22:07	64°53.543 S	63°43.439 W	Gerlache	497	S
120 *	19-Dec-14	1:36	65°03.166 S	63°12.893 W	Flandres	342	B
121 *	19-Dec-14	4:44	65°02.790 S	63°13.501 W	Flandres	287	M
122	19-Dec-14	11:43	65°02.805 S	63°13.286 W	Flandres	340	0
125 *	20-Dec-14	23:57	65°04.102 S	63°09.805 W	Flandres	559	S
126	23-Dec-14	0:50	65°04.779 S	63°10.931 W	Flandres	625	M

Note: Deployment 4 was not included in late autumn vertical distribution analysis due to methodological issues.

Table 2.2. Number of krill tracks collected over the two seasons based on totals, bay (Wilhelmina, Andvord, and Flandres), and light or dark periods.

	Total	Wilhelmina	Andvord	Flandres	Light	Dark
Late Autumn	2979	1364	1135	480	1599	1383
Late Spring	366	9	28	329	125	241

Figures:

Figure 2.1. Map of the Antarctic Peninsula (left), with inset highlighting the deployment area with the three bays and the Gerlache Strait (right).

Figure 2.2. (Top) Camera sled deployment (*left*) and diagram of camera sled (*right*). The sled is composed of a 2-m long frame on which components are mounted, including (A) stereo cameras, (B) electronics bottle with backup computer, (C) LEDs, (D) CTD sensor, and (E) ADCP. (Bottom) Example pictures of krill from the camera system in late autumn (*left*) and late spring (*right*).

Figure 2.3. Krill abundance (krill m^{-3}) versus depth (m) for (top) late autumn deployments and (bottom) for late spring deployments. Data for different bays is separated by solid black vertical lines. The dashed lines represent the bottom of the water column. Profiles which occurred during dark periods are plotted on a shaded background. Note difference in abundance scales in autumn and spring.

Figure 2.4. (top) Late autumn krill abundance (krill m^{-3}) vs. relative depth (horizon depth / total depth) from the three different bays: Andvord (square), Flandres (triangle), and Wilhelmina Bays (circle). Deployments are plotted as midwater (a) or benthic (b) and given with their deployment number (Table 1). Error bars show the standard

deviation in krill per frame. (*bottom*) Late spring krill abundance (krill m⁻³) vs. relative depth (horizon depth / total depth) from four locations: Andvord Bay (square), Flandres Bay (triangle), Wilhelmina Bay (circle) and the Gerlache Strait (diamond). Deployments are plotted as surface (c), midwater (d), or benthic (e) and given with their deployment number (Table 1). Note that krill abundances are plotted logarithmically in this season.

Figure 2.5. (a) Late autumn relative depth of maximum krill abundance as a function of average maximum irradiance. The dashed line represents the cutoff between light and dark ($3 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$). (b) Late spring relative depth of maximum krill abundance as a function of average maximum irradiance. The dashed line represents the cutoff between light and dark ($100 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$).

Figure 2.6. Vertical distributions of krill in three consecutive deployments (15, 16, and 17; Table 1) at the same station in Andvord Bay. Shaded plots represent deployments during dark periods; the light graph (middle) occurred during daylight hours. Local time is shown in the top right corner of each panel. Error bars show standard error in krill abundance.

Figure 2.7. Krill swimming speeds (a), vertical velocities (b), and turning rates (c) in late autumn and late spring. The boxes represent 25th to 75th percentiles, notched lines the median values, and error bars the 10th and 90th percentiles of swimming behavior distributions. Circles represent the means and standard errors.

Figure 2.8. Krill swimming direction in late autumn (a) and late spring (b), binned in 2° intervals. Concentric circles denote the counts of krill within each bin. In each plot, the solid linear line represents the mean swimming direction, and the dashed lines the standard error.

Figure 2.9. Swimming speeds (a, d), vertical velocities (b, e), and turning rates (c, f) for krill between light (day) and dark (night) periods in late autumn (a, b, c) and late spring (d, e, f). Plot specifics as in Figure 2.7.

Figure 2.10. Swimming direction ($^{\circ}$ from horizontal) polar histograms for krill between light (day) (a, c) and dark (night) (b, d) periods in late autumn (a, b) and late spring (c, d). Plot specifics as in Figure 2.8.

Figure 2.11. Krill motility and vertical distributions in late autumn (*left*) and late spring (*right*) illustrated using characteristic swimming tracks. In late autumn, krill swimming direction was downward, resulting in the deeper distributions of krill. In late spring, krill swimming direction was upward, resulting in shallower distributions of krill.

CHAPTER THREE

Seasonal Shifts in Krill Energetic Requirements Due to Changes in Individual Krill Movement Behaviors

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Abstract:

Krill in the Southern Ocean are important consumers of primary production in late spring and summer. However, it is not known how much food krill must consume in late autumn and winter due to limited information about krill energetic requirements in these seasons. Shifts in krill energetic requirements between late spring and late autumn were compared using individual krill swimming speeds measured during these seasons collected along three bays in the Western Antarctic Peninsula. In general, krill consumed greater quantities of carbon at larger sizes and faster swimming speeds. Krill also consumed up to 18% of their carbon weight (CW) in late spring compared to 11% CW in late autumn, larger than the estimates of carbon requirements currently assumed in most krill models. However, krill required 15 - 48% higher concentrations of carbon in the water column in late autumn than late spring to cover energetic costs. Shifts in motility over 24 hours resulted in different energetic costs and prey concentration requirements. The best method for krill to minimize energetic requirements and maximize prey encounter rates appears to be to swim faster when feeding and decrease swimming speeds when not feeding. These results suggest krill remain important consumers of lower trophic levels along the Western Antarctic Peninsula throughout the year due to their high energetic requirements, which has direct ramifications on food web dynamics, carbon sequestration, and biogeochemical cycles in this region.

Introduction:

Krill are a keystone species in the Southern Ocean and are important in the transfer of carbon from primary producers to upper trophic levels, as well as significant contributors to biogeochemical cycles and carbon sequestration (Quetin & Ross 1991; Le Fèvre *et al.* 1998; Tovar-Sanchez *et al.* 2007; Nicol & Brierley 2010; Lehet *et al.* 2012; Ballerini *et al.* 2014). Krill also constitute the largest fishery by tonnage in the Southern Ocean (Nicol 2006; Brierley 2008; Nicol *et al.* 2012; Nicol & Foster 2016). As such, it is important to understand how shifts in carbon requirements with seasonal changes in krill movement behaviors affect their carbon consumption, growth rates, and impacts on the food web.

Krill growth models attempt to predict growth and survival of krill over time under different environmental conditions, including phytoplankton abundance and seawater temperatures (Atkinson *et al.* 2006; Candy & Kawaguchi 2006; Constable & Kawaguchi 2018). However, most models of krill energetics do not incorporate krill movement behaviors when modeling carbon requirements. Krill movement is generally included in mathematically-contrived respiration rates, which do not account for how potential variation in krill swimming speeds may impact carbon requirements. In most distribution models, krill are assumed to be passive drifters within currents, not active swimmers, and thus changes in carbon requirements due to changes in krill swimming speeds are not included in food requirement estimates. To our knowledge, the only study including swimming speeds in carbon requirement calculations was from Richerson *et al.* (2015); they accounted for swimming abilities as krill migrated across the Scotia Sea from the Antarctic Peninsula to South Georgia during summer. Even though krill

distributions were largely driven by currents in the region, active swimming behavior did influence their distributions and carbon requirements (Richerson *et al.* 2015). While many of these models can predict krill growth rates and distributions, these models do not incorporate changes in individual movement behaviors and, as such, likely underestimate krill carbon requirements.

Individual krill swimming speeds are known to change when they are feeding, foraging, avoiding predators, or satiated (Hamner *et al.* 1983; O'Brien 1987; Price 1989; Hamner & Hamner 2000; Pearre 2003; Swadling 2006; Tarling & Johnson 2006). Krill motility is also affected by seasonal and diel changes. Krill swim faster in spring than late autumn or winter (Klevjer & Kaartvedt 2006; Kane *et al.* 2018). Krill swim faster at night than during the day in spring (Klevjer & Kaartvedt 2011; Tarling & Thorpe 2017; Kane *et al.* 2018); however, krill swim slightly faster during the day than at night in late autumn (Kane *et al.* 2018). Modeling the respiration requirements of krill swimming speeds under different conditions will provide a better idea of the amount of carbon they must consume to cover respiration costs, as well as how diel and seasonal shifts in swimming behaviors change carbon requirements.

In addition to shifts in movement behaviors, krill feeding behaviors and carbon requirements are known to change under different circumstances, such as seasonally and ontologically. In spring and summer, krill primarily consume phytoplankton (Price *et al.* 1988; Quetin & Ross 1991; Haberman *et al.* 2003; Saba *et al.* 2014); since phytoplankton abundances are lower in autumn and winter, krill utilize other prey items, including other zooplankton, detritus, sea ice algae, and even other krill (Boyd *et al.* 1984; Kawaguchi *et al.* 1986; Ligowski 2000; Schmidt *et al.* 2011; Atkinson *et al.* 2012a; Saba *et al.* 2014).

Sea ice algae and entrenched detritus found under sea ice is thought to be particularly important to larval and juvenile krill because they do not have lipid reserves to survive long periods of starvation in the winter (Saba *et al.* 2014; Meyer *et al.* 2017). However, as shifts in krill feeding behaviors in autumn and winter are partially dependent on resource availability, age, and location, it is very difficult to determine how much food krill consume during these seasons (Quetin & Ross 1991; Atkinson *et al.* 2002; Meyer *et al.* 2010; Flores *et al.* 2012a; Schmidt *et al.* 2014). Modeling krill energetic requirements for swimming will provide a better idea of how much carbon they must feed on during different times of the year.

To determine how shifts in swimming behaviors impact krill energetics, we modeled changes in krill carbon requirements based on changes in their swimming speeds and vertical velocities between late autumn and late spring. Krill swim almost twice as quickly in late spring as they do in late autumn, and krill in both seasons showed a difference in swimming speeds between light and dark periods (Kane *et al.* 2018). Krill vertical velocities also differed between season and between light and dark periods (Kane *et al.* 2018). Carbon requirements for seasonal and daily changes in krill motility were determined by using these swimming speed and vertical velocity measurements. Krill lengths from Cleary *et al.* (2016, 2018) and the relationship between swimming speeds and respiration rates from Swadling *et al.* (2005) were used to determine the amount of carbon utilized for krill motility under different conditions. We then modeled how much carbon krill could obtain from the water column using chlorophyll a (*chl a*) concentrations as a proxy for phytoplankton carbon. We also modeled how diel shifts in krill motility influence their carbon requirements and feeding abilities. The differences in

carbon requirements due to diel shifts demonstrate different strategies krill may utilize to optimize prey encounter rates while minimizing energetic costs, as well as how krill may need to consume prey resources other than phytoplankton.

Methods:

Collection of Krill Movement Data

Krill swimming speeds for late autumn and late spring were obtained from Kane *et al.* (2018). In summation, camera deployments were conducted in May-June of 2013 and December of 2014 on board the *R.V.I.B. Nathaniel B. Palmer* (NP-1304 and NP-1410) in three bays along the Western Antarctic Peninsula. Individual krill movement behaviors were recorded at depths from 10 m to 625 m at different light levels.

Movement behaviors were quantified from >3000 movement tracks collected from the footage over the two seasons, 366 in late spring and 2979 in late autumn. Swimming speeds (body lengths (BL) s⁻¹) were estimated from video captured at 10 Hz, with track durations of 1 to 22.7 seconds in the late autumn (average length of 2.5 s) and 1 to 14.7 seconds in the late spring (average length of 1.7 s).

Conversion of Krill Swimming Speeds and Vertical Velocities

Swimming speeds for krill of different lengths were converted from BL s⁻¹ to cm s⁻¹ by multiplying swimming speeds (Kane *et al.* 2018) by krill lengths (between 9 mm and 57 mm as measured during the same two cruises (Cleary *et al.* 2016, 2018)). To further estimate realistic energy requirements of krill, swimming speed and vertical velocity measurements were capped for each individual krill length at 21.4 BL s⁻¹, as this was the maximum movement measured in Kane *et al.* (2018). These new speed estimates were then used to determine oxygen consumption rates, and thus carbon requirements, for krill.

Determination of Effective Ascent and Descent Swimming Speeds

Ascent and descent krill swimming speeds were determined by calculating the

effective swimming speed for vertical velocities, particularly at slow vertical velocities. As krill are negatively buoyant organisms moving at intermediate Reynolds numbers, gravity must be accounted for when krill swim between -2 BL s^{-1} and 2 BL s^{-1} (Murphy *et al.* 2011).

At vertical velocities with absolute values greater than 2 BL s^{-1} , effective vertical swimming rates were considered equivalent to the measured vertical velocity as viscous forces dominate krill movement and the effects of gravity are negligible. The transitionary phase, where viscous forces become more dominant than inertial forces, is between 0.5 BL s^{-1} and 2 BL s^{-1} . As the transitionary phase is linear with increasing swimming speed (Miyashita *et al.* 1996; Murphy *et al.* 2011), the relationship between inertial and viscous forces between these speeds can be estimated using:

$$\text{Ratio} = (4/3) - (2/3) * \text{BLSS}$$

where BLSS is swim speed in BL s^{-1} . For speeds below 0.5 BL s^{-1} , inertial forces dominate, and krill must actively swim against the gravitational force.

The effective ascent and descent swimming speeds of krill vertical velocities were determined by calculating whether ascent or descent vertical velocities combined with krill sinking rates were between 0 and 2 BL s^{-1} . Sinking rates of krill were calculated using the equation from Kils (1981):

$$\text{SR} = 0.0604 * L^{1.07}$$

where SR is sinking rate in cm s^{-1} and L is krill length in mm. When effective ascent or descent vertical velocities fell between 0.5 and 2 BL s^{-1} , the ratio between inertial and viscous forces was calculated using the above equation; krill sinking rates were multiplied by this ratio and added to the ascent or descent vertical velocities to determine

their effective swimming speed. When krill effective ascent or descent vertical velocities were slower than 0.5 BL s, which mostly occurred when krill were descending very slowly, sinking rates were added to krill effective ascent or descent vertical velocity to determine their effective vertical swimming speeds.

Swim Speed and Vertical Velocity Energetics.

Krill energetic costs were determined by estimating the respiration costs of krill individual swimming speeds and effective vertical swimming speeds. Swadling *et al.* (2005) determined a relationship between krill swimming speeds and their respiration rates as well as a minimum threshold below which respiration proceeds at a minimal level, which they termed the routine respiration rate. Thus, respiration rates were estimated from swimming speeds in the late spring using:

$$\text{Resp Rate (mg O}_2\text{ g}_D^{-1}\text{ hr}^{-1}) = \begin{cases} 2.16 + 0.35 * SS, & SS > 3 \text{ cm s}^{-1} \\ 1.8, & SS \leq 3 \text{ cm s}^{-1} \end{cases}$$

where SS is swimming speed in cm s^{-1} . Respiration costs were then converted to $\text{mg O}_2 \text{ ind}^{-1} \text{ hr}^{-1}$ by multiplying the respiration rates by krill weight. Krill weight was estimated using $DW = (6.46 * 10^{-5}) * L^{3.89}$, where DW is the dry weight (in mg) of krill and L is the length of krill (in mm) (Atkinson *et al.* 2006; Richerson *et al.* 2015). Daily oxygen consumption estimates were then obtained by multiplying respiration rates of krill by corresponding weight and 24 hours to determine the daily oxygen requirement per individual.

Carbon (C) requirements of krill were estimated using both mg C required and percent carbon weight of krill (%CW) to determine absolute and relative amounts of food required. Daily oxygen consumption was converted to carbon required by multiplying the respiration rate by the mole ratio between molecular carbon and oxygen (12.011 g C

to 32 g O₂) and by a respiratory quotient of 0.72 (Lowe *et al.* 2012; Richerson *et al.* 2015). Carbon consumption in %CW was determined by dividing the mg C required by the carbon weight of krill; carbon weight of krill was based on $CW = 0.366 * DW^{1.037}$ (Hofmann & Lascara, 2000), where CW is carbon weight (in mg) and DW is dry weight (in mg).

When energetic costs of ascent and descent were estimated, krill were assumed to only move vertically. Daily oxygen consumption and carbon requirements were estimated using the same method as with swimming speed energetic estimations. Krill oxygen consumptions and carbon requirements were also estimated for distance traveled by estimating energetic requirements and time traveled for krill moving at different vertical velocities over 1 km, following the methods of Swadling *et al.* (2005) and Buskey (1998).

Feeding Abilities

In the model, the ability of krill to obtain enough carbon to cover energetic costs is dependent on the volume of water that krill can clear, as krill are efficient filter feeders and preferentially feed on phytoplankton in the water column (Kils 1983; Haberman *et al.* 2003; Schmidt & Atkinson 2016). The volume of water which a krill could filter was determined by multiplying the swimming speed by the filter area of its feeding basket to obtain the volume of water searched. The filter area of krill at different lengths was determined using the following equation modified from Kils (1981) and Schmidt & Atkinson (2016):

$$FA = 10^{(1.51 * \log_{10}(L) - 0.12)}$$

where FA is the filter area of the feeding basket (mm²) and L is length (mm).

The ability of krill to obtain carbon from the water column was modeled using several methods. The first method determined how much carbon krill could consume at various phytoplankton concentrations per hour assuming seasonal mean swimming speeds from Kane *et al.* (2018). The second method compared how long krill would have to feed at different phytoplankton concentrations to consume 2.3% CW, the minimum required to maintain routine respiration rates (Boyd *et al.* 1984); 10% CW, the maximum consumption value modeled (Boyd *et al.* 1984; Fach *et al.* 2002, 2006, 2008; Kawaguchi *et al.* 2013); 16% CW, an average concentration of how much carbon has been found in krill stomachs (Schmidt & Atkinson 2016); and 28% CW, the maximum recorded carbon content in krill gut contents caught in the Southern Ocean (Clarke *et al.* 1988; Schmidt & Atkinson 2016). The third method modeled the minimum *chl a* concentration required to be present in the water column to cover krill motility costs assuming different amounts of time spent feeding. Krill in the model fed between 1 and 6 hours, as it is considered too energetically costly for krill to feed for more than 6 hours (Boyd *et al.* 1984). The amount of carbon required for krill to maintain their motility over 24 hours was then divided by the total volume of water filtered during the times spent feeding to determine how much carbon was required to be present in the water column.

To mimic variations in krill carbon requirements due to diel shifts in swimming speeds in a 24-hour period, different swimming speeds for different periods of time were used to model daily estimates of krill movement energetic requirements, as well as the amount of carbon collected. In two variations of the model, swimming speeds switched between seasonal night and day mean swimming speeds depending on when krill were feeding; in two other variations, krill swimming speeds remained at one swimming speed,

either seasonal night or day mean swimming speeds. In the model, krill fed between 1 and 6 hours in all 4 variations; in the two variations with krill changing swimming speeds, krill fed at one speed and swam the remaining 24 hours at the other. Both carbon requirements and *chl a* concentrations needed to cover said energetic costs were then compared across the 4 variations.

Phytoplankton abundances

Phytoplankton were assumed to be the main source of food available for krill. *Chl a* concentrations were modeled by assuming a carbon to *chl a* ratio of 50:1, as this is considered a conservative estimate of the amount of carbon in phytoplankton (Fach *et al.* 2008). *Chl a* concentrations were compared to measured concentrations of 0.02 mg m⁻³ to 18.5 mg m⁻³, corresponding to a range of *chl a* concentrations measured during the two cruises (Morison & Menden-Deuer 2018); for more detailed seasonal analyses, phytoplankton concentrations were assumed not to exceed 0.4 mg m⁻³ in late autumn, while concentrations in late spring were assumed to consistently be above 0.1 mg m⁻³.

Decrease in Adult Routine Respiration Rates

Routine respiration costs of adult krill in late autumn are reported to be half of what they are in late spring (Meyer & Teschke 2016). To determine how a decrease in routine respiration rates might affect adult krill energetics and feeding requirements in late autumn, the decrease in routine respiration rates was assumed to affect only the routine respiration rates of krill larger than 25 mm, which represents adult krill greater than 1 year old. Respiration costs of movement for these krill were modeled using:

$$\text{Resp Rate (mg O}_2 \text{ g}_D^{-1} \text{ hr}^{-1}) = \begin{cases} 1.08 + 0.35 * \text{SS}, & \text{SS} > 3 \text{ cm s}^{-1} \\ 0.9, & \text{SS} \leq 3 \text{ cm s}^{-1} \end{cases}$$

with SS representing krill swimming speeds (cm s⁻¹). Carbon energetic estimates and

feeding requirements were then determined using the same methods described previously. A sensitivity analysis was conducted to determine how changes in routine respiration rates would affect respiration rates at various swimming speeds.

Results:

Krill swimming speed and vertical velocity estimates

Multiplying measured swimming speeds by krill lengths resulted in estimated swimming speed ranges of 0.1 to 105.1 cm s⁻¹ in late autumn and 0.4 to 122.1 cm s⁻¹ in late spring. Seasonal mean swimming speeds ranged from 2.5 cm s⁻¹ for krill of 9 mm length to 15.8 cm s⁻¹ for krill of 57 mm length in late autumn, and 4.8 to 30.5 cm s⁻¹ in late spring. Mean swimming speeds during light periods were between 2.7 and 17.1 cm s⁻¹ in late autumn and between 4.6 and 29.1 cm s⁻¹ in late spring; mean swimming speeds during dark periods ranged between 2.3 and 14.8 cm s⁻¹ in late autumn and between 5.0 and 31.4 cm s⁻¹ in late spring.

Multiplying krill lengths by measured vertical velocities resulted in velocities ranging from -69.5 to 80.4 cm s⁻¹ in late autumn and from -120.8 to 95.8 cm s⁻¹ in late spring, with negative vertical velocities representing downward movement and positive velocities representing upward movement. Mean vertical velocities were between -0.09 cm s⁻¹ for krill of 9 mm length and -0.57 cm s⁻¹ for krill of 57 mm in length in late autumn, and between 0.30 and 1.88 cm s⁻¹ in late spring. Vertical velocities ranged between -50.7 and 54.7 cm s⁻¹ during the day and -69.5 and 80.4 cm s⁻¹ at night in late autumn, while in late spring they ranged between -61.0 and 89.5 cm s⁻¹ during the day and -120.8 and 95.8 cm s⁻¹ at night.

Swimming Speed Energetic Costs

Across the range of swimming speeds, faster and larger krill consumed more oxygen. Oxygen consumption increased linearly with swimming speed and exponentially with increasing krill size (Figure 3.1). The model indicated krill consume

from between 2.96×10^{-3} and $19.4 \text{ mg O}_2 \text{ hr}^{-1}$ for krill of increasing size (from 9 to 57 mm) when swimming at the maximum possible swimming speeds of 22.1 BL s^{-1} , which resulted in estimated maximum swimming speeds between 19.9 and 126.0 cm s^{-1} . At mean swimming speeds modeled, krill would consume between 5.99×10^{-4} and $3.39 \text{ mg O}_2 \text{ hr}^{-1}$ in late autumn and 12.9×10^{-3} and $5.65 \text{ mg O}_2 \text{ hr}^{-1}$ in late spring. When swimming at similar speeds, smaller krill utilize more carbon relative to their body carbon weight than larger krill, with krill 9 mm in length using 30.4% more carbon relative to their body weight than krill 57 mm in length (Figure 3.2).

As modeled, krill swimming at seasonal mean swimming speeds generally used 24 to 40% more carbon per day in late spring than in late autumn (Figure 3.3). In the late spring, krill daily carbon consumption rates were 3 to 6% greater when swimming at night mean swimming speeds compared to day mean swimming speeds (Figure 3.4). In the late autumn, the daily carbon consumption rates of krill greater than 12 mm were between 5 and 12% greater when swimming at day mean swimming speeds compared to night mean swimming speeds; carbon consumption rates of krill smaller than 12 mm were between 0 and 90% greater due to errors with the Swadling *et al.* (2005) respiration requirements and thus not shown.

Vertical Velocity Energetic Costs

Energetic requirements of vertical velocities followed the same pattern as general swimming speeds, with krill consuming more oxygen when larger or swimming faster (Figure 3.5). At slower vertical velocities, when inertial forces are involved, krill used more energy moving upward than downward over sustained intervals. However, when comparing energetic costs over traveling 1 km, krill used almost 94 times more oxygen at

slower speed than faster speeds, since it takes considerably longer to move 1 km at slower velocities than faster velocities.

Late autumn mean vertical velocities were similar to mean vertical velocities in late spring, with modeled daily oxygen costs slightly greater as krill get larger (Figure 3.5). Krill used up to 11% more energy to maintain average vertical velocities in late spring than in late autumn. Additionally, krill used between 22 and 37% more energy to ascend and between 18 and 32% more energy to descend in late spring compared to late autumn; however, krill use more energy for ascent than descent in both seasons. In spring, krill use 10 to 30% more energy to move up and down at night than during the day (Figure 3.6); in contrast, in late autumn, krill utilize 5 to 10% less energy to move up and down at night than during the day (Figure 3.6).

Feeding Abilities

In general, larger krill were able to obtain more carbon from the water column than smaller krill (Figure 3.7); this was due to both faster mean swimming speeds and the larger areas of the feeding baskets of larger krill, as the filter area of the feeding basket of a krill increased between 1.3 and 8.5% with increasing krill length, with the largest relative increases in area happening between the smallest krill lengths. However, the model suggests that smaller krill are able to obtain more carbon compared to their body mass than larger krill in both seasons at the same phytoplankton concentrations. Slower mean swimming speeds in late autumn suggest krill would acquire about 48% less carbon than in late spring. In late spring, krill obtain about 7.3% less carbon per hour at mean day swimming speeds when compared to night swimming speeds, whereas in late autumn, krill obtain about 15% more carbon per hour at mean day swimming speeds

when compared to night swimming speeds.

Due to the decreased volume of water krill were able to filter due to slower mean swimming speeds, krill in late autumn need almost twice the time to collect equivalent amounts of carbon as in late spring. For all krill in both seasons, the model estimated it takes 435, 696, and 1217% more time to collect 10% CW, 16% CW, and 28% CW than it takes to collect 2.3% CW filter feeding. In late spring, it takes approximately 8% more time at mean day swimming speeds to collect as much carbon as at mean night swimming speeds. In late autumn, however, it takes 13% less time to collect equivalent carbon amounts at day swim speeds as at night swim speeds.

The model showed that krill require lower concentrations of carbon be present in the water column to cover energetic costs when they are able to feed for longer periods of time. If routine respiration rates did not decrease in late autumn, krill would require 15 – 48% more carbon in the water column to meet their energetic requirements. In late spring, krill would need 1– 4% higher *chl a* concentrations in the water column to fulfill their energetic requirements during the day than at night. In late autumn, krill would require 4 – 9% lower *chl a* concentrations in the water column to fulfill their energetic requirements during the day than at night.

Carbon Balance with Changing Swimming Speeds

Modeled shifts in krill swimming speeds caused by changes in feeding and non-feeding behaviors resulted in differences in movement energetic requirements and the *chl a* concentrations necessary to cover energetic costs (Figure 3.8). In late spring, swimming at the slower speeds results in krill utilizing less carbon. However, the combination of swimming slightly faster at night to feed and swimming at slower speeds

during the remaining 24 hours results in 6% lower *chl a* concentration needed to cover energetic costs than if krill swam slowly over 24 hours. A similar pattern is observed in late autumn, with the slight increase in speeds during the day and the decrease in speeds at night resulting in 12% lower *chl a* concentration required to obtain enough carbon to cover energetic costs than if krill swam slowly over 24 hours.

Decrease in Routine Respiration Rates

The model shows that decreases in routine respiration rates, or the lowest possible respiration rates, of adult krill, as occur in late autumn and winter (reviewed in Meyer & Teschke 2016), result in a notable decrease in overall respiration rates when routine respiration rates have a greater contribution to the overall energetic requirement of krill, particularly at swimming speeds closer to 0 cm s⁻¹. As krill swimming speeds increase, changes in routine respiration rates have less of an effect on overall changes in respiration rates, such that decreases in routine respiration rates have a negligible effect on total respiration rates at speeds above 30 cm s⁻¹.

When routine respiration rates of adult krill were assumed to be 50% lower in late autumn than late spring, modeled oxygen consumption was more than 48% lower in late autumn than spring, and was 14 to 26% lower than autumn oxygen consumption when routine respiration rates were held constant. This decrease in oxygen requirement in late autumn, which decreases their carbon requirement, means larger krill require prey carbon concentrations in the water column to be 0.6 to 1.1% lower in late autumn than late spring, and 14 to 24% lower than carbon concentrations required when routine respiration rates were held constant.

Discussion:

Changes in carbon requirements and feeding abilities of krill between late spring and autumn were modeled utilizing recently published measurements of individual krill seasonal swimming behaviors. Krill required up to 18% CW in late spring and up to 11% CW in late autumn to maintain mean swimming speeds, both of which are greater than the assumed maximum consumption of 10% CW used in most models and closer to the 16-18% CW observed in the guts of krill collected in the field (Boyd *et al.* 1984; Clarke *et al.* 1988; Hofmann & Lascara 2000; Fach *et al.* 2002, 2006, 2008; Schmidt & Atkinson 2016). Modeling energetic requirements of krill vertical velocities demonstrated that while it is more energetically efficient for krill to ascend or descend quickly in the water column when conducting diel vertical migrations, it is less energetically costly over time for krill to sink slowly over time than to remain at a particular depth. Remarkably, the model indicated that while high swimming speeds yielded higher energetic demands in late spring, slower swimming speeds in late autumn did not necessarily support sufficient prey exposure to meet prey intake requirements. The predicted optimal solution to address the energetic imbalance between different swimming speeds is for krill to swim faster while feeding and decrease swimming speeds when not feeding, balancing tradeoffs between the high energetic cost of swimming and the need to clear adequate volumes of water to meet prey requirements. These results imply krill must continuously feed throughout the year, which may drive the biological pump in the late spring when phytoplankton are in abundance and may potentially reverse the biological carbon pump in late autumn when krill are primarily feeding on sediment.

Krill likely require large amounts of carbon to maintain the estimated mean

swimming speeds that were measured in late spring and late autumn. Because krill swim almost twice as fast in late spring as in late autumn (Kane *et al.* 2018), krill energetic requirements are up to 40% higher in late spring than late autumn; when the seasonal decrease in respiration rates is included (Meyer *et al.* 2002, 2010; Meyer 2012; Brown *et al.* 2013; Meyer & Teschke 2016), larger krill consume almost 50% more carbon in late spring than they do in late autumn. Most krill growth models assume krill consume up to 10% CW per day (Boyd *et al.* 1984; Hofmann & Lascara 2000; Fach *et al.* 2002, 2006, 2008). However, our results demonstrate that krill likely consume up to 18% CW per day on a consistent basis in late spring to cover movement costs; this is similar to field observations of the amount of carbon in krill gut contents (Clarke *et al.* 1988; Schmidt & Atkinson 2016). Moreover, current models of krill energetic requirements in late autumn likely underestimate the carbon requirements of krill, particularly if they only assume the energetic costs of krill routine respiration rates (Hofmann & Lascara 2000; Meyer 2012). Our model results indicate krill likely feed throughout the year to maintain higher levels of energetic movements observed in both late autumn and late spring.

While krill may conserve energy by moving at slower vertical velocities over time, it is more energetically efficient for krill to move up and down in the water column at faster vertical velocities towards particular water column depths than moving at slower velocities. Krill diel vertical migrations in the water column generally show a strong ascent at the beginning of the night followed by more variable, generally slower descent behaviors until the end of the night, when the remaining krill move quickly down to depth (Ohman 1986; Sourisseau *et al.* 2008; Tarling & Thorpe 2017). These faster movements at the beginning and end of the night are the most efficient method for krill to

move between depths, both to obtain food and hide from air-breathing predators. The slow descent of krill in the middle of the night may be linked to the hunger-satiation hypothesis, which postulates krill will slow their movement as they become satiated to increase ingestion (Pearre 2003; Swadling 2006; Tarling & Johnson 2006). The results presented here support that sinking is less energetically costly for krill than maintaining their position in the water column over time.

Krill likely require greater carbon concentrations in the water column in late autumn than in late spring to meet carbon consumption requirements despite the decrease in krill energetic costs in late autumn. This is primarily due to the decrease in krill swimming speeds in late autumn compared to late spring, as the volume of water krill are able to filter is directly proportional to swimming speeds (Kils 1981; Schmidt & Atkinson 2016; Kane *et al.* 2018). In particular, these results demonstrate the importance of food availability for juvenile krill. Sea ice algae and other carbon found under sea ice are considered important food sources for juvenile krill to survive the winter due to their lack of lipid reserves (Flores *et al.* 2012b; Saba *et al.* 2014; Meyer & Teschke 2016; Meyer *et al.* 2017). Juvenile krill need a consistent food source in late autumn; due to their slower motility in late autumn, juvenile krill require prey concentrations in this season to be almost twice as dense as in late spring in order to meet movement energetic requirements. The decrease in routine respiration rates of adult krill decreases their energetic requirements, which implies adult krill may be able to cover energetic costs at slightly lower *chl a* concentrations in late autumn than late spring. Additionally, if krill are able to feed for longer periods of time, they are capable of meeting their energetic requirements at *chl a* concentrations of $\leq 0.4 \text{ mg } chl a \text{ m}^{-3}$, similar to those measured

during our late autumn cruise (Morison & Menden-Deuer 2018). Overall, the model indicates krill require higher concentrations of carbon to be present to cover their energetic costs in late autumn than they do in late spring, due to the decrease in prey encounter rates caused by decreasing krill motility; however, krill may be able to obtain enough carbon to cover energetic costs at realistic late autumn *chl a* concentrations the longer they are able to feed.

Diel shifts in krill swimming speeds have significant impacts on krill energetic requirements, feeding capabilities, and food requirements. In both seasons, the most energetically-optimal pattern of swimming speeds was for krill to move more quickly when feeding and revert to slower swimming speeds when not. This particular pattern follows previous observations of krill increasing their swimming speed when feeding and decreasing their speed when not (Price 1988; Hamner & Hamner 2000; Pearre 2003; Swadling 2006; Tarling & Johnson 2006). In late spring, faster swimming speeds were associated with dark periods and slower swimming speeds with light periods (Kane *et al.* 2018). As krill were generally found at shallow depths in the water column at night in late spring, krill were likely feeding on phytoplankton in the surface layers of the water column (Godlewski 1996; Kawaguchi *et al.* 1999; Hamner & Hamner 2000; Kane *et al.* 2018). In contrast, krill in late autumn moved faster during light periods than during dark periods; additionally, krill were found close to the sediment during light periods and in the middle of the water column at night (Kane *et al.* 2018). Krill are known to regularly feed on carbon in the sediment throughout the year, particularly when there is limited food in the water column (Kawaguchi *et al.* 1986; Ligowski 2000; Clarke & Tyler 2008; Schmidt *et al.* 2011, 2014). Based on the most optimal energetics model for late autumn,

our results support krill actively consuming detritus during light periods in late autumn and not feeding while in the water column during dark periods due to the increase in swimming speeds during light periods and the decrease in swimming speeds during dark periods. By increasing swimming speeds near food sources and decreasing swimming speeds when not feeding in both seasons, krill are able to increase prey encounter rates to obtain enough carbon to cover their energetic costs at lower food concentrations than by swimming consistently at slower speeds over 24 hours.

As the purpose of this model was to examine how seasonal and diel shifts in krill movement behaviors influence their energetic costs and feeding abilities, there are several limitations with our analysis of total krill carbon consumption. There are differences in energetic costs between male, female, and juvenile krill; for example, male and juvenile krill have a lower respiration rate for movement than adult females (Johnson & Tarling 2008). Additionally, males and females incur different reproductive costs, which was not modeled here (Nicol *et al.* 1995; Virtue *et al.* 1996). We also did not explore how changes in the length-weight relation of krill might impact their energetic requirements. There are a number of different length-weight relationships from studies of Antarctic krill (reviewed in Siegel 2016); however, we only used one relation between krill length and weight to keep comparisons of energetic costs consistent between seasons. Furthermore, changes in krill respiration rates and krill weight are affected by changes in life stage, season, temperature, food availability, growth rate, and molt stage (Daly 1990; Quetin *et al.* 1994; Swadling *et al.* 2005; Atkinson *et al.* 2006; Tarling *et al.* 2006; Meyer *et al.* 2010; Meyer & Teschke 2016; Ryabov *et al.* 2017; Benkort *et al.* 2018; Constable & Kawaguchi 2018). While these many differences may provide more nuanced predictions

of krill carbon requirements, the basic conclusions of krill consuming more carbon in late spring than late autumn due to increased motility, and the higher carbon concentration required to be in the water column to cover their energetic costs in late autumn compared to late spring, will likely be similar.

Shifts in krill carbon consumption requirements due to seasonal changes in motility have implications for their contributions to carbon cycling in the Southern Ocean. In the model, larger krill may consume up to 37 mg C per day to cover movement costs in late spring, closer to 18% CW; a single krill 57 mm long can search through 0.4 m³ of water per hour and obtain enough carbon to cover energetic requirements during phytoplankton blooms with minimum *chl a* concentrations of 0.33 mg m⁻³. This means that large swarms of krill, with hundreds or thousands of individuals, can consume entire phytoplankton blooms very quickly (Le Fèvre *et al.* 1998; Ryabov *et al.* 2017). Krill egestion rates increase with greater ingestion rates, so the consumption of phytoplankton blooms by krill would support nutrient recycling in the upper portion of the water column and increase krill contributions to the biological pump in spring (Le Fèvre *et al.* 1998; Tovar-Sanchez *et al.* 2007; Atkinson *et al.* 2012b; Lehet *et al.* 2012). In late autumn, larger krill need to consume up to 22 mg C per day to cover energetic costs. However, since measured phytoplankton concentrations were ≤ 0.4 mg *chl a* m⁻³ in late autumn and averaged 0.28 mg *chl a* m⁻³, the model indicates larger krill would not obtain enough carbon to cover energetic costs by feeding only on phytoplankton in the surface waters (Boyd *et al.* 1984; Morison & Menden-Deuer 2018). The sediment along the Antarctic Peninsula accumulates large amounts of organic carbon throughout the year and contain regions with organic carbon concentrations of between

18 and 35 mg cm⁻² (Mincks *et al.* 2005; Smith *et al.* 2006; Glover *et al.* 2008; Isla 2016). Individual krill would be able to cover energetic costs by feeding on the sediment during late autumn even assuming larger krill were only able to filter 50% of the smaller particles due to decreasing filter efficacy with smaller particle size (Kils 1983; Kawaguchi *et al.* 1986; Schmidt & Atkinson 2016). However, krill consuming carbon from the sediment would reduce the amount of carbon sequestered. Krill feeding at the benthos may also resuspend particles into the water column, as krill flick the sediment into the water column to feed (Clarke & Tyler 2008; Schmidt & Atkinson 2016); when krill move up from the sediment at night, they may bring resuspended particles through water column movement to the middle of the water column (Ritz *et al.* 2011; Houghton *et al.* 2018). The combination of krill flicking up and consuming carbon from the sediment reintroduces carbon towards surface waters, either through predation by air-breathing predators or advection of particles into surface waters. In contrast to larger adult krill, the model suggests smaller juvenile krill may be able to cover movement costs with sea ice algal concentrations of 0.4 mg chl *a* m⁻³. While this may not be enough to sustain optimal growth rates, these results demonstrate that juvenile krill may be able to access enough sea ice algae or organic carbon to survive until the next spring (Fritsen *et al.* 2008; Meyer *et al.* 2017). The estimates of energetic requirements from our model, based on observed swimming behaviors, imply krill are important consumers of phytoplankton in late spring and other food resources in late autumn; furthermore, large adult krill are important contributors to the biological pump in late spring and may prevent carbon sequestration in late autumn.

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Tables:

Table 3.1. Model descriptions for shifts in krill swimming speed (in body lengths (BL) s^{-1}) when feeding and when not feeding.

	Spring		Autumn	
	Feeding	Not Feeding	Feeding	Not Feeding
Model 1	5.1 BL s^{-1}	5.1 BL s^{-1}	3.0 BL s^{-1}	3.0 BL s^{-1}
Model 2	5.1 BL s^{-1}	5.5 BL s^{-1}	3.0 BL s^{-1}	2.6 BL s^{-1}
Model 3	5.5 BL s^{-1}	5.5 BL s^{-1}	2.6 BL s^{-1}	2.6 BL s^{-1}
Model 4	5.5 BL s^{-1}	5.1 BL s^{-1}	2.6 BL s^{-1}	3.0 BL s^{-1}

Figures:

Figure 3.1. Changes in individual krill respiration rates (in mg O₂ ind⁻¹ hr⁻¹) with changes in swimming speed (in cm s⁻¹) and length (in mm). The solid black line is the respiration rates of krill swimming at mean average swimming speeds in late spring, and the dashed line represents the respiration rates of krill swimming at mean average swimming speeds in late autumn assuming no decrease in routine respiration rates.

Figure 3.2. Carbon utilized by krill of different lengths to maintain motility at given swimming speeds. Krill of 9 mm, 21 mm, 33 mm, and 45 mm length were assumed to be able to swim to speeds up to 19.1, 44.9, 70.6, and 96.3 cm s⁻¹, respectively.

Figure 3.3. Daily oxygen consumption for krill of different lengths at seasonal mean (solid lines) and standard error (dashed lines) swimming speeds.

Figure 3.4. Percent differences in carbon requirements for maintaining mean swimming speeds between day and night. Percent differences for krill of lengths greater than 12 mm are shown here due to errors occurring in carbon consumption estimates due to the Swadling *et al.* (2005) equation for krill below lengths of 12 mm.

Figure 3.5. Individual respiration rates (in $\text{mg O}_2 \text{ ind}^{-1} \text{ hr}^{-1}$) for krill of different lengths (in mm) and swimming at different vertical velocities (in cm s^{-1}) with spring (solid) and autumn (dashed) mean swimming speeds, as well as average 10% upward and downward swimming speeds.

Figure 3.6. Percent differences in carbon requirements between day and night upper (dashed) and lower (dot-dashed) vertical velocity averages for late spring and autumn.

Figure 3.7. Carbon (mg C hr⁻¹) obtained by krill of different lengths assuming mean swimming speeds of spring (a) and autumn (b) at different chlorophyll *a* (*chl a*) concentrations measured in both seasons.

Figure 3.8. Comparison of carbon requirements due to energetic costs (a, b) and chlorophyll a (*chl a*) concentration required to cover swimming costs (c, d) in late spring (a, c) and late autumn (b, d) under different diel models (see Table 3.1) and assuming 6 of 24 hours spent feeding.

CHAPTER 4

Shifts in Individual Krill Motility With Changes in Aggregation Density

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Key Words:

Abstract:

Antarctic krill in the Southern Ocean are traditionally defined as an obligate schooling species, meaning they form and maintain aggregations throughout their adult lives. However, recent studies have suggested krill may swim alone more often than previously thought. Additionally, aggregation studies have focused primarily on describing the size, shape, and density of aggregations and how individuals maintain the aggregations. The focus of this study was to examine how individual krill movement behaviors were influenced by krill aggregation density and nearest neighbor distances. In general, swimming speeds increased by 39% to 42% between solitary krill and krill in dense aggregations. During light periods, krill swimming speeds increased between solitary krill and dense krill abundances by 34% and 91% in late autumn and spring, respectively. In the late autumn, krill turning rates increased with increasing krill density. Krill swimming speeds also increased with increasing nearest neighbor distance, and the variance in turning rates decreased with increasing krill density. Energetic models evaluating the effect of increased swimming speeds associated with krill density showed individuals consume enough carbon to cover energetic costs at 17 to 19% lower prey concentrations than swimming speeds associated with solitary krill. These results suggest that denser aggregations are likely to intensify krill contributions to local nutrient recycling, the biological carbon pump, and food web dynamics in the late spring, as well as enhance particle resuspension caused by krill feeding on the carbon in the sediment in late autumn.

Introduction:

Antarctic krill are important in the Southern Ocean as a key food source for many iconic megafauna (Quetin & Ross 1991; Ballerini *et al.* 2014). Krill are also important in benthic-pelagic coupling, biogeochemical cycles, and the biological carbon pump, in part due to the large biomass of the population (Le Fèvre *et al.* 1998; Tovar-Sanchez *et al.* 2007; Atkinson *et al.* 2008; Lehet *et al.* 2012). However, krill are not found uniformly throughout the Southern Ocean but are instead concentrated in aggregations in the Southwestern Atlantic Sector (Miller & Hampton 1989; Atkinson *et al.* 2008; Siegel & Watkins 2016; Tarling & Fielding 2016).

Krill have long been considered an obligate schooling species, meaning they were thought to spend the majority of their adult life cycle in groups (Marr 1962; Miller & Hampton 1989; Hamner & Hamner 2000; Tarling & Fielding 2016). Studies of krill distributions generally find large portions of biomass of krill in larger groups; when coming across superswarms, studies may even find that >50% of the krill biomass observed resides in a single group (Tarling *et al.* 2009; Krafft *et al.* 2012; Tarling & Thorpe 2014; Tarling *et al.* 2018). However, krill are known to swim alone when the nearest aggregation consists of krill not of similar size, possibly to avoid being more easily targeted by visual predators (Hamner & Hamner 2000). Additionally, it has recently been suggested that forming aggregations may not be a successful strategy for larger adult krill due to their visibility (Tarling & Fielding 2016). This shift from assuming krill are an obligate schooling species to observing that krill schools form under specific conditions illustrates the importance of understanding what conditions induce krill to establish aggregations.

There are very few studies on how krill densities influence individual krill swimming behaviors. The majority of *in situ* studies of krill aggregations have been conducted using acoustics to characterize the aggregations as a whole more than the behaviors of individuals within the aggregations (Tarling *et al.* 2009; Atkinson *et al.* 2012a; Siegel & Watkins 2016; Tarling & Fielding 2016); acoustic studies are also likely to miss individual krill swimming alone as solitary krill are much smaller than the area averaged by acoustics at any given time (Atkinson *et al.* 2012a). Most individual krill behaviors studied in aggregations using photographic methods have focused on quantifying nearest neighbor distance and orientation differences between individuals (Hamner & Hamner 2000; Kubilius *et al.* 2015). Laboratory studies of krill aggregating behaviors have primarily focused on contrasting the differences in nearest neighbor distances and swimming speeds between schooling and swarming krill, as well as determining at which density they are likely to form schools (Strand & Hamner 1990; Kawaguchi *et al.* 2010). To our knowledge, there have been no studies, either *in situ* or in the laboratory, on how individual swimming behaviors are affected by shifts in krill density within aggregations, particularly swarms.

Determining the differences in individual krill motility due to changes in density may provide a better understanding of how krill deal with the trade-offs associated with aggregating. Collective motion of a group of organisms is defined as the summation of individual behaviors interacting with and reacting to one another (Vicsek 2001; Vicsek & Zafeiris 2012). However, recent studies into organism behaviors within groups have revealed that the interactions are slightly more complicated. Starlings, for example, follow up to seven neighbors based on topographical distances rather than all neighbors

visible (Ballerini *et al.* 2008). Fish behaviors are influenced by how close their neighbors are but not necessarily by how dense their aggregation is (Katz *et al.* 2011; Shelton *et al.* 2014). It has also been theorized that aggregations of krill are able to find and stay near food resources more easily than a single krill (Grünbaum 1998; Flierl *et al.* 1999). Clearly, there is a trade-off between aggregation size and the degree of resource competition among krill (Flierl *et al.* 1999; Parrish & Edelstein-Keshet 1999; Brierley & Cox 2010). Understanding how differences in krill density influence individual krill movement behaviors will clarify some of the strategies krill may employ as competition for resources increases.

Using footage collected along the Western Antarctic Peninsula during May-June 2013 and December 2014 (for details, see Kane *et al.* 2018), we quantified differences in individual krill swimming behaviors within aggregations of different densities, both with overall density shifts and changes in nearest neighbor distances. We then modeled how changes in krill movement behaviors at these densities influence their carbon requirements and feeding abilities on phytoplankton abundances, using chlorophyll *a* (*chl a*) as a proxy for carbon concentrations in the water column.

Methods:

Data collection

Krill movement and abundance data for late autumn and spring were collected as described in detail in Kane *et al.* (2018). In brief, video observations of krill swimming *in situ* were collected from camera deployments conducted in three bays along the Western Antarctic Peninsula between 13 May and 6 June 2013 and 6 to 23 December 2014. Footage of krill was collected using a camera system and sampling throughout the day under various conditions at depths from 10 m up to 625 m at distinct stops, which will be further referred to as horizons. Movement behaviors were quantified from 366 movement tracks collected in late spring and 2979 in late autumn. Swimming speeds (BL s^{-1}) were estimated from video captured at 10 Hz. These data have been used in a prior study to estimate seasonal effects on individual swimming behaviors and energetic requirements (Kane *et al.* 2018; Kane & Menden-Deuer, *in prep.*; Chapters 2 and 3 of this dissertation).

Determination of krill abundances

In both seasons, densities of krill were manually determined at horizons which contained tracked krill. To determine krill abundances, footage at each horizon was visually reviewed and the number of krill averaged for the 30 s with the greatest abundance of krill present. Krill density was then calculated by dividing the average number of krill seen by the 2.4 m^3 volume of water the camera system sampled (for details, see Kane *et al.* 2018; Chapter 2).

Comparison of Krill Abundance and Individual Movement

Krill movement tracks from each season were separated into four categories based

on the density of krill at the horizon: $< 0.1 \text{ krill m}^{-3}$, $0.1 - 1 \text{ krill m}^{-3}$, $> 1 - 10 \text{ krill m}^{-3}$, and $> 10 \text{ krill m}^{-3}$. As light is known to influence krill behaviors and densities (Kawaguchi *et al.* 2010; Meyer & Teschke 2016; Kane *et al.* 2018), a second analysis was conducted to compare krill movement behaviors at different densities under light or dark conditions (Table 4.1). Krill movement behaviors were compared using a Kruskal-Wallis test and a Tukey post-hoc test to determine which densities significantly influenced krill behaviors.

Comparison of Nearest Neighbor Distance

Distances between tracked krill were measured to determine how nearest neighbor distances influenced krill movement behaviors. To determine 2-D distance between krill, the distance between krill centroids was calculated; the centroid, or the center of the krill, was determined by applying the MATLAB (The Mathworks Inc, ver. 2015b) function *regionprops* to the images. The pixel distance between krill was converted to body length distance between krill by dividing the distance by the length of the krill being tracked. Movement behaviors and nearest neighbor distances were then compared by determining the coefficient of covariance between the variables.

Determining Krill Orientation

Three different approaches were compared to determine the most accurate method to measure krill orientation. The first approach was to measure the angle of the krill major axis using the *regionprops* function. The second approach measured the angle between the krill's centroid and weighted centroid, or the center of the krill based on its weighted shape, with the centroid and weighted centroid having been determined by the function *regionprops*. The third approach, which was determined to be the most accurate

approach for measuring krill orientation, involved multiplying the absolute value of the major axis angle by the vertical direction between the weighted centroid and centroid of the krill, where positive direction indicated krill orienting upwards and negative direction indicated krill orienting downwards (for details, see Appendix 4A). This third approach was used as the method to measure krill orientation.

Differences in orientation, from 0° to 180° , between tracked krill in the same image were then calculated to determine the characterization of the krill group (i.e., school or swarm). Krill were considered to be schooling if the difference between krill orientation for all nearest neighbors was less than or equal to $\pm 15^\circ$; krill were considered to be swarming and not oriented to one another when orientation differences between all krill were larger than $\pm 15^\circ$.

Comparison of Carbon Budget Costs and Requirements

Krill energetic requirements and feeding abilities were compared between krill movement behaviors associated with different aggregation densities using the methods described in Kane & Menden-Deuer (*in prep.*, Chapter 3). In brief, energetic requirements for krill of sizes 9 - 57 mm (Cleary *et al.* 2016, 2018) were modeled by multiplying swimming speeds and lengths to convert swimming speeds from BL s^{-1} to $cm s^{-1}$. Swimming speeds were converted to oxygen consumption rates in $mg O_2$ per gram dry weight (g_D^{-1}) per hour (hr^{-1}) based on the relationship found by Swadling *et al.* (2005). Krill daily oxygen consumption rates were then determined by multiplying the resulting oxygen consumption rates by krill dry weights estimated using the length-weight equation from Atkinson *et al.* (2006) and 24 hours. Carbon consumption requirements were modeled by converting oxygen consumption rates using the molar

conversion factor between carbon and oxygen and then multiplying the amount of carbon by the respiration quotient of 0.72 (Lowe *et al.* 2012; Richerson *et al.* 2015). Feeding abilities were modeled by calculating the amount of water a krill was able to filter through its feeding basket at different swimming speeds (Kils 1981; Schmidt & Atkinson 2016). The carbon concentration required to be in the water column for krill to meet their energetic costs was determined by dividing the amount of carbon consumed by the amount of water a krill could filter in 6 hours, assuming krill can feed for a maximum of 6 hours (Body *et al.* 1984).

Modeled energetic and carbon requirement differences were compared between density behaviors. Swimming behaviors at different densities were compared to determine required carbon concentrations in the water column, using *chl a* as a proxy (Morison & Menden-Deuer 2018). Based on these energetic differences, the number of krill which could be supported at a given carbon concentration assuming different behaviors was compared.

Results:

Krill Swimming Behaviors with Density

In general, there was a positive correlation between krill swimming speeds and increases in density in both seasons, with swimming speeds at densities $> 10 \text{ krill m}^{-3}$ and $> 1 \text{ krill m}^{-3}$ being 39% and 42% greater than swimming speeds associated with krill densities $< 0.1 \text{ krill m}^{-3}$ in late autumn and spring, respectively (Figure 4.1a, 4.2a) (late autumn: $p < 0.001$; late spring: $p = 0.008$) (Table 4.2). The trend of increased swimming speeds with greater density was particularly strong during light periods in both seasons, with speeds being 34% and 91% faster at densities $> 10 \text{ krill m}^{-3}$ and $> 1 \text{ krill m}^{-3}$ compared to densities $< 0.1 \text{ krill m}^{-3}$ in late autumn and spring, respectively (Figure 4.3a, c) (late autumn: $p < 0.001$; late spring: $p < 0.001$). During dark periods, however, there was no statistical relationship between swimming speeds and density in late spring (Figure 4.3d) ($p = 0.767$), and late autumn swimming speeds were ~5% greater at densities between 0.1 and 1 krill m^{-3} compared to swim speeds at greater or lower densities (Figure 4.3b) ($p < 0.001$).

In late autumn, turning rates increased with greater krill densities, with turning rates being 23% faster at densities $> 10 \text{ krill m}^{-3}$ compared to turning rates at densities $< 0.1 \text{ krill m}^{-3}$ ($p = 0.003$) (Figure 4.1b) (Table 4.3). In late spring, turning rates were relatively similar between different densities ($p = 0.163$), although there was a decrease in turning rates when krill densities were $< 0.1 \text{ krill m}^{-3}$ (Figure 4.2b). There was a positive correlation between krill turning rates and densities during light periods in late autumn (Figure 4.4a) ($p = 0.015$); there was also a slight, although not statistically significant, increase in turning rates with density during dark periods in this season

(Figure 4.4b) ($p = 0.259$). In late spring, krill turning rates were fastest when krill densities were between 0.1 and 1 krill m^{-3} during both light and dark periods, with krill turning at similar rates when krill densities were > 1 krill m^{-3} or < 0.1 krill m^{-3} , although this relation was not statistically significant (Figure 4.4c, d) (light periods: $p = 0.621$; dark periods: $p = 0.102$).

There was no statistical difference in krill vertical velocities at different densities in both seasons (late autumn: $p = 0.465$; late spring: $p = 0.444$) (Figure 4.1c, 4.2c), including when light and dark periods were taken into consideration in either season (Table 4.4). There was also no difference in swimming directions with regards to density in late autumn or late spring (late autumn: $p = 0.941$; late spring: $p = 0.520$) (Figure 4.1d, 4.2d) (Table 4.5).

Krill Swimming Behaviors and Nearest-Neighbor Distance

There was a slight positive correlation between nearest neighbor distance and swimming speeds, with speed increasing with average nearest neighbor distance in both late spring ($p \ll 0.001$, $r = 0.44$) and late autumn ($p \ll 0.001$, $r = 0.23$) (Figure 4.5a). There was no direct correlation between turning rates, vertical velocities, or changes in swimming directions with nearest neighbor distances in both seasons. However, there was a decrease in the variance of turning rates and changes in swimming directions with increasing nearest neighbor distance in late autumn (Figure 4.5b, d).

Krill Orientation and Swimming Behaviors

Differences in orientation between neighboring krill varied between 1° and 166° in late autumn and between 5° and 155° in late spring, with mean differences in orientation being $63 \pm 1^\circ$ in late autumn and $65 \pm 4^\circ$ in late spring. In general,

differences in orientation between krill were less than 80° (Figure 4.6). There was also no relation between nearest neighbor distance or individual swimming behavior and the differences in orientation between neighboring krill.

Energetic Requirements and Feeding Abilities

Krill energetic requirements increased with the faster swimming speeds associated with greater krill densities (Figure 4.7a, c). In late autumn, krill energetics increased between 12 and 27% when krill swam at speeds associated with densities > 10 krill m^{-3} compared to mean swimming speeds associated with densities < 0.1 krill m^{-3} . In late spring, carbon requirements were between 18% and 34% greater with mean swimming speeds associated with densities of > 1 krill m^{-3} when compared to mean swimming speeds associated with densities of < 0.1 krill m^{-3} . In both seasons, these faster speeds were associated with lower carbon concentration requirements due to increases in the amount of water column searched (up to 19% in late autumn and up to 17% in late spring) (Figure 4.7b, d); this decrease in carbon concentration requirements means higher densities are supported by faster-moving krill at similar carbon concentrations in the water column when compared to slower-moving krill.

Discussion:

Krill aggregations are known to vary in terms of their size, shape, and density (Lawson *et al.* 2008; Tarling *et al.* 2009; Krafft *et al.* 2012; Tarling & Thorpe 2014; Tarling *et al.* 2018). However, there is very little known about how individual krill movement behaviors are affected by different aggregation densities. We examined how individual krill swimming behaviors and the associated energetic requirements varied with differences in krill densities. While krill swimming speeds decreased with decreasing nearest neighbor distance, krill motility generally increased with increasing densities, particularly during light periods in both seasons. In late spring, this increase in swimming speeds with increasing density was likely due to increased competition between individuals; additionally, the decrease in krill swimming speeds with decreasing aggregation densities may have decreased the predation risk of solitary krill. In late autumn, the increase in swimming speeds with increasing density likely improved the ability of krill to forage on the sediments. In both seasons, the increased swimming speeds associated with increased densities improved prey encounter rates, which may enable greater abundances of krill to cover energetic costs at carbon concentrations similar to what solitary krill swimming more slowly require. Changes in individual motility due to changes in krill density point to mechanisms krill utilize to balance the trade-offs between aggregation formation and intraspecific competition.

Krill motility may increase with greater aggregation densities because of heightened intraspecific competition. It has been theorized krill in groups are more likely to find and stay within phytoplankton patches than individual krill (Ritz 1994; Grünbaum 1998; Flierl *et al.* 1999). However, krill within these aggregations are also competing

against one another for resources. Krill moving at faster speeds will obtain more food than krill swimming more slowly because the former will clear a greater volume of water, have higher encounter rates with particles, and be able to filter particles from the water column more efficiently (Kils 1983; Vissier 2001; Ritz *et al.* 2011). Faster swimming speeds also assist with keeping krill feeding baskets open, which increases the surface area in the feeding baskets and allows for more water to be filtered (Kils 1983). Furthermore, the faster swimming speeds may fragment marine snow particles encountered into smaller pieces, providing another potential food source for krill (Goldthwait *et al.* 2004). In addition to faster swimming speeds, increased turning rates enable krill to remain within a food patch while simultaneously avoiding neighbors (Hamner *et al.* 1983; Price 1989; Hamner & Hamner 2000). Thus, increased krill motility may allow krill within aggregations of higher density to more successfully forage on phytoplankton and detritus.

Concurrently, krill motility may decrease with decreasing density due to predation pressures. Krill in large groups are thought to be less susceptible to predation (O'Brien 1987; Ritz 1994; Ritz *et al.* 2011; Tarling & Fielding 2016). As krill movement produces a continuous wake that is 1 – 4 body lengths or more around them, solitary krill may swim more slowly to decrease their wake in the water column, making it more difficult for predators to sense them (Kils 1981; Vissier 2001; Catton *et al.* 2011; Murphy *et al.* 2013). Krill at lower densities may also be moving more slowly to visually search for and avoid predators in the water column (Wiese 1996). Krill in aggregations with higher densities may deal with a greater foraging cost, but solitary krill may be more susceptible to predation pressures and must utilize other behaviors, such as decreasing motility, to

avoid being consumed.

In late spring, the large shift in swimming speeds associated with different densities between light and dark periods is likely due to a combination of anti-predatory strategies, competition, and feeding behaviors. During dark periods, when krill are thought to come up to the surface to feed on phytoplankton, individual krill swimming speeds were very similar between different densities (Quetin & Ross 1991; Godlewski 1996; Hamner & Hamner 2000; Kane *et al.* 2018). Due to the limited dark time in this season, foraging on phytoplankton in shallower waters likely becomes a higher priority compared to actively avoiding visual predators. During light periods, however, there is an almost two-fold increase in krill swimming speeds between solitary krill and krill within a swarm. Due to increased intraspecific competition, krill within denser aggregations may be more actively foraging and searching for higher quantities of food than krill in less dense aggregations. Comparatively, solitary krill may also be swimming more slowly to avoid visual predators (O'Brien 1987; Wiese 1996). Differences in krill motility with both density and light in late spring are likely a reflection of complex strategies used by krill to maximize prey encounter rates and minimize predation risks.

In late autumn, the increase in swimming speed observed in denser aggregations during light periods may enable krill to obtain more carbon from the sediment. Krill were found in large abundances at the bottom of the water column during light periods and were thought to be foraging on the carbon in the sediment (Clarke & Tyler 2008; Schmidt *et al.* 2011, 2014; Kane *et al.* 2018). The ability of krill to obtain carbon from the sediment is likely influenced by their sizes: larger krill are likely able to shift larger portions of sediment than smaller krill, thus obtaining more carbon. However, higher

concentrations of krill foraging at the benthos may be able to suspend larger amounts of sediment, including organic carbon, into the water column than solitary krill (Clarke & Tyler 2008; Catton *et al.* 2011; Isla 2016; Houghton *et al.* 2018). Greater swimming speeds may be a mechanism to enhance particle suspension and break up larger particles (Goldthwait *et al.* 2004; Ritz *et al.* 2011). Suspending and decreasing the sizes of particles would enable krill to filter more carbon from “food bank” regions at the benthos in the Antarctic Peninsula (Mincks *et al.* 2005; Smith *et al.* 2006; Glover *et al.* 2008; Isla 2016). As phytoplankton populations are very low in this season (Morison & Menden-Deuer 2018), utilizing organic carbon from the sediment as their primary food source will facilitate krill survival during late autumn and winter (Meyer 2012).

The camera system utilized in this study provides high resolution observations of individual krill, small groups of krill, and krill behaviors within larger aggregations. This detailed observation capacity comes at the cost of a limited observation volume, preventing us from observing the full range of behaviors of krill within large aggregations (Kane *et al.* 2018). Additionally, we were not able to observe how krill movement behaviors change between different types of aggregations, as the krill observed in the footage were either in swarms, as evidenced by the large and varying differences in krill orientations between neighbors, or solitary. However, this study does provide some of the first evidence that the density of krill in the water column does influence their individual movement behaviors.

Faster individual krill swimming speeds associated with greater aggregation densities intensify the impacts krill have on biogeochemical cycles and the biological carbon pump along the Western Antarctic Peninsula. Increased speeds allow krill to filter

larger volumes of water; in late spring, higher feeding rates result in greater egestion rates of krill, which increases the amount of carbon being pumped out of the surface of the water column to depth (Le Fèvre *et al.* 1998; Atkinson *et al.* 2012b; Lehet *et al.* 2012). In the late autumn, krill likely feed on the sediment as an alternative food source due to low levels of primary productivity (Kawaguchi *et al.* 1986; Schmidt *et al.* 2011, 2014; Kane *et al.* 2018; Morison & Menden-Deuer 2018). Since krill are capable of producing large vortices of moving water behind them as their pleopods move (Kils 1981; Catton *et al.* 2011; Murphy *et al.* 2013), large amounts of sediment containing nutrients and organic carbon may be resuspended into the water column when krill aggregations feed on the benthos. This resuspension of sediment enables more nutrients, such as silica and iron, to be reintroduced to the upper portions of the water column through advection caused by the vertical movement of krill (Isla 2016; Houghton *et al.* 2018; Kane *et al.* 2018). However, sediment resuspension may prevent carbon from being sequestered and may, in fact, enhance the return of carbon from depth to surface waters. Consequently, larger densities of krill will enhance local effects on biogeochemical cycles in benthopelagic coupling throughout the year along the Western Antarctic Peninsula, with the consumption of phytoplankton in late spring resulting in large movements of carbon to depth through fecal pellet production and the resuspension of sediment in the late autumn resulting in the reintroduction of nutrients and carbon from depth towards the surface.

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Tables:

Table 4.1. Sample size of seasonal krill tracks at each of the 4 density categories. Krill densities in late spring did not reach > 10 krill m^{-3} .

	Late Autumn			Late Spring		
	All	Light	Dark	All	Light	Dark
< 0.1 krill m^{-3}	98	62	36	35	22	13
$0.1 - 1$ krill m^{-3}	920	544	376	120	58	62
$1 - 10$ krill m^{-3}	1852	884	968	211	45	166
> 10 krill m^{-3}	109	109	0	-	-	-

Table 4.2. Means and standard errors for krill swimming speeds (in body lengths (BL) s⁻¹).

	Late Autumn			Late Spring		
	All	Light	Dark	All	Light	Dark
< 0.1 krill m ⁻³	2.63 ± 0.14	2.72 ± 0.18	2.47 ± 0.24	4.07 ± 0.38	3.38 ± 0.43	5.24 ± 0.61
0.1 – 1 krill m ⁻³	2.83 ± 0.06	2.81 ± 0.08	2.85 ± 0.09	4.97 ± 0.28	4.71 ± 0.38	5.21 ± 0.41
1 – 10 krill m ⁻³	2.72 ± 0.04	2.97 ± 0.06	2.49 ± 0.06	5.78 ± 0.25	6.45 ± 0.51	5.59 ± 0.28
> 10 krill m ⁻³	3.65 ± 0.19	3.65 ± 0.19	-	-	-	-

Table 4.3. Means and standard errors for krill turning rates (in ° s⁻¹).

	Late Autumn			Late Spring		
	All	Light	Dark	All	Light	Dark
< 0.1 krill m ⁻³	96 ± 7	104 ± 3	97 ± 12	99 ± 12	100 ± 16	98 ± 18
0.1 – 1 krill m ⁻³	98 ± 3	92 ± 4	106 ± 4	133 ± 10	124 ± 10	141 ± 18
1 – 10 krill m ⁻³	111 ± 2	95 ± 9	117 ± 3	116 ± 6	109 ± 15	118 ± 6
> 10 krill m ⁻³	119 ± 10	119 ± 10	-	-	-	-

Table 4.4. Means and standard errors for krill vertical velocities (in body lengths (BL) s⁻¹).

	Late Autumn			Late Spring		
	All	Light	Dark	All	Light	Dark
< 0.1 krill m ⁻³	-0.30 ± 0.20	-0.53 ± 0.27	0.10 ± 0.27	-0.14 ± 0.47	0.21 ± 0.45	-0.74 ± 1.00
0.1 – 1 krill m ⁻³	-0.16 ± 0.07	-0.14 ± 0.09	-0.19 ± 0.10	0.07 ± 0.35	-0.05 ± 0.35	0.19 ± 0.60
1 – 10 krill m ⁻³	-0.05 ± 0.06	0.04 ± 0.09	-0.13 ± 0.07	0.55 ± 0.30	0.92 ± 0.66	0.45 ± 0.34
> 10 krill m ⁻³	-0.25 ± 0.30	-0.25 ± 0.30	-	-	-	-

Table 4.5. Means and standard errors for krill swimming directions (in Δ° horizontal).

	Late Autumn			Late Spring		
	All	Light	Dark	All	Light	Dark
< 0.1 krill m ⁻³	-8.52 ± 4.26	-10.11 ± 5.34	-5.77 ± 7.13	-4.45 ± 6.79	-1.24 ± 8.53	-9.88 ± 11.51
0.1 – 1 krill m ⁻³	-5.32 ± 1.28	-2.73 ± 1.73	-9.06 ± 1.87	-0.22 ± 3.50	0.38 ± 4.60	-0.79 ± 5.28
1 – 10 krill m ⁻³	-5.01 ± 1.01	-0.30 ± 1.54	-9.32 ± 1.33	2.39 ± 2.81	8.51 ± 5.55	0.73 ± 3.23
> 10 krill m ⁻³	-5.36 ± 4.51	-5.36 ± 4.51	-	-	-	-

Figures:

Figure 4.1. Late autumn krill swimming behaviors as a function of krill density: swimming speed (a), turning rate (b), vertical velocities (c), and swimming directions (d). Means are represented by the black circles, median values by the lines in the box plots, the 25th to 75th percentile values by the bottom and top of the box, and the highest and lowest 10% values are represented by the horizontal lines. Note that standard error is contained within the mean symbol.

Figure 4.2. Late spring swimming behaviors as a function of changes in krill density: swimming speed (a), turning rate (b), vertical velocities (c), and swimming directions (d). See Figure 4.1 legend for details.

Figure 4.3. Individual swimming speeds at different krill densities in late autumn (a, b) and late spring (c, d) during light periods (a, c) and dark periods (b, d). See Figure 4.1 legend for details.

Figure 4.4. Individual turning rates at different krill densities in late autumn (a, b) and late spring (c, d) during light periods (a, c) and dark periods (b, d). See Figure 4.1 legend for details.

Figure 4.5. Comparison of nearest neighbor distance to swim speeds (a), turn rates (b), vertical velocities (c), and changes in swimming direction (d) in late autumn (blue) and late spring (green). Histogram of nearest neighbor distances are plotted below.

Figure 4.6. Histogram of differences in orientation between krill neighbors in late autumn (blue) and late spring (green).

Figure 4.7. Percent differences between krill carbon requirements (a, c) and required carbon concentration in the water column to support krill movement (b, d) for late autumn (a, b) and late spring (c, d). Carbon requirements and concentrations were compared to carbon requirements and concentrations based on swimming behaviors associated with the lowest krill density (i.e., $< 0.1 \text{ krill m}^{-3}$).

Appendix 4A:

Determination of Accuracy of Krill Orientation Methods

To determine the orientation of krill from the collected images, two different approaches using properties measured in the function *regionprops* in Matlab (The Mathworks Inc, v. 2015b) were compared: (1) measuring the angle between the centroid and weighted centroid of the krill; and, (2) measuring the angle of the major axis of the krill. Orientations from 1995 krill in 540 test images were determined by manually measuring the vertical angle between the telson and the eye of the krill. Krill orientations determined using the automated methods were compared to manually measured krill orientations using a Model II Regression. The angles measured using the centroids were more accurate ($r^2 = 0.745$) than those measured using the major axis angle ($r^2 = 0.0052$). However, when the absolute values between the manual and algorithmically-determined krill orientations were compared, measuring the angle of the major axis resulted in more accurate angle estimates ($r^2 = 0.912$) than measuring the angle between the centroid and weighted centroid ($r^2 = 0.845$) (Figure 4.A2). Therefore, a combination between the two automated methods was developed and compared, where the angle was determined using the angle of the major axis and the direction of the angle was determined using the centroid and weighted centroid. This provided a slightly tighter fit between krill measured angles and the more correct direction of the orientation and was used in further analysis ($r^2 = 0.745$) (Figure 4.A3).

Figure 4.A1. Comparison of the absolute values of measured krill orientations to krill orientations determined using the angle between the centroid and weighted centroid of a krill (a) and krill orientations measured using the angle of the major axis length of the krill (b).

Figure 4.A2. Orientation of krill determined using the combined method of using the absolute value of the major axis orientation with the directionality of the angle determined using the centroid and weighted centroids.

CHAPTER 5

CONCLUDING REMARKS

Studying individual krill behavior throughout the water column in the Southern Ocean was difficult until recently, largely due to the lack of available technologies (Nicol & Brierley 2010). Using a novel stereo camera system, krill were filmed throughout the water column along the Western Antarctic Peninsula during the late austral autumn and late spring. This approach provided unique and unprecedented observations of individual krill movement behaviors and vertical distributions throughout the water column in two contrasting seasons. Using these data sets, this dissertation addressed gaps in the understanding of seasonal and diel shifts in individual krill movement behaviors, vertical distributions, and energetic requirements, as well as the concentration of attainable carbon required to cover these different energetic costs. These *in situ* data sets also enabled one of the first analyses of how aggregation density influences individual krill swimming behaviors.

We were able to quantitatively show that krill were actively swimming in both seasons, although motility was greater in late spring than late autumn. Based on the energy required to support the measured motility in late spring, krill were estimated to utilize up to 18% of their carbon weight (CW) in food per day to cover their energetic costs; this is greater than most models of krill energetics which assume movement and respiration energetics require up to 10% CW (Hofmann & Lascara 2000; Fach *et al.* 2002, 2006, 2008; Constable & Kawaguchi 2018). In late autumn, krill required up to 11% CW to cover motility costs. Meyer (2012) demonstrated that, assuming krill maintained slower routine metabolic rates and are able to catabolize most of their lipid

reserves, krill still need to feed to survive during the winter. The results of this study support the hypothesis that krill must continue to feed in late autumn and winter and suggest krill feeding requirements are greater in these seasons than previously suspected due to their active movement. Our novel findings of seasonal shifts in krill motility and the estimated energetic requirements imply krill remain important consumers of lower trophic levels in both late autumn and late spring, although their impact on the food web and biogeochemical cycles is not consistent across seasons.

Surprisingly, while krill did require more carbon to meet energetic costs in late spring than late autumn, our findings suggest krill required a higher concentration of carbon in the water column to cover energetic costs in late autumn than late spring. Our model assumed krill only fed on phytoplankton in both seasons, which is their preferred food source (Quetin & Ross 1991; Haberman *et al.* 2003). However, while there were plenty of phytoplankton to cover energetic requirements for krill in late spring, phytoplankton abundances were low in late autumn (Morison & Menden-Deuer 2018). Adult krill are known to consume copepods, detritus, and even other krill when there is limited phytoplankton abundance (Boyd *et al.* 1984; Kawaguchi *et al.* 1986; Ligowski 2000; Schmidt *et al.* 2011; Atkinson *et al.* 2012; Saba *et al.* 2014). These prey resources, being at different trophic levels, have different chemical compositions which change the amount of energy krill gain from consuming them (i.e., copepods are more lipid-heavy than phytoplankton (Fach *et al.* 2008)). The results presented here emphasize the need to quantify the availability of all potential food sources krill may be able to consume in the Southern Ocean. Additionally, further studies of how much energy krill obtain from metabolizing different food sources are needed to provide a better concept of krill prey

preferences, particularly at different times of the year.

The images collected enabled us to study how the density of an aggregation influences individual krill movement behaviors. Most studies have focused on how to characterize krill aggregations, how aggregations form, why such aggregations are maintained, and advantages of aggregating behaviors (Miller & Hampton 1989; Ritz 1994; Atkinson *et al.* 2008; Tarling *et al.* 2009; Ritz *et al.* 2011; Siegel & Watkins 2016; Tarling & Fielding 2016). Our study shows that krill swimming speeds generally increased with increasing aggregation density. This has implications in particular for modeling krill contributions to the biological carbon pump and nutrient recycling in the Southern Ocean. Our findings show that the amount of food krill consumed, and thus the amount of fecal pellets produced, cannot be calculated simply by multiplying how much food one krill consumes by the number within the aggregation; the density of the aggregation influences krill motility and carbon consumption, possibly intensifying the local effects on biogeochemical cycles. Unfortunately, our study only was able to look at changes with krill swimming behaviors in aggregations where krill orientations varied drastically between individuals, i.e., swarming. Other studies have suggested that krill may conserve energy and move more quickly when all krill within the aggregation orient towards one another, i.e., schooling (Ritz 2000; Kawaguchi *et al.* 2010). Further research is needed to determine if the density of schools also influences individual krill behaviors.

Our study demonstrates that krill motility shifts between light and dark periods, both between late autumn and spring, and with changes in density. The diel shifts in krill motility may provide an indication of where krill are feeding in different seasons. Krill swam faster during light periods in late autumn when krill were concentrated at the

bottom of the water column and during dark periods in late spring when krill were closer to the surface. As krill swimming speeds increase while krill actively feed (Price 1989), the diel shift in swimming speeds suggests krill were foraging on the sediment in late autumn and phytoplankton in surface waters in late spring. This suggests further studies of individual krill motility, particularly diel shifts, may provide more information about what krill are feeding on in different seasons. Moreover, further studies of individual krill motility over 24 hours in different seasons will provide more information about their energetic requirements and how shifts in their motility influence their food requirements.

In the late autumn footage, dense abundances of krill were found carpeting the sediment. Combined with our results of krill late autumn energetic requirements, these observations suggest krill were consuming carbon from the sediment in this season. In order to feed on sediment, individual krill flick the sediment into the water column to filter out the carbon for consumption (Clarke & Tyler 2008; Schmidt & Atkinson 2016). As krill swimming speeds increase with density, these aggregations of krill feeding on the seafloor may resuspend large quantities of sediment into the water column. Furthermore, it is hypothesized that dense krill aggregations may be able to keep particles suspended in the water column for longer periods of time (Ritz *et al.* 2011). As the ambit of krill vertical migrations are 150 m in late autumn (Siegel 2005), krill may bring large quantities of resuspended material up from the bottom to shallower depths in the water column. This may reintroduce key nutrients for phytoplankton from depth to the euphotic zone either through convection of the water column or through defecation in shallow waters by air-breathing krill predators. However, krill may simultaneously reintroduce carbon from the sediment to shallower waters through these same processes,

decreasing the amount of carbon which can be sequestered in the sediment. Modeling how much sediment krill are able to resuspend may further our understanding of their contributions to nutrient recycling and carbon sequestration. The resuspension of nutrients may intensify the initial spring phytoplankton blooms or provide nutrients necessary for autumn primary production, while the resuspension of carbon into the water column may indicate that krill are a vector for the reintroduction of carbon from the sediment to surface waters in late autumn, decreasing the amount of carbon on the seafloor which might otherwise have been sequestered or utilized by benthic fauna.

This dissertation provides some of the first quantitative information on krill motility in late autumn and spring in the Western Antarctic Peninsula. However, krill are known to behave differently in different sections of the Southern Ocean, and shifts in krill motility may differ in other regions of the Southern Ocean (Flores *et al.* 2012; Schmidt *et al.* 2014). Moreover, krill populations also show a cyclic pattern, where krill abundances decrease for several years until enough food is available to support large quantities of juvenile krill (Ryabov *et al.* 2017). Further spatial and temporal studies are necessary to study how shifts in individual krill motility contribute to their energetic requirements and survival in a seasonally-dynamic environment.

Prior to this thesis, krill motility measurements were restricted to laboratory measurements or acoustic estimates. Laboratory settings, particularly small tanks, are known to affect routine respiration rates and behaviors of krill (McWhinnie & Marciniak 1964; Ngan *et al.* 1997; Lehetto *et al.* 2012). Acoustic observations provide *in situ* mean estimates of krill swimming speeds but are limited in depth resolution and do not incorporate krill movement variability. We now have the technology to observe and

quantify the averages and variations of individual krill behaviors throughout the water column. Our study provides the first seasonal comparison of krill movement behaviors throughout the water column in the Western Antarctic Peninsula, which enabled us to explicitly model how shifts in krill motility impact their energetic requirements and feeding abilities. Due to the resolution of our observations, we were also the first to be able to quantify how differences in krill aggregation density, whether krill are solitary or in dense aggregations, influence individual krill movement behaviors. While important questions remain about seasonal, annual, and spatial differences in krill motility, and how schooling densities influence individual krill motility, this research establishes a new standard for studying krill within their environment and biological context.

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