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The carapace matters: refinement of the instantaneous growth rate method for Antarctic krill *Euphausia superba* Dana, 1850 (Euphausiacea)

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ABSTRACT

Growth of Antarctic krill *Euphausia superba* Dana, 1850 is commonly calculated using the Instantaneous Growth Rate (IGR) method based on the difference between the uropod lengths of the moulted exoskeleton and the uropod lengths after moulting. To date, this method has not accounted for sex-dependent differences in body proportion, relying only upon uropod measurements. We measured the carapace, uropod, and total body lengths of gravid females, non-gravid females, males, and juvenile krill from the Indian Sector of the Southern Ocean. Growth rates derived using a combination of the carapace and uropod measurements for gravid females were different from those derived through the traditional uropod-only based IGR, whereas non-gravid females, male, and juvenile growth rates showed no significant difference between methods. The refined method we propose successfully reflects dimorphism in growth between the sexes of krill, with gravid females having enlarged carapaces during the reproductive season. The interaction between growth and reproduction must be considered to improve the reliability of predictions from krill life history models, which is possible through the use of sex-dependent IGR measurements. We propose that, whenever possible, measurements of carapace and total length should be made along with uropod measurements. Together with assessments of maturity stages of krill that did not moult during experiments, these measurements will aid in further informing krill stock assessments.

Key Words: gravid females, Instantaneous Growth Rate (IGR) method, life history, sex dependent, Southern Ocean, sexual dimorphism

THIRD INTERNATIONAL SYMPOSIUM ON KRILL

INTRODUCTION

Antarctic krill *Euphausia superba* Dana, 1850, hereafter krill, has been recognised as a key species in the Southern Ocean, being an integral component of many Antarctic marine food webs and acting as a major link between primary producers and higher-level predators (O'Brien *et al.*, 2011, Tarling *et al.*, 2016). The ecological importance of krill stems from their very high biomass, estimated to be *circa* 500 million tonnes (Cavanagh *et al.*, 2016), their high nutritional content, and their swarming behavior that concentrates its biomass (Tarling *et al.*, 2016). These ecological factors also contribute to commercial importance, making krill a readily exploitable species that has been commercially harvested for almost 50 years (Kawaguchi & Nicol, 2007; Cavanagh *et al.*, 2016).

Despite their ecological and commercial importance, there are some aspects of the life history of krill that remain poorly understood, including their growth, which is an essential parameter required for the development of an adequate management regime (Brown *et al.*, 2010). The krill fishery in the Southern Ocean is managed through the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), which employs ecosystem-based management (EBM) procedures (Cavanagh *et al.*, 2016). Krill growth trajectory is important for EBM as this is one of the fundamental parameters used in generalised yield

models to calculate the precautionary catch limit in CCAMLR (Constable & De la Mare, 1996). There are various methods for estimating and/or describing krill growth, including the use of length-frequency distributions (Reid, 2001), somatic growth such as an increase in weight or carbon content (Nicol, 2000), biochemical indications (Shin *et al.*, 2003), on-shore laboratory examinations (Reiss, 2016), and instantaneous growth rate (IGR) (Quetin & Ross, 1991). Length-frequency curves from two different time points were routinely used to assess growth; however, this method is based on the assumption that the same population is sampled, which is difficult to ensure for pelagic organisms. As a result, growth rates derived from this method are difficult to relate over temporal and spatial scales, and age-dependent mortality cannot be accounted for (Quetin *et al.*, 2003; Kawaguchi *et al.*, 2006; Saba *et al.*, 2014). Somatic growth measurements also assume that the same population is sampled, but have the advantage that they can be used as an indicator of the response krill show to their environment, as they are the sum of major physiological processes (Nicol, 2000; Tarling *et al.*, 2006). The use of biochemical indicators, e.g. the ratio between the content of ribonucleic acid (RNA) and deoxyribonucleic acid (DNA), is efficient and less labour-intensive, although the results are confounded by temperature, developmental stages, age, and diel rhythms (Shin *et al.*, 2003; Arnold *et al.*, 2004). Laboratory examinations can provide data across all seasons because conditions are readily manipulated, although the krill are not wild and often exposed to unnatural experimental conditions (Reid, 2001; Brown *et al.*, 2010; Reiss, 2016).

We used the IGR method, which measures growth directly from individual live krill from the wild that moulted within a few days of capture. Results obtained using this method can be related to ambient environmental conditions, come from a large sample size, and account for growth during discrete periods (Shin *et al.*, 2003; Arnold *et al.*, 2004; Kawaguchi *et al.*, 2006). Growth in length in crustaceans occurs in a series of steps, coinciding with each moult, and this is the principle upon which the IGR method is based (Atkinson *et al.*, 2006). Due to their stepwise growth, the length of the moulted exoskeleton represents the length of the krill before their moulting event (Kawaguchi *et al.*, 2006). The IGR method measures the linear growth increments of individuals and assumes that the percentage increase (or decrease) in krill length at moult during the first four days of incubation after being sampled from the wild is representative of growth rates in the field (Nicol *et al.*, 1992).

The IGR method has been refined over time as its importance to krill growth measurements became more apparent. The original methodology was outlined by Quetin & Ross (1991) and then modified by Nicol *et al.* (1992). This modification was made to exclude data where there were possible effects of capture on krill growth, and to make the method more efficient so as to increase the sample size. Kawaguchi *et al.* (2006) developed a model to summarise large amounts of IGR data and Candy & Kawaguchi (2006) extended this model to obtain daily growth rates that could be generalised to seasonal growth patterns, with the inclusion of both growth and shrinkage. The IGR method currently relies on measurements of the uropod (tail) of the moult and that of the post-moult krill and does not account for sex-dependent differences in body proportion. At the end of the reproductive season, females no longer need to contain large ovarian and fat-body masses in their carapaces, leading to reductions in size of their cephalothorax. Tarling *et al.* (2016) more recently suggested that estimates of growth need to consider the differences between the sizes of male and female carapaces. They hypothesised that as the carapace decreases in size there would be a corresponding reduction in total body length. To test this hypothesis Tarling *et al.* (2016) suggested comparing the carapace size to the total body length of krill during different seasons.

The aims of the our study were to develop a sex-dependent growth rate equation for Antarctic krill with the inclusion of the carapace and total length measurements, based on the hypothesis outlined by Tarling *et al.* (2016), and to compare the results from the sex-dependent IGR (SIGR) to the traditional IGR (TIGR) and evaluate similarities and differences, discussing the use of the method and possible caveats.

MATERIALS AND METHODS

Sampling protocol

Live krill were collected with a rectangular mid-water trawl (RMT 8) (Baker *et al.*, 1973) during two Southern Ocean voyages in the Indian Ocean sector (January to February 2016 and December

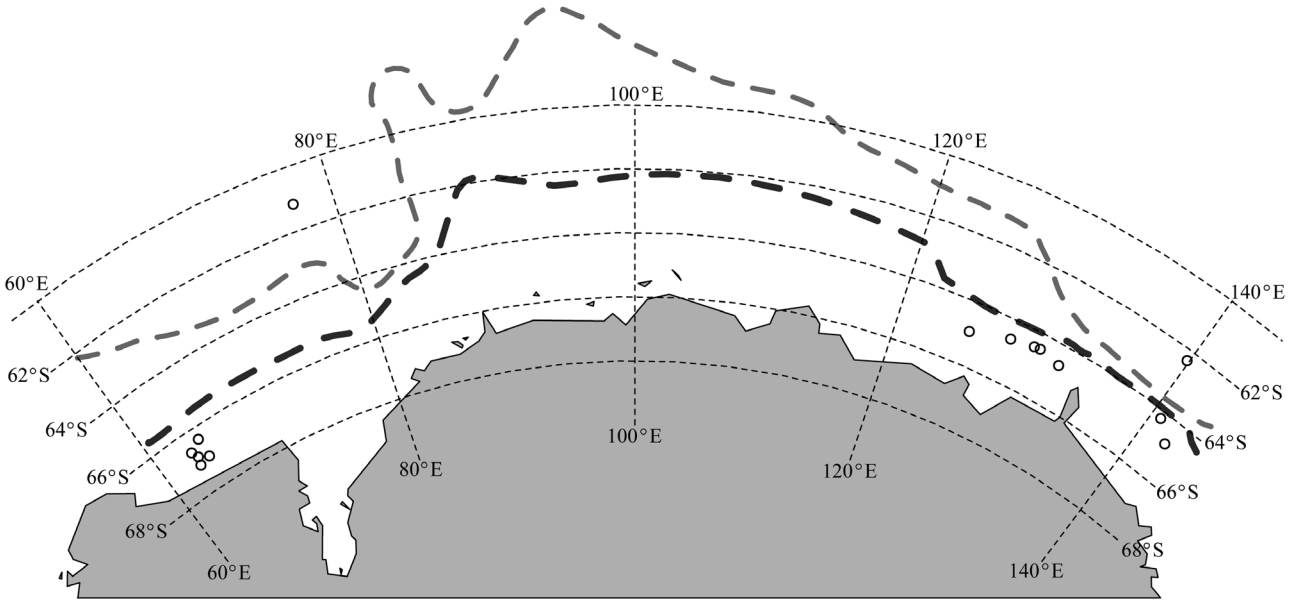

Figure 1. Sites (black-outlined circles) where IGR experiments were run. Voyage 1 was west of 100 °E and sampled during January and February in the 2015/16 season. Voyage 2 was east of 100 °E and sampled during December and January in the 2016/17 season. Black dashed line, Southern Boundary of the Antarctic Circumpolar Current; Grey dashed line, Southern Antarctic Circumpolar Current front.

2016 to January 2017) on board the RSV *Aurora Australis*. A total of 14 experiments were run across the two voyages (Fig. 1). After each RMT 8 deployment, 288 freshly caught krill individuals were randomly selected and immediately transferred to individual jars. The experiments were undertaken on board in a flow-through seawater system as described by Kawaguchi *et al.* (2006). Krill were checked for moulted exoskeletons every 24 h, and the experiments ran for up to four days. Individuals that moulted were frozen, together with their respective moulds, in liquid nitrogen to be measured onshore or measured immediately on board and frozen in liquid nitrogen after measurements were taken.

Measurements of growth rate

All length measurements made using the Leica Application Suite V4.2 image analysis software (Leica Microsystems, Mannheim, Germany) and images were captured with a digital colour camera DFC380 on a Leica MZ9.5 microscope.

TIGR method. The total length of the uropod exopodites on both the left and right sides of the individual and its moult were measured (Fig. 2A, B). Developmental stage or sex (hereafter state) was recorded as either juvenile, male, non-gravid female (hereafter females), or gravid female according to the existence or absence of petasma (males) or thelycum (females) as well as ovarian development in the post-moult females. An average of the length measurements for the left and the right uropods was calculated for the krill and its moult, if both uropods were intact. A uropod was not included in growth measurements if it was damaged in an individual or its moult, so growth was based only on a single uropod for the individual and its moult. If both uropods were damaged the krill was excluded from the analysis. The TIGR was calculated with direct measurements using Equation 1 (Table 1) for each individual krill. This method assumes that uropod growth rates are proportional to the growth rate of the entire body.

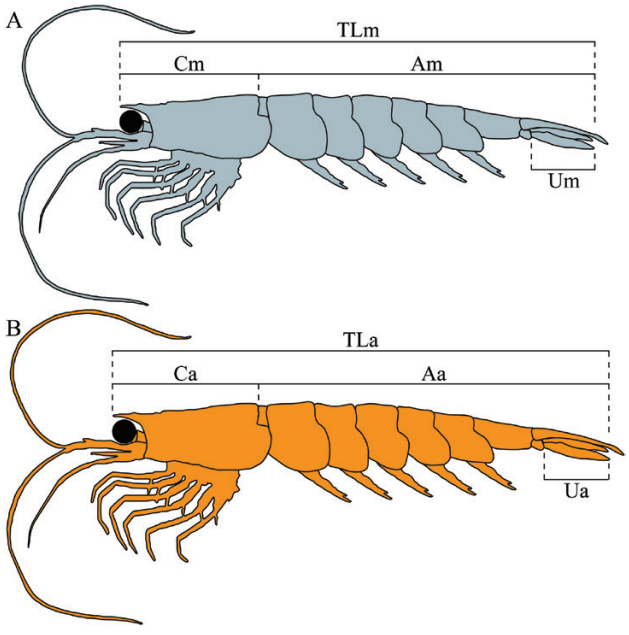

Figure 2. Length measurements needed to derive sex-dependent (SIGR) and traditional (TIGR) growth rates for the moulted exoskeleton from the krill before (**A**) and after (**B**) the moulting event. TLa, total length of the krill after moulting, measured as described by Standard 1 in Mauchline (1980); Ua and Um, average of left and right uropod lengths measured from the distal tip to its external intersection with the basipodite (Brown *et al.*, 2010); Ca and Cm, carapace length measurements, as depicted by Hill (1990). TLa, Ca, Cm, Ua, and Um are direct measurements; TLm and Aa are calculated parameters.

SIGR method. To develop the SIGR equation, total body length of the post-moult krill and carapace length of both the moulted exoskeleton and the post-moult krill (Fig. 2A, B) were also measured, in addition to what had already been measured for TIGR: uropod length and state. SIGR values were calculated for each individual krill using Equation 2 (Table 1). The concept behind this method is to calculate the growth rate based on the difference in total body size before and after moulting, rather than representing the growth rate only by the uropod measurements. The length of the moulted exoskeleton sections of the carapace and uropod can be directly measured as they are readily distinguishable and whole. The abdomen, however, involves multiple segments and it is not possible to measure the size of this section directly from the moulted exoskeleton and therefore the total length of the moulted exoskeleton (TLm; Fig. 2A) cannot be measured. As shown by Equation 3 (Table 1), TLm was estimated by assuming that the growth rate of the abdomen is equal to the growth rate of the uropods, where the krill post-moult abdominal length (Aa, Fig. 2B) was calculated from subtracting the carapace length post-moult from the total length of the krill post-moult.

Calculation of daily growth rates and intermoult period. Daily growth rates (DGR) for each experiment were calculated using Equation 4 (Table 1). The intermoult period (IMP) was derived using Equation 5 (Table 1) based on the proportion of individuals moulted within the first four days of incubation. There was not sufficient information to calculate IMP for each state as the krill that had not moulted at the end of each experiment (parameter N, Equation 5; Table 1) were not sexed. IMP is required to calculate DGR and therefore it was not possible to determine for each state. The IMP calculated for the whole experimental population was nevertheless assumed to be equal for each state.

Statistical Analysis

Data from both voyages were pooled and all analyses were undertaken using the R statistical package (R Core Team, 2017). The carapace lengths and total lengths for males and females post-moults were used to create a scatterplot and identify the relationship between the two variables to test whether a difference in carapace lengths existed that was dependent on state. When this relationship was apparent, predictor and confidence intervals were calculated, based on equal error variances, to calculate uncertainty in the parameters and the uncertainty due to measurement. Analysis of Variance (ANOVA) and Wald tests were used to judge significance levels.

RESULTS

A total of 253 krill (97 females, 49 males, 33 gravid females, 74 juveniles) was measured and used for calculation using both growth-rate methods. An average of 0.70% of the incubated krill died on Voyage 1 and an average of 1.6% died on Voyage 2. The mean IMP, which was calculated based on experiment regardless of state, was 24 d (range 12–50 d). Models in this study were fitted to krill with post-moult lengths of 20–55 mm, therefore the relationships presented are only valid within this range.

Comparison of carapace lengths

The linear regression relationship of carapace length to total length post-moult was derived for:

$$\text{Females TLa} = -3.23 + 0.422\text{Ca} \left(R^2 = 0.89, P < 0.001\right), \text{ and}$$

$$\text{Males TLa} = -0.304 + 0.33\text{Ca}\ \left(R^2 = 0.96, P < 0.001\right).$$

The slope of the relationship was similar for both males and females, although the intercepts differed. The carapace length was equal for males and females at a total post-moult length of 30.5 mm, and the relation diverged beyond that length (Fig. 3). An ANOVA revealed a significant difference between the female and male linear models (ANOVA, $P < 0.001$).

Comparison of growth rate methods

SIGR for each state (mean and standard deviations in brackets), from highest to lowest growth percentages were as follows: juveniles 5.2% (2.2), males 4.2% (2.6), females 1.5% (2.7), and gravid females 0.8% (2.7); the corresponding TIGR for each state were: juveniles 4.4% (1.9), males 3.3% (2.1), females 2.1% (1.8), and gravid females 0.3% (2.0).

Model fit

Linear regressions for each state were calculated to examine model fit (Fig. 4 A–D). The relationship of TIGR to SIGR for each state was as follows:

$$\text{Juveniles SIGR} = 1.31 + 0.885\text{TIGR}\ \left(R^2 = 0.53, P < 0.001\right),$$

$$\text{Males SIGR} = 0.712 + 1.05\text{TIGR}\ \left(R^2 = 0.62, P < 0.001\right),$$

$$\text{Females SIGR} = -0.791 + 1.08\text{TIGR}\ \left(R^2 0.54, P < 0.001\right) \text{ and}$$

Table 1. Equations and parameters used for growth rate calculations and statistical analysis.

Equation number	Equation name	Units	Formula	Parameters
1	Traditional IGR (TIGR)	Percentage (%)	$\left(\frac{Ua - Um}{Um}\right) \times 100$	Figure 2
2	Sex-dependent IGR (SIGR)	Percentage (%)	$\left(\frac{TLa - TLm}{TLm}\right) \times 100$	Figure 2 and equation 3
3	Total Length of Moult (TLm)	Millimetres (mm)	$Cm + \left[(TLa - Ca) \times \left(\frac{Um}{Ua}\right)\right]$	Figure 2
4	Daily Growth Rate (DGR)	Millimetres per day ($mm.d^{-1}$)	$\frac{(TLm \times IGR)}{(IMP \times 100)}$	Figure 2
5	Intermoult Period (IMP)	Days	$\frac{(N + m) \times d}{m}$	N = total number of krill alive at end of experiment d = total length of incubation m = number of krill that moulted

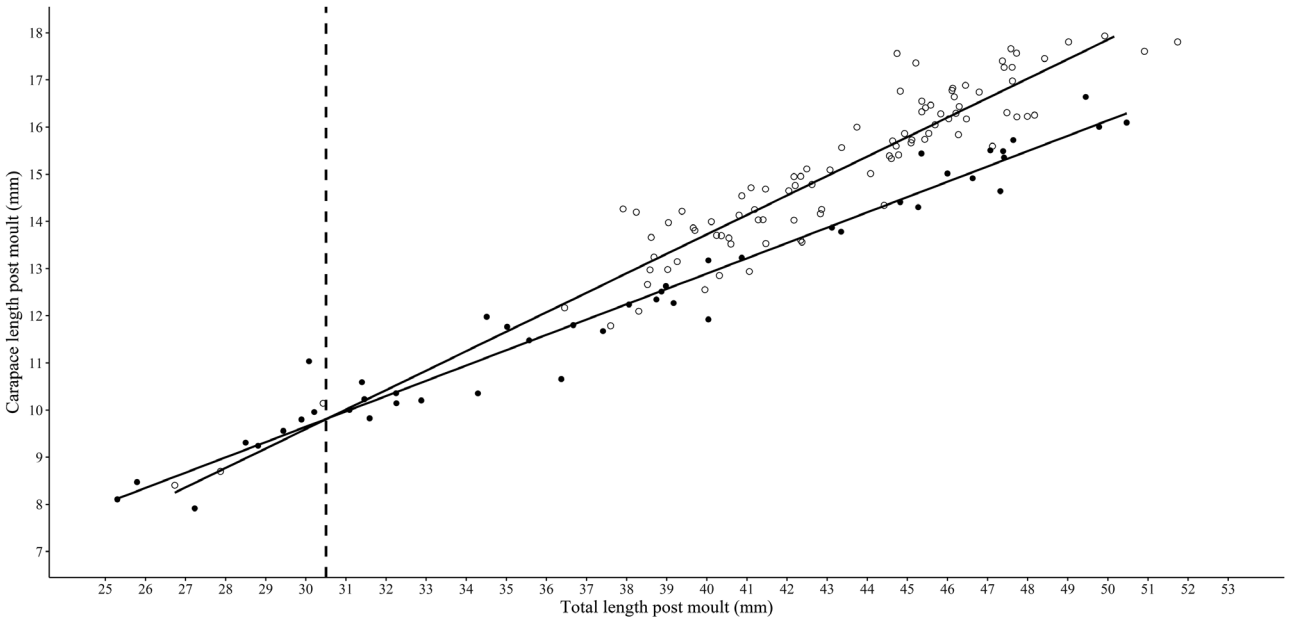

Figure 3. Carapace length (mm) as a function of krill total length post-moult (mm) for males (closed circles) and females (open circles). Dashed line represents where total body length and carapace length were equal for males and females. Solid black lines represent fitted regression lines.

$$\text{Gravid females SIGR} = 0.454 + 1.33\text{TIGR}\ \left(R^2 = 0.73, P < 0.001\right).$$

No significant differences were found between the 1:1 ratio line and slope of the 'line of best fit' for male ($P = 0.66$), juvenile ($P = 0.25$), and female ($P = 0.46$) krill between the growth rate methods. The gravid females had the most dissimilar trend, with the 1:1 ratio line and 'line of best fit' intersecting at approximately –1% TIGR and –4% SIGR (Fig. 4B) with a significant difference between the two lines ($P < 0.01$).

Cumulative DGR

Daily growth rate for both methods was generally consistent with previous estimates (Table 2). The DGR shows how much a krill grows or shrinks in millimeters per day, whereas IGR shows the growth or shrinkage, as a percentage of their body size per

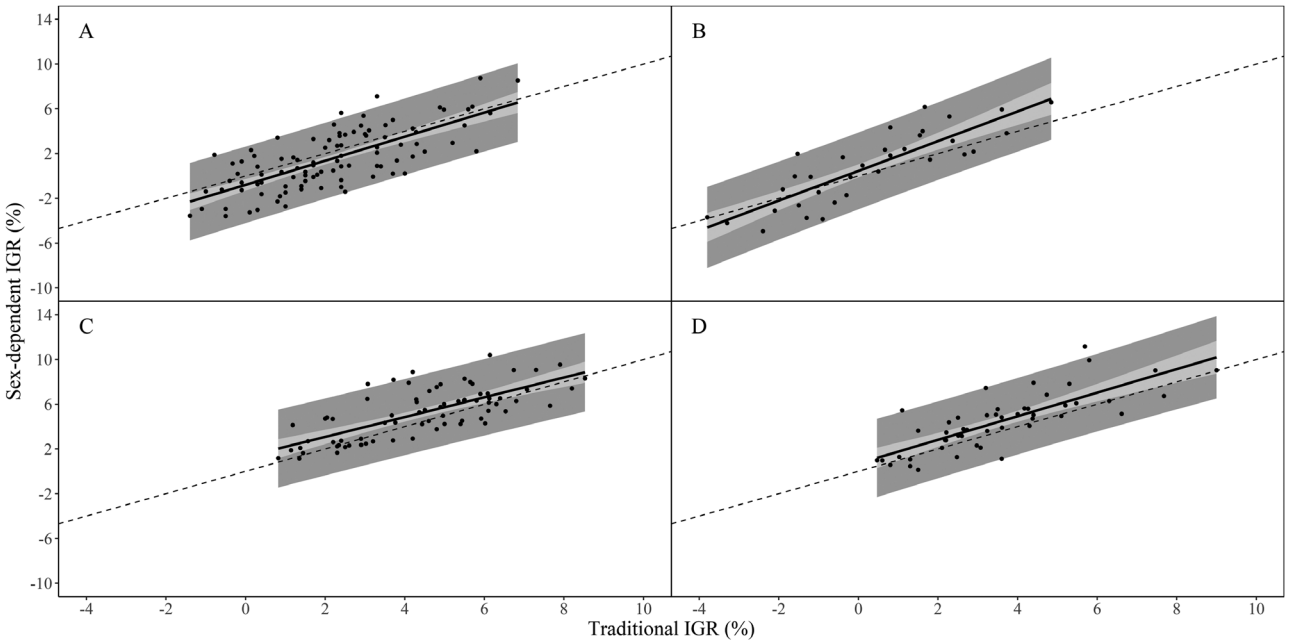

Figure 4. Sex-dependent IGR (SIGR) as a function of traditional IGR (TIGR) for non-gravid females **(A)**, gravid females **(B)**, juveniles **(C),** and males **(D)**; 95% prediction intervals (dark grey box) and 95% confidence intervals (light grey box), with the regression line for each state (solid black line) and the 1:1 ratio (dashed black line).

Table 2. Summary of daily growth rates (DGR) of *Euphausia superba* obtained from the literature and this study, all in chronological order of collections.

Sex	Daily growth rate (mm day^{-1})	Region and timing	Reference
Juveniles	Maximum mean 0.047	Laboratory study, caught in 1984 and 1985	Ikeda & Thomas (1987)
Juveniles	December 0.204 to 0.279	Indian Ocean sector, 10 summers from 1992 to 2003	Kawaguchi *et al.* (2006)
	April 0.012		
Adult females	December 0.083 to 0.126		
	April –0.014 to –0.003		
Adult males	December 0.05 to 0.136		
	April 0.010		
Juveniles and adults	0.013 to 0.32	Southwest Atlantic sector, January and February 2002 and 2003	Atkinson *et al.* (2006)
Juveniles and adults	0.00 to 0.45	Southwest Atlantic sector, January and February 2002 and 2003	Tarling *et al.* (2006)
Adult females	August to December –0.07 to 0.13	Laboratory study, Krill caught March 2006 in Indian Ocean sector; seasons simulated in lab	Brown *et al.* (2010)
	January to July –0.23 to 0.07		
Adult males	August to December –0.12 to 0.13		
	January to July –0.19 to 0.10		
Juveniles and adults	0.003 to 0.169	Indian Ocean sector, 2 summers, December to January 2016 and January to February 2017	Sex-dependent measurements (SIGR); this study (2017)
	0.011 to 0.113		Traditional uropod-only measurements (TIGR); this study (2017)

moulting event. The cumulative DGR derived for TIGR and SIGR methods, assuming growth for 90 d, will be: 3.56 and 2.68 mm for females, 0.49 and 1.45 mm for gravid females, and 4.44 and 5.81 mm for males, respectively, using the simple IMP calculated for the whole experimental population.

DISCUSSION

Our results support the hypothesis outlined by Tarling *et al.* (2016) that sexual dimorphism in the carapace may cause a difference in the measurement of growth rates between males and females, as there was a statistically significant difference between growth rate methods for gravid females. The results of this method development indicate a need for further analysis to enhance TIGR approaches to estimating sex- and stage-specific krill growth and the need to parametrise the models for it to allow accurate description of the relationship between reproduction and growth

Carapace and total body length

Adult krill are sexually dimorphic, with the carapace being 30% longer in females than in males of a similar total body length (Goebel *et al.*, 2007). Total carapace length of juvenile krill is closely related to total body length and is often described by an allometric relationship (Reid & Measures, 1998). The different relationship found for gravid females in this study can be attributed to variations in carapace length due to the ovaries and lipid stores, with this body section containing up to 40% of total individual wet mass in fully gravid females (Tarling *et al.*, 2007). There has been no modification to growth rate measurements to include the carapace length as a standard parameter of the IGR method. Our results indicate that 30.5 mm total body length signifies the point where total carapace length diverges between males and females. There is no differentiation in the relationship between the carapace lengths of males and females of an equal size in individuals smaller than 30 mm. Beyond this critical body length, females were found to have longer carapace lengths than males of an equal size, indicating that the growth rates of males and females differ (Siegel, 1982; Miller, 1983; Goebel *et al.*, 2007). This gave us reason to continue our development of a sex-dependent relationship for the IGR method, highlighting that carapace sexual dimorphism was apparent.

Comparison of growth rate methods

The development of the SIGR method ultimately led to the need to compare the length of the moulted exoskeleton, which is too difficult to measure directly due to its condition after the moulting event, with the total length of the krill post-moulting. Relying solely on the change in size of uropods (TIGR methods) results in the inability to distinguish sex-dependent differences in growth (Miller, 1983).

Regardless of whether SIGR or TIGR was used, IGR results for each state were consistent with previous estimates (Table 3). Juvenile krill had the highest average IGR of all stages in both methods due to their need to grow and develop faster to reach a size where they can overwinter effectively (Kawaguchi *et al.*, 2006). Males had the second highest average IGR, consistent with findings that males tend to grow faster than females (Kawaguchi *et al.*, 2007). Females had an overall higher IGR than gravid females because they do not need to divert energy away from growth and into reproduction (Nicol *et al.*, 1995; Atkinson *et al.*, 2006).

Differences between the DGR derived using TIGR and SIGR may appear small but there are notable differences in cumulative growth if applied over the reproductive season (90 d between

Table 3. Summary of data on growth increments (% per moult) in *Euphausia superba* obtained from the literature and this study, all in chronological order of collection dates.

Sex	IGR ranges (% per moult)	Region	Reference
Adults	Autumn 2 to 5 Winter –0.1 to 2	Waters west of Antarctic Peninsula, March to April and August to September 1985	Quetin & Ross (1991)
Juveniles	2.42 to 9.05	Indian Ocean sector	Nicol *et al.* (1992)
Adults	0.35 to 7.34	Over 4 summers, 1988, 1990–1992	
Juveniles	2 to 10	Within 3.7 km of Palmer Station, West Antarctica, Spring and Summer from 1991 to 1996	Ross *et al.* (2000)
Juveniles and adults	0.58 to 15	Southwest Atlantic sector, January and February 2002 and 2003	Atkinson *et al.* (2006)
Juveniles	–1.09 to 15.11	Western Indian Ocean sector (BROKE-West Survey), summer 2006	Virtue *et al.* (2010)
Adult females	–3.60 to 15.32		
Adult males	–1.66 to 22.10		
Adult females	August to December –4.21 to 34 January to July –11.55 to 5.40	Laboratory study, Krill caught March 2006 in Indian Ocean sector	Brown *et al.* (2010)
Adult males	August to December –5.85 to 35 January to July: –6.80 to 6.53		
Juveniles and adults	–4.60 to 4.60	Indian Ocean sector (SIPEX survey), September to October 2007	O'Brien *et al.* (2011)
Juveniles	1.13 to 14.82	Indian Ocean sector, 2 summers, December to January 2016 and January to February 2017	Sex-dependent measurements (SIGR), this study (2017)
Adult females	Adult: –4.54 to 10.16 Gravid: –4.93 to 6.59		
Adult males	–0.30 to 15.41		
Juveniles	–0.82 to 12.74		Traditional uropod-only measurements (TIGR), this study (2017)
Adult females	Adult: –1.40 to 8.70 Gravid: –3.80 to 4.85		
Adult males	–0.76 to 9.00		

spring and summer). It is noteworthy that Tarling *et al.* (2006) reported female krill IMP could be as short as half that of male IMP, depending on temperature and total length of krill. With this IMP assumption factored in for DGR calculations, the DGR for the two methods in our study will double for females, in comparison to DGR for males, which will not change. The cumulative growth rates for TIGR and SIGR for each state will thus be 7.11 and 5.35 mm for females, 0.97 and 2.91 mm for gravid females, and no change from 4.44 and 5.81 mm for males, respectively. This implication for DGR estimations highlights the need for future studies to include the maturity stages of krill that did not moult during the experiment in order to derive sex-dependent IMP and therefore sex-dependent DGR.

Future recommendations

The SIGR method can add approximately 25 to 50% more time per measurement, dependent on the skills of the researcher and the quality of the sample. Even though the SIGR method adds time to an already labour-intensive process, we have shown the value of including carapace length to increase the accuracy of the growth measurement. The inclusion of maturity stages with the SIGR method in future studies would lead to the development of a growth model that accurately describes differential growth between males and females under various environmental conditions. It would also provide the data required for the calculation of sex-specific IMP so that sex-specific DGR does not need to be assumed.

Processes limiting krill growth and reproduction, as terms included in models, can include the exoskeleton, gonadal masses, and the seasonal cycle (Meyer & Teschke, 2016). At present, models do not fully account for these factors and so cannot give realistic outputs related to sex-dependent energetics. Constable & Kawaguchi (2018) highlighted the need for future models to include the interaction between reproduction and growth, and understand the way in which they interact with the factors listed above; the SIGR method is a way for this interaction to be included.

The use of the SIGR method for future studies will be dependent on the purpose of the research. As the size of carapace dictates the size of the ovary (Tarling *et al.*, 2007), growth rates that reflect female carapace size are an important proxy for the increase rate of egg carrying capacity during the reproductive season. The proposed SIGR method does not replace TIGR. The accumulation of data, however, which allows for SIGR calculations to be conducted at a later date will add value to the TIGR method. Future IGR experiments should include, where possible, the total length of the krill post-moult, uropod and carapace lengths of the moult and the specimen itself, sex and maturity stages of individual krill, as well as maturity staging of krill that did not moult during the experiments. These measurements will enable sex and stage-dependent differences to be represented in growth-rate calculations. The inclusion of these factors will allow for accurate measurements to be included as parameters in life history models to contribute to our understanding of life cycle and population dynamics of krill.

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