

## Natural growth rates in Antarctic krill (*Euphausia superba*): I. Improving methodology and predicting intermolt period

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### Abstract

The growth rates of postlarval krill (*Euphausia superba*) were measured across a wide range of environments in the Scotia Sea and around South Georgia using the Instantaneous Growth Rate (*IGR*) method. Each *IGR* experiment determined the intermolt period (*IMP*) and growth increment at molt (*GI*) of an average of 120 individuals incubated for 5 d in through-flowing ambient, filtered seawater. We examined the results from 51 *IGR* experiments involving 5,927 animals ranging between 25 mm and 62 mm. Animals were collected from an area that covered a latitudinal range of 10° and surface temperatures of between -0.85°C and 4.75°C. The measurement of *IMP* has rarely been achieved in *IGR* experiments because synchronous molting biases estimates. We overcame this by applying a binary logistic regression model to our data. This related *IMP* to temperature, body length, and maturity stage. Food did not influence *IMP*. Our model estimated that krill within our experiments had *IMPs* ranging from 9 d to 57 d. Temperature affected the *IMP* of females more than that of males. The *IMPs* of females were shortest around 2°C and increased at lower and higher temperatures. *IMP* increased with body size and altered according to gender, with male *IMPs* being 50% longer than those of equivalently sized females. One of the main assumptions of the *IGR* method is that the *GI* measured in the first few days reflects the *in situ* conditions experienced by krill in the previous intermolt period. However, we found that the *GIs* declined immediately and rapidly after capture, particularly when growth was initially high. Thus, conditions at time of molt also influence *GI*. We developed a method of correcting measured *GIs* to natural growth in field conditions. These refinements to *IGR* methodology (*IMP* and *GI* estimation) enable more accurate and precise predictions of krill growth rates in summer to be made.

Antarctic krill have been a widely studied species because of their economic importance and fundamental position in the Southern Ocean food web (Everson 2000). However, their biology also makes them an ideal species with which to examine important ecological questions. Being crustaceans, krill grow in length in a punctuated fashion at each molt. Unlike most other crustaceans, however, krill continue to molt frequently through adulthood, even if there is no further somatic growth (Mauchline and Fisher 1969; Hartnoll 1982). Molt frequency and growth at molt are key indices to the physiological state of the animal and reflect its response to environmental conditions. We are capable of measuring this at all stages in the life of a krill.

Somatic growth is a good indicator of the response of an animal to its environment, since it is the sum of a number of major physiological processes (e.g., ingestion, assimila-

tion, respiration, excretion, locomotion). However, it is difficult to obtain growth measurements that are suitably direct and unaffected by experimental conditions. The most widely adopted method is to determine the change in the mean length of the sampled population over time (e.g., Marr 1962; Mackintosh 1972). Such studies have problems when it comes to sampling the same population repeatedly (Clarke and Morris 1983) and accounting for age-dependent mortality (Nicol 2000). They also give poor spatial and temporal resolution.

Measuring krill growth through incubation in laboratories over long periods (e.g., Murano et al. 1979; Buchholz 1985; Nicol and Stolp 1990) overcomes some of the above problems. The animals are maintained for the duration of their intermolt period or longer, so that the total length of the intermolt period as well as the increment of growth at molt can be measured. Nevertheless, it is impossible to simulate the exact environmental conditions, such as the concentration and taxonomic structure of food. This is likely to introduce error through experimental stress.

In the case of krill, it is possible to adopt an alternative method that measures growth directly but minimizes exposure to experimental conditions. The Instantaneous Growth Rate (*IGR*) was originally adapted for use in krill by Quetin and Ross (1991) and Nicol et al. (1992). The method involves taking around 100 krill (minimum) and incubating them for 2–3 d in individual containers. The animals must be checked daily and any molted animals extracted from the experiment with the cast-exoskeleton and the newly molted animal measured to determine the percent change in length at molt (growth increment, *GI*). The daily molt rate (*MR*)

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### Acknowledgments

We thank the crew and scientists aboard the RRS *James Clark Ross* during the cruises JR70 and JR82 for their assistance in collecting material. We also thank Peter Ward, who managed operations as Principal Scientific Officer on JR70, Doug Bone for assembling and maintaining the net gear, Steve Nicol, in sharing with us his design for the bulk rearing of krill in *IGR* experiments, and Fred Buchholz and Janine Cuzin-Roudy for formative discussions on this subject. We are grateful to the three anonymous referees who made considerable efforts to improve this manuscript. Pete Rothery expertly guided us through binary logistic regression statistical analysis. This work was carried out as part of the DYNAMOE program at the British Antarctic Survey.

can be estimated through dividing the total number of krill at the start of the incubation into the number molting per day. Intermolt period (*IMP*) is the inverse of *MR* (Eq. 1), so we call this the *1/MR* method.

$$IMP = \frac{1}{MR} \quad (1)$$

Dividing *IMP* into the *GI* gives the percent change in length per day. Relating this back to the premolt length of the original krill ( $L_{pre}$ , mm) allows the daily growth rate (*DGR*, mm d<sup>-1</sup>) to be determined using the equation of Ross et al. (2000):

$$DGR = \frac{L_{pre} \cdot GI}{IMP \cdot 100} \quad (2)$$

The technique is based on three major premises: (1) that the number molting each day is relatively constant and equal to the inverse of the molt duration; (2) that the *GI* is not affected by the incubation conditions for several days postcapture (Nicol et al. 1992); and (3) that *IMP* is not affected by incubation.

Previous studies using this technique have understood that these premises are violated to some extent and have used their results judiciously to avoid many of the potential errors (e.g., Nicol et al. 2000; Ross et al. 2000; Quetin et al. 2003). The *IMPs* of experiments calculated with the *1/MR* method have been found to be variable (Nicol 2000), probably because of molt synchrony (Buchholz et al. 1996). Over a small number of incubation days, such synchrony would result in either very few or almost all of the krill molting, biasing the estimate of *IMP* using Eq. 1.

One solution, that employed by Quetin et al. (2003), was to use an average *IMP* calculated over all experiments. However, one of the main justifications for employing the *IGR* method is to determine how environmental fluctuations affect krill growth, and such large-scale averaging compromises this ability. Another approach is to consider growth only in relative units (i.e., *GI* per molt; e.g., Nicol et al. 2000; Ross et al. 2000). Although this is a valid unit when comparing among *IGR* experiments, it has limited use with regard to population dynamic studies, which use absolute units such as growth in length (mm d<sup>-1</sup>). Therefore, the challenge is to devise an alternative means of predicting *IMP* for individual *IGR* experiments.

The measurement of *GI* presents a different type of challenge. Krill are unable to feed at natural rates in the incubations. Like some other studies, we have incubated in filtered seawater to standardize conditions. The basic premise is that the *GI* of a krill is dictated by the environment in the sea and is relatively unaffected by a couple of days of captivity just prior to molting. It is understood that this starvation will eventually affect the growth of the krill, but the trade-off comes in deciding how many days are possible before incubation results become biased. If the number of days is too few, the sample size of molters will be insufficient for making robust estimates. However, holding thousands of krill to ensure a large enough sample size becomes logistically unfeasible. Our approach, therefore, is to correct

results so that the experimental effects of incubation are accounted for.

In 2002 and 2003, we measured the molting performance and growth increments of >5,000 krill during two field surveys of South Georgia and the Scotia Sea. The large geographic coverage of the surveys meant that they encompassed a large span of the conditions encountered by krill within their biogeographic range. In Part I of this pair of articles, we investigate some of the biological and environmental factors affecting *IMP* and develop methods that allow *IMP* to be estimated in different situations. We also examine the effect of incubation time on *GI* and provide a simple method of correcting *GI* to in situ values. Part II (Atkinson et al. this issue) investigates the factors affecting *GI* and develops functional relationships between daily growth rates and krill length, maturity stage, temperature, and food. Together, these studies enable other investigators to use refined methodology to predict growth in postlarval *Euphausia superba* using easily measured and readily obtainable variables. The data set also represents a major description on the impacts of food, temperature, and maturity stage on the *IMP* of krill.

## Materials and methods

*Sampling protocol*—Capture of live specimens: Surveys aboard RRS *James Clark Ross* were carried out in January and February 2002 near South Georgia and in January and February 2003 across the Scotia Sea (Fig. 1). Krill were caught by locating krill schools with multifrequency acoustics (38 kHz, 120 kHz, 200 kHz) and sampling them with a Rectangular Midwater Trawl (RMT8). The RMT8 was rigged with two remotely operated opening/closing nets, thus enabling sampling from separate schools when there were several located close together. The stress of capture was minimized through use of a nonfiltering cod end on each net and by hauling immediately once an acoustically monitored swarm had been sampled. Once on board, the cod end contents were diluted immediately into ambient surface seawater in 160-liter circular containers held in a constant-temperature room maintained at ambient sea-surface temperature. Each of the separate experiments is summarized in Table 1 of Atkinson et al. (this issue). We examined the 51 experiments in which incubations lasted for 5 d or longer.

*Environmental parameters*: Atkinson et al. (this issue) give full details of the collection and primary analysis of environmental variables, so only a summary is given here. Surface temperature and salinity were recorded at high temporal frequency along the cruise track using a thermosalinograph connected to the ship's nontoxic pumped seawater supply. This water was taken from a nominal depth of 6.5 m. A SeaBird 911+ CTD was deployed at regular intervals throughout both surveys. Water samples were collected on the upcast of the CTD with 10-liter Niskin bottles housed in a SeaBird 12-position carousel water sampler.

Samples taken in the top 20 m were analyzed taxonomically to determine the concentrations of different microplankton groups, following the protocol of Utermöhl (1958). Chlorophyll *a* (Chl *a*) samples were taken either from the

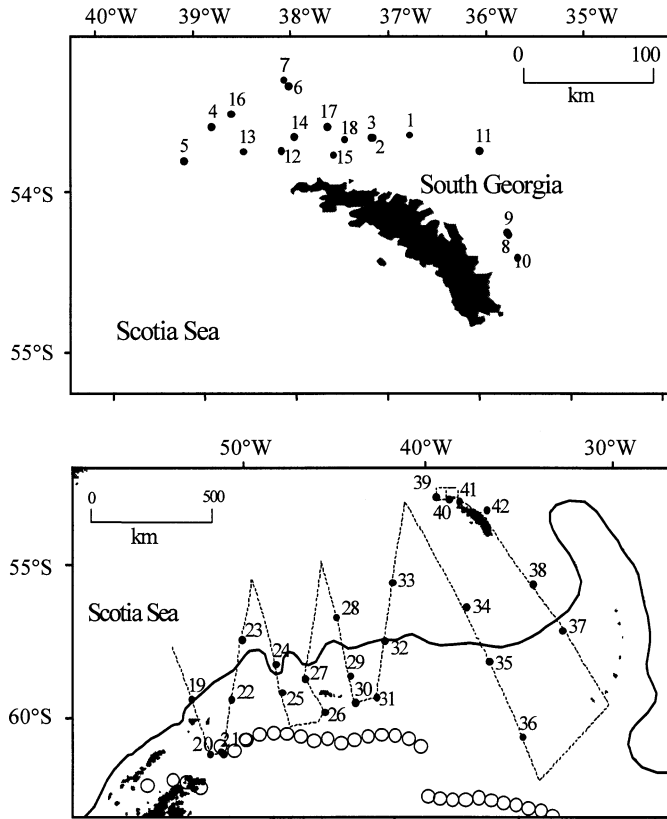


Fig. 1. Distribution of krill catches (black circles) used for IGR incubations in 2002 upper and 2003 lower. The numbers refer to the sequence in which krill catches were taken. The position and dates of these catches are given in a table in Atkinson et al. (this issue). Note that up to two experiments were set up at each station from separately caught swarms. The dotted line refers to the cruise track in 2003; the open circles, the position of ice-edge in February 2003; and the bold line, the average position of the Southern Boundary of the Antarctic Circumpolar Current Front.

pumped seawater supply (6.5 m) or from equivalent depth CTD samples and analyzed fluorometrically after transfer onto GF/F ( $<0.7 \mu\text{m}$ ) filters. Surface Chl *a* concentration was also determined remotely through analysis of monthly SeaWiFS level-3 standard-mapped images with a  $9 \times 9$ -km resolution, which were analyzed using ARC GIS 8.2 software (Environmental Systems Research Institute).

**Experimental studies**—Incubation methods: Krill were incubated in a constant-temperature room. They were held at ambient sea-surface temperature in individual containers within a flow-through tank, in a manner similar to that described by Nicol et al. (2000). For each experiment, an average of 120 krill (standard deviation [SD]  $\pm 73$ ) were taken from the holding containers and transferred individually into separate 500-mL perforated polycarbonate jars before being placed into the flow-through tank (500-liter capacity). Once seeded with a single krill, the jars were stacked within perforated tubes (9-cm-diameter plastic drainage pipes) within these tanks to increase space efficiency and facilitate regular maintenance checks. The checks were made to be quick and easy by attaching a string to the bottommost pot of each

stack to help lift the pots from the tank. Seawater was taken from the pumped seawater supply and was filtered to remove all particles larger than  $2 \mu\text{m}$  before being pumped into the holding tanks at a rate that replaced their volume three times per day. There were three holding tanks connected in a series, with a combined total capacity of around 1,000 krill. Often there were four or five different incubation experiments within these tanks at any one time. Temperature in each tank was monitored daily. Experiments were set up within 1 h of the net coming aboard.

**Experimental analysis:** We checked the krill every 24 h after capture for 5 d, with newly molted and dead animals being removed from the incubation. On average, 1% of krill died on the first day, dropping to below  $0.5\% \text{d}^{-1}$  thereafter. At the end of the experiment, animals were analyzed fresh for length, sex, and maturity stage: total length (mm) was measured from the front of the eye to the tip of the telson; maturity staging followed the method of Morris et al. (1988), which was based on the key provided by Makarov and Denys (1980). Molted animals that were removed during the course of the incubation period were analyzed in the same way. The same investigator (R.S.S.) always carried out the measurements under the same working conditions in order to minimize biases.

We calculated the IMP of an experiment, using the  $1/MR$  method, as follows:

$$IMP = \frac{N \cdot d}{m} \quad (3)$$

where  $N$  represents the total number of krill that were alive at the end of the experiment plus those that molted during the incubation period,  $m$  is the number that molted, and  $d$  is the total length of the incubation (5 d in this instance).

We obtained growth increments ( $GI$ ) through measuring the left and right uropods on both the animal and its recently molted exoskeleton under a binocular microscope fitted with an eyepiece graticule. Usually, left and right uropod measurements were combined to give an average uropod length for the animal and for the molt, but in some instances it was necessary to use the values from just one of the uropods because the other was damaged.  $GI$  was defined as the percentage difference between the uropod length of the animal ( $U_a$ ) and the molt ( $U_m$ ), as follows:

$$GI = \frac{U_a - U_m}{U_m} \cdot 100 \quad (4)$$

Buchholz (1991), among others, used a function to convert uropod length to total body length before determining  $GI$  to avoid any allometric errors (i.e., the problem of different body parts growing at different rates). We found that converting uropod lengths to body lengths before carrying out the calculation of  $GI$  made virtually no difference to the results ( $GI_U = 0.0001 + 1.0297 \cdot GI_{TL}$ ,  $R^2 = 0.99$ ,  $p < 0.0001$ ; where  $GI_U$  is the  $GI$  based on differences in uropod size and  $GI_{TL}$  is the  $GI$  based on differences in equivalent total body length). The uropod method was used in further analysis since it was more direct and was based on measured rather than estimated values.

Table 1. A list of parameters used.

Parameter	Description	Unit
<i>GI</i>	Growth increment	%
<i>U</i>	Uropod length	mm
<i>MR</i>	Moult rate	d <sup>-1</sup>
<i>IMP</i>	Intermoult period	d
Observed <i>IMP</i>	Intermoult period calculated using <i>1/MR</i>	d
Predicted <i>IMP</i>	Intermoult period calculated using functional relationships in Table 3	d
<i>DGR</i>	Daily growth rate	mm d <sup>-1</sup>
<i>P</i>	Probability of moult	
<i>N</i>	Total number of krill in an <i>IGR</i> experiment	individuals
<i>d</i>	Number of incubation days	d
<i>m</i>	Total number of animals moulting in an <i>IGR</i> experiment within 5 d	individuals
$\Delta GI$	Decline in <i>GI</i> over unit time in an <i>IGR</i> experiment	%
<i>GI</i>	Mean <i>GI</i> of an experiment	%
in situ	The state had the animal remained in the sea	
<i>GI<sub>in situ</sub></i>	<i>GI</i> at time of capture	%
<i>GI<sub>obs</sub></i>	<i>GI</i> measured during <i>IGR</i> experiment	%
<i>h</i>	Time elapsed	h
<i>F</i>	Food proxy: mean SeaWiFS Chl <i>a</i>	mg m <sup>-3</sup>
<i>T</i>	Surface temperature at time of capture	°C
<i>L</i>	Measured total body length	mm
<i>L<sub>pre</sub></i>	Estimated total body length before moult	mm
<i>DW</i>	Dry weight	mg
<i>J</i>	Energy	joules
<i>R</i>	Respiration rate	joules d <sup>-1</sup>
<i>W</i>	Weight	
<i>a, b</i>	Constants or coefficients	

## Results

**Intermolt period (IMP)**—Calculating the *IMP* from an individual experiment using the *1/MR* method (Eq. 3) results in *IMP* estimates that span almost an order of magnitude (10–120 d; Fig. 2). Such variance is unrealistic given that laboratory studies, which follow the molting performance of

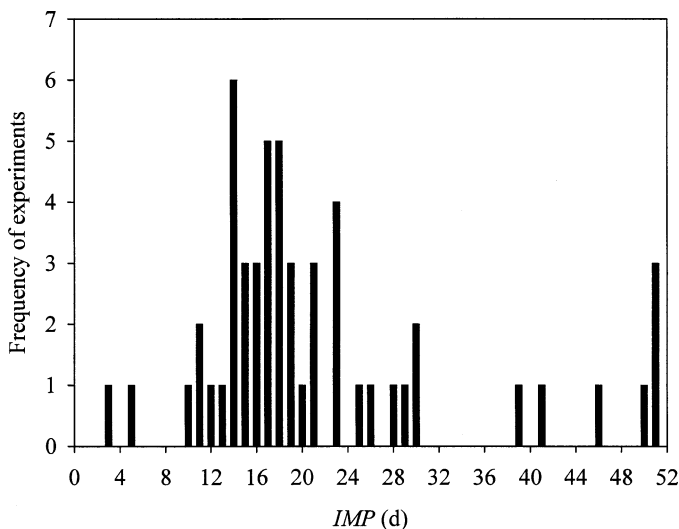


Fig. 2. *IMP* for each experiment determined by the *1/MR* method.

individual postlarval krill, estimate *IMP* to be within the range of 10 to 30 d (Buchholz 1991). Synchronized molting is a likely cause of much of the variation between our experiments. Applying the *1/MR* method to data from a single experiment is therefore an unreliable way to estimate *IMP*.

To overcome this problem, our new method was to identify any functional relationships between *IMP* and biometric and environmental variables. We treated the data set in its entirety as one large experiment rather than as 51 separate experiments. This had the effect of mixing the krill; individuals from experiments with molt-synchrony were combined with others without synchrony; situations in which molt-synchrony may have increased the probability of molting were combined with others in which the probability was decreased.

Molt data were recorded in a binary format (1 or 0), since an individual did (1) or did not (0) molt during the 5-d incubation period. Such data can be analyzed with a Binary Logistic Regression Model (Hosmer and Lemeshow 1989), in which the probability of an event (molting) is related to the values of one or more explanatory variables. The relationship between the event probability and the explanatory variables is described by the following logistic response curve:

$$P = \frac{e^{a+bx+cy\dots}}{1 + e^{a+bx+cy\dots}} \quad (5)$$

where *P* is the probability of the event (molting within 5 d),

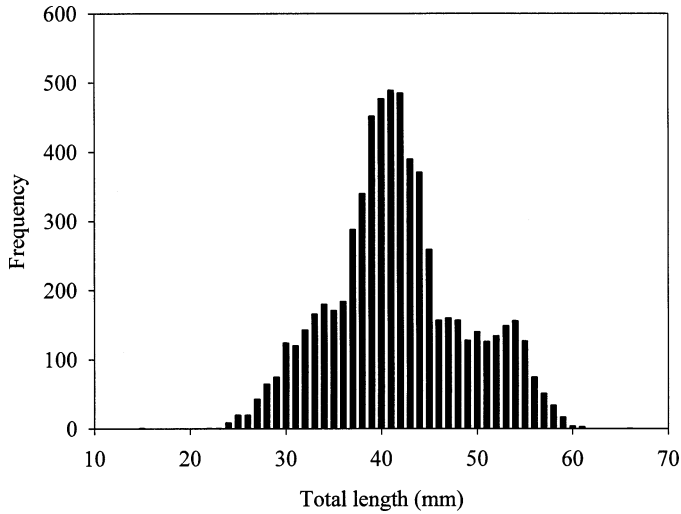


Fig. 3. Length frequency distribution of krill from all catches carried out in 2002 and 2003.

$a$ ,  $b$ , and  $c$  are fitted constants or coefficients, and  $x$ ,  $y$ , etc. are explanatory variables.  $IMP$  is derived by

$$IMP = \frac{d}{P} \tag{6}$$

where  $d$  is the number of incubation days (5 d in this instance). It is to be noted that this method means that it is not possible to determine  $IMP$  of a population containing individuals that molt more frequently than every 5 d. We assumed that *E. superba* postlarvae did not molt so frequently based on the typical  $IMP$  ranges for this species reported elsewhere (Buchholz 1991; Ross et al. 2000).

**Choosing explanatory variables**—Factors believed to influence  $IMP$  include temperature (Quetin et al. 1994), food (Buchholz 1991), and body size (Mauchline 1977). We used proxies of these factors as explanatory variables in the logistic models.

For temperature ( $T$ ), our proxy was near-surface temperature (~5 m in depth) at time of capture, which ranged between  $-0.85^{\circ}\text{C}$  and  $4.75^{\circ}\text{C}$  within our surveys. The alternative is the water temperature during the incubation, which

was correlated to near-surface temperature (Pearson correlation coefficient 0.825,  $p < 0.001$ ) but had a smaller overall range. We considered near-surface temperature at time of capture preferable for biological and practical purposes. Biologically, krill must pass through a number of molt stages during its molt cycle (Buchholz 1985). For the krill in the present incubation experiments, the majority of these stages would have been spent in the environment rather than in the incubation. Therefore, it is likely that alterations to the probability of molting made by incubation conditions will be relatively minor. Practically, developing models based on near-surface temperature is more applicable to other studies, since such data are readily accessible. For food ( $F$ ), we used the mean SeaWiFS Chl  $a$ , which was found by Atkinson et al. (this issue) to have a higher explanatory power than other food proxies when predicting  $GI$  and  $DGR$ . Values ranged between 0.07 and  $12.00 \text{ mg Chl } a \text{ m}^{-3}$  during the surveys. We used total length ( $L$ ) as a proxy for body size, which ranged from 26 mm to 60 mm (Fig. 3).

**Model selection**—We constructed a number of logistic models using various combinations of the above explanatory variables. Squared values of temperature and total length were included to examine suitability of quadratic functions in models. Ten models were constructed with different combinations of explanatory variables (Table 2).

The data set was divided into two halves by randomly allocating each of the 5,927 krill into one of two subsets. The models were fitted to one half of the data set and tested on the second half. The fitting procedures were carried out on subset 1 by the software package MINITAB v. 14 (Minitab) by determining the maximum likelihood of the model fitting the data. We carried out further tests on the accuracy and precision of model predictions by extracting 200 krill randomly from subset 2 and comparing the observed number of molters to the number predicted. These further tests were carried out 1,000 times for each model.

Models 1, 2, 8, and 10 were rejected at the fitting procedure stage because the routines failed to find any significant relationships. Our further tests found that model 7 underestimated observed  $IMP$  by 40% and model 9 overestimated  $IMP$  by 30%, and thus both were rejected. The four remaining models underestimated observed  $IMP$  by 2%.

Table 2. Logistic models fitted to the moult data set. Explanatory variables differ between each model. Each model was ranked according to its level of fit, accuracy of prediction, and number of explanatory variables (models with fewer variables ranked higher).

Model No.	Explanatory variables	Rejected (R)/ Accepted (A)	Ranking of model	Reason for rejection
1	L, L <sup>2</sup> , T	R	5	No significant relationships during fitting
2	L, L <sup>2</sup> , T, T <sup>2</sup> , F	R	5	No significant relationships during fitting
3	L, T, T <sup>2</sup> , F	R	3	Additional variable ( $F$ ) did not improve fit
4	L, T, F	R	3	Additional variable ( $F$ ) did not improve fit
5	L, T	R	2	Maximum likelihood of fit worse than model 6
6	L, T, T <sup>2</sup>	A	1	
7	L	R	4	Underestimation of $IMP$ by 40%
8	L, L <sup>2</sup>	R	5	No significant relationships during fitting
9	T	R	4	Overestimation of $IMP$ by 30%
10	T, T <sup>2</sup>	R	5	No significant relationships during fitting

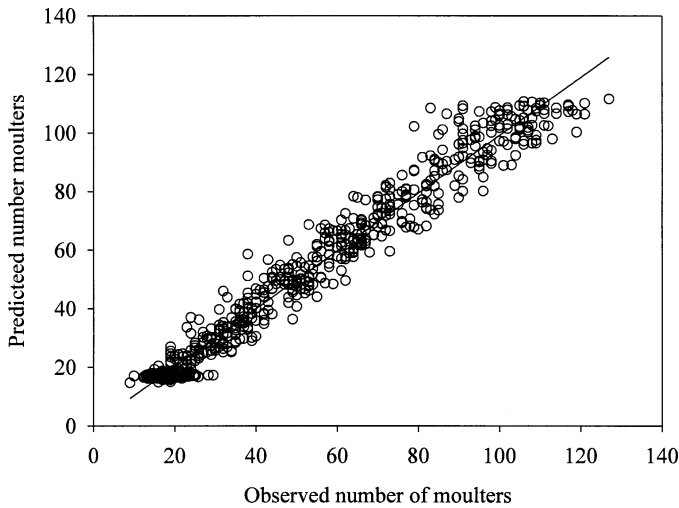


Fig. 4. The observed and predicted number of molters in simulated experiments containing different numbers of randomly selected krill monitored for 5 d. The *IMP* model (Table 3) was used to make the predictions.

We excluded the two models containing the food proxy ( $F$ , mean SeaWiFS Chl  $a$ ), since this additional explanatory variable added little to our predictive capability. Of the two remaining models, we selected model 6 over model 5 since its maximum likelihood value during the fitting procedure was better. The functional form of model 6 is

$$P = \frac{e^{a+bL+cT+dT^2}}{1 + e^{a+bL+cT+dT^2}} \quad (7)$$

Equation 7, when used with the best-fitting constants and coefficients, underpredicted the number of molters in any one experiment by 2% (SD 9%). We tried to eliminate this bias by subdividing the data set according to maturity stage and fitting model 6 to each stage separately. The data set was divided into three maturity stages: females, males, and juveniles. The performance of the maturity stage models was tested on 1,000 subsets of 200 randomly chosen animals, as described above. The predictions of these models were an improvement, since they differed from observations by an average of 0.1% (SD 9%).

**Model robustness and sensitivity**—Observed variation in the molt behavior of individuals within our data set may stem from a variety of sources. We examined some of these sources by dividing the entire krill data set according to various criteria and comparing the predicted and observed number of molters in each division. We focused on three major sources of variation: size of experimental population, total body length, and temperature.

**Experimental population size:** Our incubation experiments contained varying numbers of krill depending on how many healthy specimens were contained in net catches. We simulated this situation by creating 500 subsets of between 50 and 375 individuals chosen randomly from the entire data set. The observed and predicted number of molters in each subset was calculated and compared. Regressing the ob-

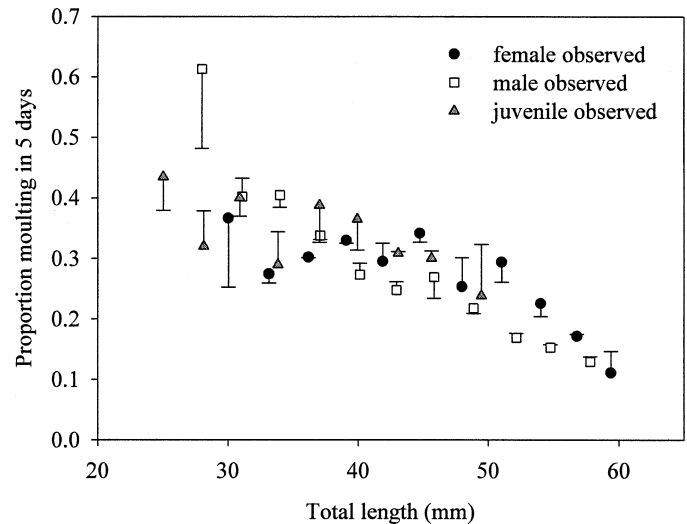


Fig. 5. The observed (symbols) and predicted (end-bar of vertical lines) proportion of molters in 3-mm increments of the female, male, and juvenile data sets. The *IMP* model (Table 3) was used to make the predictions. Observed and predicted proportions are based on 5 d of monitoring.

served (*Obs*, individuals) against the predicted (*Pre*, individuals) values produced a slope close to 1 and a y-intercept close to 0 ( $Obs = 0.62 + 0.99 \cdot Pre$ ,  $R^2 = 0.95$ ,  $p < 0.0001$ ; Fig. 4). We concluded that there was little bias in model predictions as a result of varying the number of krill in each experiment.

**Effect of total body length:** There was a wide range of krill lengths within the data set, and we investigated whether the accuracy and precision of model predictions were equal throughout this range. The male, female, and juvenile data sets were subdivided into 3-mm increments and the number of observed and predicted molters in each increment were determined. This value was expressed as a proportion by relating it to the total number of molters in the respective increment.

Predicted values were spread evenly on either side of the observed values in males and juveniles, with an average difference of 0.02 (Fig. 5). There was less accuracy in the case of females, with predictions becoming increasingly larger than observations as total length increased, reaching a difference of 0.1 above 55 mm. The majority of individuals in this upper size range were mature, reproductive females (IIC, D and E, according to Makarov and Denys [1980]; FA3–5 according to Morris et al. [1988]). To minimize this bias, we separated the female data into two subsets: one containing mature females and the other all remaining females, which included subadults and those with immature ovaries. Equation 7 was fitted to these two data sets separately. This improved the accuracy of the fit, with the difference between observed and predicted proportions being reduced to a maximum of 0.04 in the upper size classes (Fig. 5). The resulting level of fit between observed and predicted proportions of female molters was significant ( $R^2 = 0.66$ ,  $F_{8,2} = 8.76$ ,  $p < 0.02$ ), as was that in males ( $R^2 = 0.90$ ,  $F_{8,2} = 39.02$ ,  $p < 0.0001$ ). Although predictions were free of

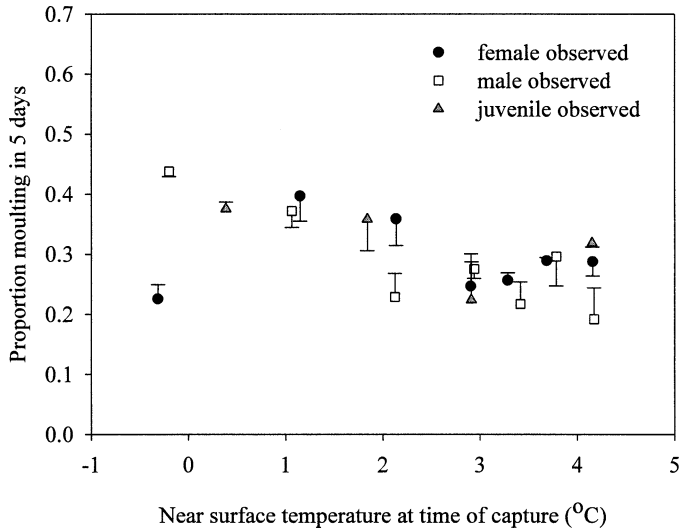


Fig. 6. The observed (symbols) and predicted (end-bar of vertical lines) proportion of molters in 0.75°C increments of the female, male, and juvenile data sets. The *IMP* model (Table 3) was used to make the predictions. Observed and predicted proportions are based on 5 d of monitoring.

bias in juveniles, they were relatively imprecise ( $R^2 = 0.23$ ,  $F_{6,2} = 1.05$ ,  $p > 0.5$ ), which reflects the fact that length is not the most important determinant of *IMP* in juveniles.

Effect of temperature: Krill were not distributed evenly over the range of surface temperatures in which experiments were conducted. Smaller juveniles were most abundant in colder waters, larger animals more prevalent in warmer waters. We investigated the importance of this potential bias by determining the proportion of predicted and observed molters in temperature increments of approximately 0.75°C. Calculations were carried out on each maturity stage separately.

In each maturity stage, predictions were distributed evenly around observations in all parts of the temperature range (Fig. 6). The average difference between the predicted and observed proportions of molters was 0.02. The  $R^2$  values for females and males were similar to those in the total length analysis (see above), while those for juveniles were higher. None were significant (Females  $R^2 = 0.66$ ,  $F_{4,2} = 3.81$ ,  $p > 0.5$ ; Males  $R^2 = 0.81$ ,  $F_{4,2} = 8.45$ ,  $0.05 < p < 0.1$ ; Juveniles  $R^2 = 0.49$ ,  $F_{1,2} = 0.49$ ,  $p > 0.5$ ), but the comparatively low degrees of freedom indicate that this may be Type II error (i.e., the true difference being masked by the low number of samples). Overall, the model was successful at predicting the proportion of molters throughout the temperature range of  $-0.85^\circ\text{C}$  to  $4.75^\circ\text{C}$ .

Effect of incubation on *IMP*—We tested the effect of incubation on *IMP* by determining the proportion of molters on each incubation day for each experiment. A one-way analysis of variance (ANOVA) found there to be no statistical difference between the proportions found on each day ( $F_{4,255} = 1.318$ ,  $p = 0.264$ ). As a result, we assumed that *IMP* was unaffected by the incubation conditions. We did not consider it necessary to make any adjustments to the model to take incubation time into account.

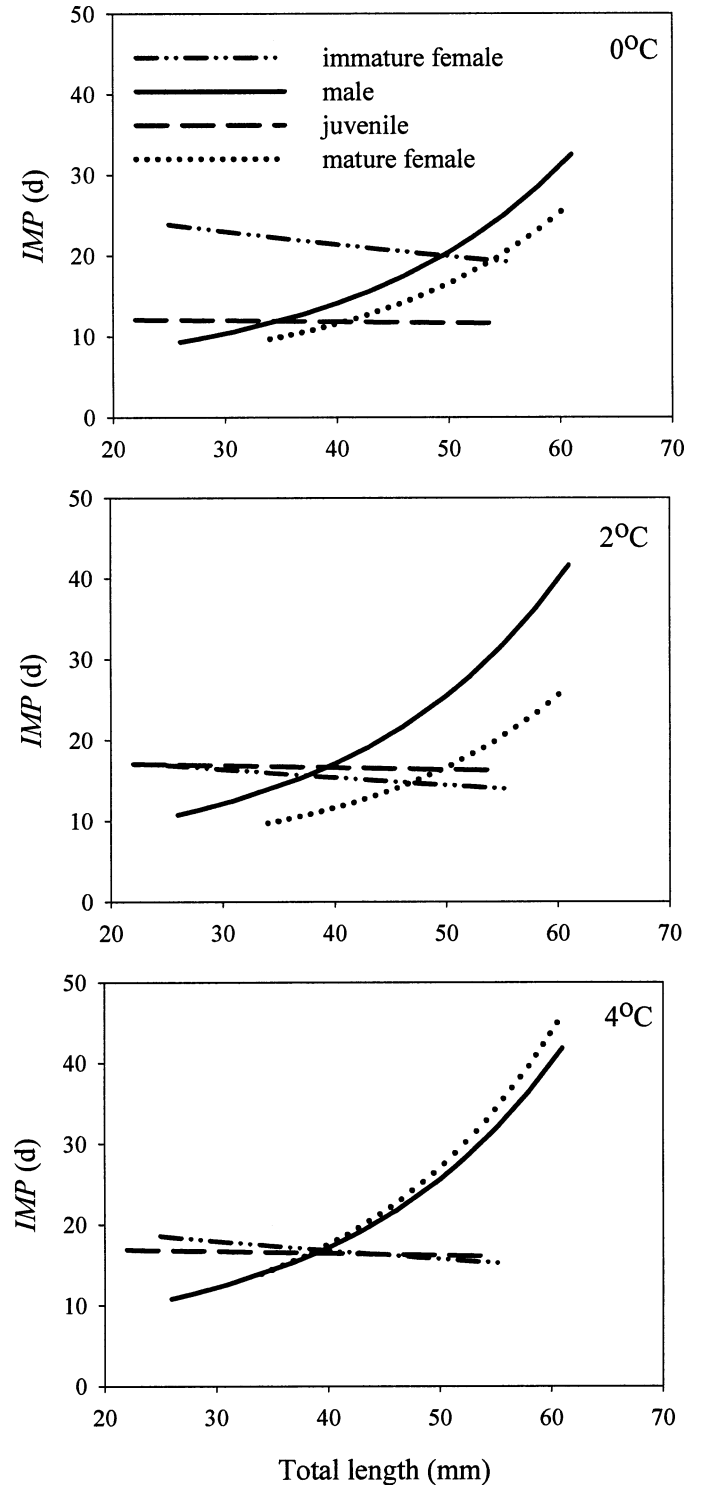


Fig. 7. The relationship between *IMP* and total length (mm) for different maturity stages at 0°C, 2°C, and 4°C, as predicted by the *IMP* model (Table 3).

Model predictions—The model predicts the *IMP* of a krill as a function of total length and the near-surface temperature at time of capture. Figures 7 and 8 illustrate the separate influence of each of these variables, through altering one variable while fixing the other.

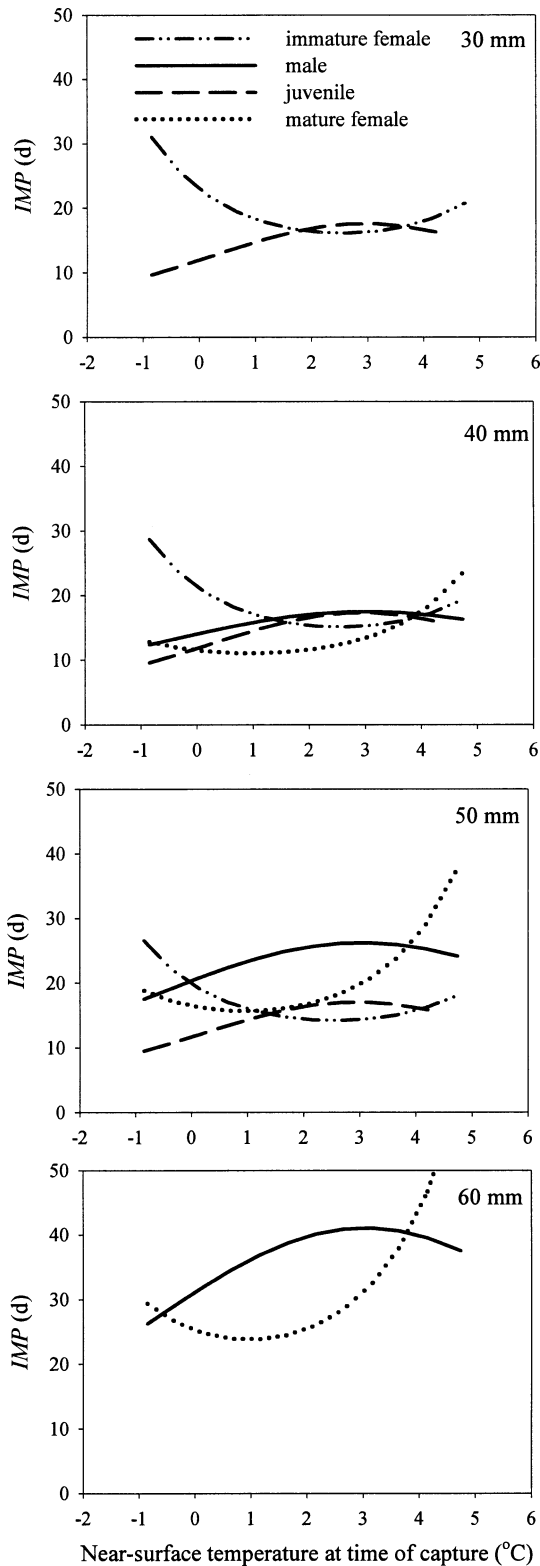


Fig. 8. The relationship between *IMP* and near-surface temperature at time of capture ( $^{\circ}\text{C}$ ) for 30-mm, 40-mm, 50-mm, and 60-mm krill of different maturity stages, as predicted by the *IMP* model (Table 3). Note that not all sexes/maturity stages are present in the upper and lower size categories.

The influence of total length on *IMP* differed according to maturity stage. For mature krill, *IMP* increased at an accelerating rate as individuals became larger. In Fig. 7, *IMP* increased from 10 d to 25 d in mature females and from 10 d to 35 d in males at  $0^{\circ}\text{C}$  and  $2^{\circ}\text{C}$ . The *IMP* of mature males was around 8 d ( $\sim 50\%$ ) longer than that of equivalently sized mature females. The *IMP* of immature individuals varied little with length. At  $2^{\circ}\text{C}$ , juveniles molted every 12–13 d, whereas immature and subadult females molted every 14–17 d.

The response to temperature differed mainly between sexes (Fig. 8). Mature and immature/subadult females show a minimum *IMP* toward the midpoint of the temperature range ( $\sim 2^{\circ}\text{C}$ ) and increased toward the upper and lower temperature extremes. Juveniles and males were less affected by temperature, although *IMP*s tended to be slightly shorter in colder waters. Mature female krill have one of the shortest *IMP*s of any maturity stage through most of the temperature range. The difference between male and female *IMP* is greatest at midpoint temperatures in the largest size categories, where male *IMP* is almost double that of females.

*Implementation of IMP model*—The constants and coefficients that were fitted to the data sets of each maturity stage are provided in Table 3, along with the method for implementing the model. We applied this model to the original data set, experiment by experiment, to compare its performance with the  $1/MR$  method (Fig. 9). The maximum *IMP* predicted for any experiment by the model was 46 d, as opposed to 177 d by the  $1/MR$  method. The minimum predicted by the model was 12 d, whereas two experiments had *IMP*s of less than 6 d according to the  $1/MR$  method. Nevertheless, both approaches found that most experiments had *IMP*s of between 16 and 20 d and both had medians of 18 d. The consistency at midrange values shows that there is little evidence of bias with the two methods. However, the *IMP* model is more precise, because its *IMP* estimates are free of the potential error from molt synchrony.

*Percent growth increment (GI)*—*GIs* decreased significantly during the incubation period (Fig. 10). Compared with incubation day 1, the mean *GI* fell by an average of 26% by day 3 and by more than 50% by day 5. The rate of decrease in *GI* over time was greatest in those animals with the highest mean rates of growth (Fig. 11). The growth increments of individuals with high *GI* (4.5–12%) at the start of the experiment fell at a rate of around  $1\% \text{ GI d}^{-1}$  (ANOVA,  $F_{1,55} = 16.88$ ,  $p < 0.05$ ), whereas those with a medium *GI* (2.5–4.5%) fell at a rate of around  $0.4\% \text{ d}^{-1}$  (ANOVA,  $F_{1,102} = 24.06$ ,  $p < 0.05$ ). A significant drop in *GI* over the incubation period was not detected in krill with initial *GIs* of less than 2.5%.

Determining the true *GI* of a krill, as it would have existed in natural conditions (in situ), therefore requires adjustment to allow for (1) the time between capture and molting and (2) whether or not the animal was growing rapidly. To achieve this, we developed a simple correction that could adjust measured *GI* values ( $GI_{\text{obs}}$ ) to an equivalent had the krill remained in situ ( $GI_{\text{in situ}}$ , defined as the value at time of capture). As a first step, the rate of decline in *GI* in each

Table 3. A method for determining the *IMP* of krill based on a number of influential factors. The method is valid for krill between 26 mm and 60 mm in total length.

**Step 1**

Obtain data

- (i) krill total body length (*L*, front of eye to tip of telson)
- (ii) maturity (Morris et al. 1988)
- (iii) surface temperature at time of capture (*T*)

**Step 2**

Divide data set into subsets according to maturity stage

- (i) juvenile, (ii) male (MS and MA), (iii) subadult (FS) and immature (FA1–2) female, (iv) mature female (FA3–5)

**Step 3**

Determine probability of moult (*P*) for each krill as a function of temperature (*T*) and body length (*L*)

$$P = \frac{e^{a+bL+cT+dT^2}}{1 + e^{a+bL+cT+dT^2}}$$

- (i) juvenile:  $a = -0.392315$ ,  $b = 0.0021159$ ,  $c = -0.404726$ ,  $d = 0.0687522$
- (ii) male:  $a = 1.52581$ ,  $b = -0.0529790$ ,  $c = -0.213042$ ,  $d = 0.0350464$
- (iii) subadult/immature female:  $a = -1.55926$ ,  $b = 0.0093231$ ,  $c = 0.375765$ ,  $d = -0.0733018$
- (iv) mature female:  $a = 2.00098$ ,  $b = -0.0566740$ ,  $c = 0.152815$ ,  $d = -0.0786357$

**Step 4**

Convert to *IMP*

$$IMP = \frac{d}{P} \quad \text{where } d = 5 \text{ d}$$

**Step 5**

Where the *IMP* of the experiment is required, average the *IMP*s of all individuals.

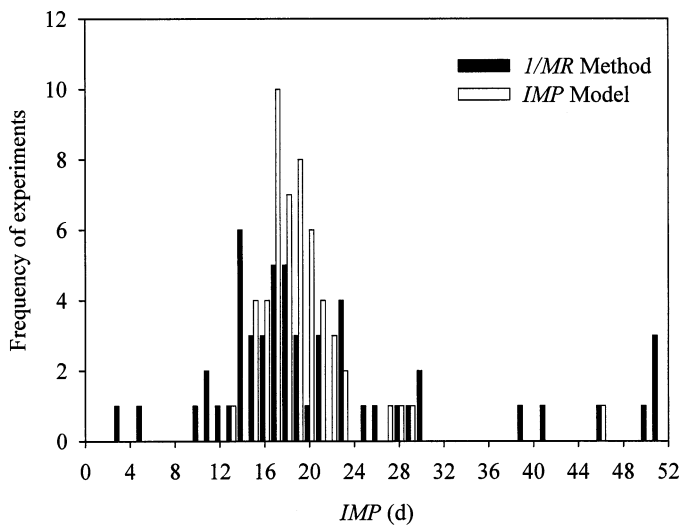


Fig. 9. The frequency of occurrence of different *IMP* estimates among experiments. The 1/MR method and the *IMP* model were used to calculate the *IMP* of each experiment.

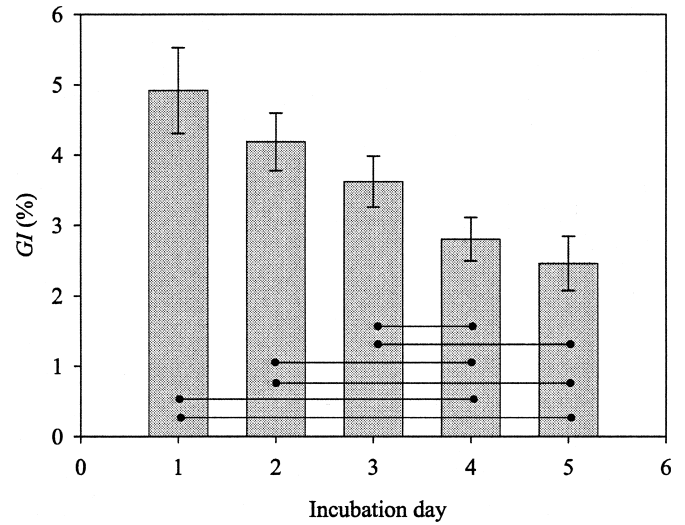


Fig. 10. The percent growth increment (*GI*) on each incubation day averaged over all experiments. A Kruskal–Wallis ANOVA on ranks found a significant difference between days ( $H_4 = 62.73$ ). Horizontal “dumbbell” lines indicate which days were significantly different from each other (Dunn’s method: all pairwise multiple comparison procedure). Vertical lines indicate  $\pm 95\%$  confidence intervals.

experiment ( $\Delta GI$ ) was determined as a function of incubation time (in hours) in each of the experiments in which more than 10 molters were observed (this reduced the original 51 experiments to 37). A linear regression was fitted to each of the experiments and coefficients of between  $-0.01$  to  $0.08$  were obtained (a positive value indicating *GI* declined with time). We also calculated the arithmetic mean *GI* ( $\bar{GI}$  in %) for the first 5 d of incubation in each experi-

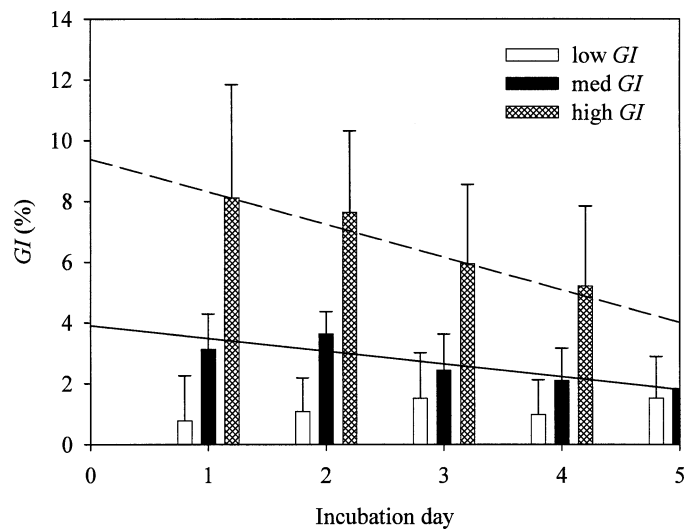


Fig. 11. *GI* versus incubation day for experiments with high *GI* values ( $>4.5\%$ ; horizontal lines), medium values ( $2.5\text{--}4.5\%$ ; cross-hatched), and low values ( $<2.5\%$ ; diagonal lines). Solid and dashed lines represent significant regressions for high and medium *GIs*, respectively. There was no significant relationship over time for low *GIs*. Errors bars denote  $\pm 1$  SD.

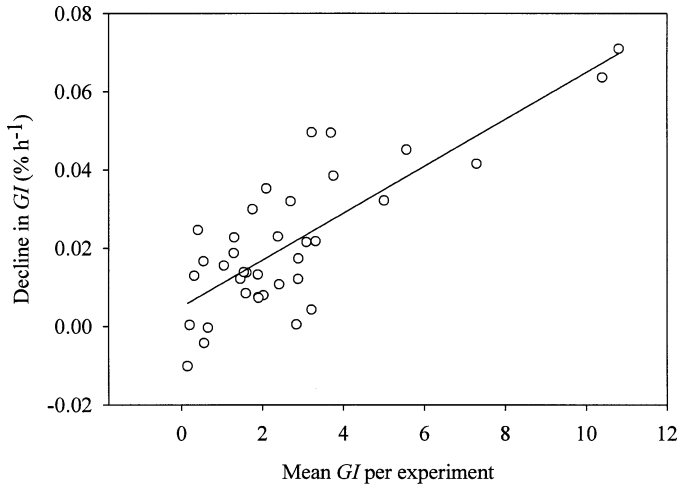


Fig. 12. The change in  $GI\ h^{-1}$  as a function of the mean  $GI$  of the respective experiment (averaged over 5 d of incubation).

ment and plotted it against  $\Delta GI$  (Fig. 12). The relationship was significant (ANOVA,  $F_{1,35} = 60.15$ ;  $p < 0.05$ ), with the rate of decline in  $GI$  relating to the mean  $GI$  in each experiment, as follows:

$$\Delta GI = -0.005 + (0.006 \cdot \overline{GI}) \quad R^2 = 0.64 \quad (8)$$

We can predict  $GI_{in\ situ}$  for each krill in each experiment through, first of all, estimating the total amount of decline that has occurred since capture and then adjusting  $GI_{obs}$ , as follows:

$$GI_{in\ situ} = GI_{obs} + (\Delta GI \cdot h) \quad (9)$$

where  $h$  is the time between capture and molt (in hours).

The implications of this result are (1) that the  $GI$  of a krill will decline as soon as it is caught and (2) that this rate of decline will be greater if the krill's initial growth rate was higher.

*Application of the correction factor to experiment-specific GI estimates*—Experimental means of  $GI_{obs}$  varied between 0.6% and 15.2% (Fig. 13), with an overall average of 2.6%. At this mean rate, a 40-mm krill would lengthen by 1 mm at molt. When  $GI$  values were adjusted to take experimental effects into account (i.e.,  $GI_{in\ situ}$ ), the overall average increased to 3.9%. This would result in a 40-mm krill growing by 1.5 mm at its next molt. Postlarval krill typically molt between 8 and 10 times in a summer season, which means that the correction could make as much as a 5-mm difference in the annual growth estimate.

*Calculation of daily growth rate (DGR  $mm\ d^{-1}$ )*—DGR can be calculated by combining  $IMP$  and  $GI$ , as given in Eq. 2. The following four DGRs were calculated to distinguish between the effects of  $GI$  and  $IMP$  corrections: (1) original  $GI$  and  $1/MR$  method estimate of  $IMP$ ; (2) corrected  $GI$  and  $1/MR$  method estimate of  $IMP$ ; (3) original  $GI$  and model estimate of  $IMP$ ; and (4) corrected  $GI$  and model estimate of  $IMP$ .

DGR calculations were carried out for every individual

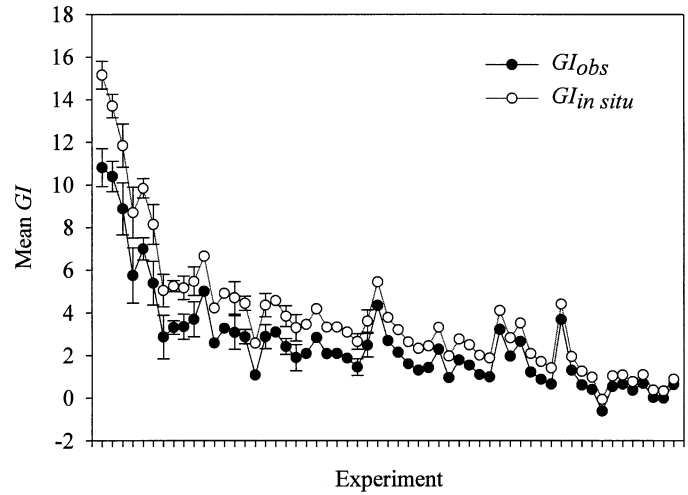


Fig. 13. Comparison of the mean  $GI$  observed in IGR experiments ( $GI_{obs}$ ) and the  $GI$  corrected to the likely in situ values ( $GI_{in\ situ}$ ). Bars indicate 95% confidence intervals and are plotted only in instances in which there is no overlap between observed and corrected values. Experiments are ordered along the x-axis according to the difference between the two estimates of  $GI$ , the largest difference being toward the left-hand side.

that molted during the incubations. All DGR estimates were derived for the premolt length ( $L_{pre}$ ) of krill. This was not measured directly but can be estimated through taking measured  $GI$  away from the measured total length ( $L$ ), as follows:

$$L_{pre} = \frac{L \cdot 100}{100 + GI} \quad (10)$$

The DGR of an experiment was derived as the average DGR of all individuals in that experiment.

The corrections increased estimated individual DGRs by 20%, from an average of 0.09  $mm\ d^{-1}$  to 0.11  $mm\ d^{-1}$  (Table 4; Fig. 14). Of the two growth parameters, the correction of  $GI$  had most influence on the new estimate of growth. Nev-

Table 4. Summary of daily growth rates estimates (DGR,  $mm\ d^{-1}$ ) based on a sample set of all individuals that molted during the experiments (above) and on a sample set of average DGRs per experiment (below). DGR is calculated using different combinations of the original and corrected estimates of  $GI$  and  $IMP$ .

	Original $GI, 1/MR$	Corrected $GI, 1/MR$	Original $GI,$ model $IMP$	Corrected $GI,$ model $IMP$
Individuals				
Mean	0.09	0.14	0.08	0.11
SD*	0.11	0.13	0.08	0.09
Minimum	-0.24	-0.14	-0.13	-0.09
Maximum	0.87	0.87	0.45	1.00
Experiments				
Mean	0.07	0.10	0.06	0.09
SD	0.08	0.11	0.05	0.06
Minimum	-0.01	0.00	-0.01	0.00
Maximum	0.31	0.45	0.24	0.32

\* SD, standard deviation.

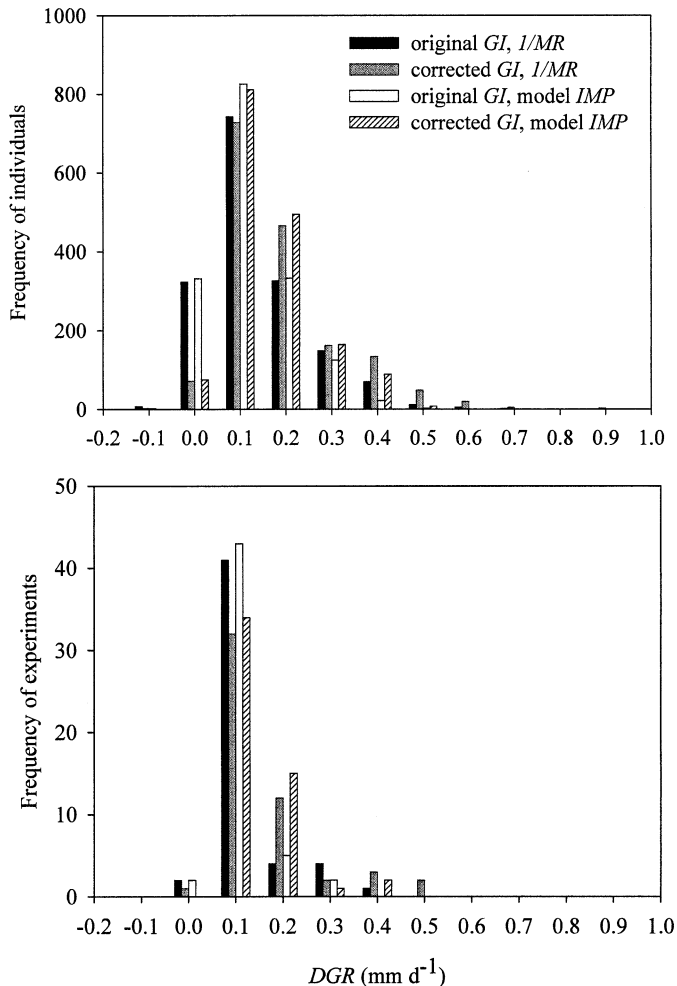


Fig. 14. The frequency of occurrence of different estimates of daily growth rate ( $DGR$ ,  $\text{mm d}^{-1}$ ) among individuals (upper) and experiments (lower).  $DGR$  was calculated in four different ways according to whether  $GI$  was the original or the corrected estimate and  $IMP$  was the  $1/MR$  method or the model estimate. The  $DGR$  of an experiment represents the average  $DGR$  of all individuals within that experiment.

ertheless, correcting  $IMP$  made substantial differences to certain experiments, reducing some particularly high growth rate values (e.g., 0.27, 0.31  $\text{mm d}^{-1}$ ) to ones that were more moderate (0.11, 0.12  $\text{mm d}^{-1}$ , respectively).

## Discussion

Our study has shown that three major factors affect the  $IMP$  of postlarval krill in summer: temperature, body length, and the sex/maturity stage. We established functional relationships between  $IMP$  and these factors to produce a simple model that is capable of predicting  $IMP$  based on easily obtainable information. A method that considers the multiple controls on  $IMP$  is an improvement on previous studies, in which only relationships with a single factor, mainly temperature, were taken into account (Buchholz 1991; Quetin et al. 1994). Furthermore, our model overcame problems, such

as molt synchrony, that have prevented the calculation of  $IMP$  in previous  $IGR$  experiments.

The most useful unit of growth for population dynamics is  $\text{mm d}^{-1}$ . Although users of the  $IGR$  technique can calculate this value by dividing the  $GI$  (converted into  $\text{mm}$ ) by the  $IMP$ , many chose not to do so because  $IMP$  measurements were potentially biased. Our new method allows this calculation to be performed with greater confidence. Past as well as future  $IGR$  experiments now have the capacity to produce growth measurements in  $\text{mm d}^{-1}$ , which allows results to be compared with other techniques of measuring growth.

Our study demonstrated that growth is reduced even within the first few days of incubation. This effect was most dramatic in those animals that were growing the fastest. We constructed an algorithm, built as a function of the day of incubation and the rate of growth, which corrected for this error (Eq. 9). Below, we discuss first the controls on  $IMP$  and second the modifications to  $IGR$  methodology that improve our ability to estimate daily growth rate in natural krill populations.

*Influence of temperature, body length, and maturity on  $IMP$* —Several studies have indicated that temperature has a strong influence on  $IMP$  (Poleck and Denys 1982; Ikeda et al. 1985; Buchholz 1991; Quetin et al. 1994, and references therein), with  $IMP$  decreasing as conditions warm. Quetin et al. (1994) considered the pattern regular enough to calculate a  $Q_{10}$ , deriving a value of 3.5. We found that the pattern of decreasing  $IMP$  with increasing temperature was far from regular.  $IMP$  decreased as temperature increased from  $-1^{\circ}\text{C}$  to  $2^{\circ}\text{C}$  in immature and adult females, a result that is in line with the findings of Quetin et al. (1994). However, this trend reversed above  $2^{\circ}\text{C}$ , and  $IMP$  increased as temperature increased. Temperature had less of an effect on the  $IMP$  of juveniles and males, although if anything, there was a slight increase in  $IMP$  with increasing temperature. The complexity of these results indicates that molt rate is not simply a function of metabolic rate but rather a trait under maturity- and sex-specific selective pressures.

$IMP$  increased rapidly with increasing length in adult males and females. In juveniles and immature females, however,  $IMP$  barely altered over the entire range of total lengths. A simple explanation is that somatic growth is pre-programmed to slow once a certain age or maturity has been reached, and  $IMP$  becomes longer as a result. In addition, Antarctic krill divert considerable resources to reproductive tissue when reaching adulthood (Virtue et al. 1996; Cuzin-Roudy 2000). The decrease in surplus energy means that somatic growth will inevitably slow.

We found that the  $IMP$ s of adult males could be up to twice as long as those of females at certain sizes and temperatures (Figs. 7, 8). The phenomenon may be explained by the interlinking of spawning and molting, first proposed for northern krill (*Meganctiphanes norvegica*) by Cuzin-Roudy and Buchholz (1999). They demonstrated that spawning mainly occurs in the D2 molt stage in every other molt cycle. The interlinking of spawning and molting results in a situation in which processes governing molt rate in females are different from those observed in males. An acceleration

Table 5. A calculation of the energy lost through maintaining a 40-mm krill in filtered seawater during the course of an *IGR* experiment. The calculation is based on the assumption that the *IMP* is 20 d. Energy used for growth was determined as the difference between the average energetic content of (i) a 40-mm krill and (ii) a 40-mm multiplied by *GI*; total length (*L*) was converted to joules through converting body length to dry weight, *DW* ( $DW = 1.41 \cdot 10^{-6} L^{2.98}$ , Kils 1981), and then *DW* to joules, *J* ( $J = 25.12 \cdot DW$ ; Norrbin and Bämstedt, 1984). Energy for metabolism was calculated using Kils (1981). The sum of the energy for growth and for metabolism was taken as the energy obtained per unit time had the animal remained in situ. The remainder of the calculation determines what effect incubating the animal in filtered seawater had on *GI* through reviewing two scenarios: (a) when the animal moulted on incubation day 2 and (b) when the animal moulted on incubation day 5. Predicted values are compared to the decrease in growth observed in the *IGR* experiments, described by Eq. 8.

$GI_{in\ situ}$ (%)	Energy used for growth in situ ( $J\ IMP^{-1}$ )	Energy for metabolism ( $J\ d^{-1}$ )	Total energy assimilated in situ ( $J\ d^{-1}$ )	Day of moult (incubation day)	Lost energy through starvation ( $J\ IMP^{-1}$ )	Predicted en- ergy available for growth ( $J\ IMP^{-1}$ )	Predicted <i>GI</i> (%)	Predicted change in <i>GI</i> $h^{-1}$	Observed change in <i>GI</i> $h^{-1}$ in <i>IGR</i> experiments
5	363.3	7.5	25.7	2	51.4	311.9	4.3	-0.014	-0.035
5	363.3	7.5	25.7	5	128.5	234.7	3.3	-0.014	-0.035
1	68.8	7.5	11.0	2	22.0	46.8	0.7	-0.007	-0.011
1	68.8	7.5	11.0	5	55.0	13.8	0.2	-0.007	-0.011

of the ability to mature eggs in stage D2, for instance, may result in females increasing their molt rate, whereas in less suitable conditions for egg maturation, molt rate may slow down. The concurrent molt rate of males may be less affected by such conditions, making it faster in some circumstances and slower in others.

Patterns of food availability across the Scotia Sea did not help in explaining the observed variability in *IMP*. Furthermore, we found that *IMP* was unaffected by the starvation conditions during incubation, since there were no statistically significant differences in the number of molters between days. This indicates that *IMP* in krill is relatively inflexible in the shorter term and that longer term factors, such as prevailing temperature, maturity, and body length, have a greater influence. By contrast, the relationship between food availability and *GI* found by Atkinson et al. (this issue) shows that *GI* is probably more responsive to immediate conditions. This is supported by observations in the present study in which starvation conditions in the *IGR* experiments contributed to an instantaneous and dramatic decrease in *GI*. Altering *GI* rather than *IMP* in response to food is a pattern common to many euphausiids (Buchholz 1985). The pattern contrasts with that of many other Crustacea, in which varying food affects mainly *IMP* (Hartnoll 1982).

The present study was carried out in summer, when the highest growth rates are achieved. In winter, when growth is more limited, the relationship between *IMP* and food availability may be stronger. Quetin et al. (2003) found that half of the extremely long *IMPs* observed in wintertime *IGR* experiments came from larvae in open water (as opposed to under ice), where food levels were probably very low. Accompanying experiments showed that the mean molting frequency of fed larvae was 4.4% per day, whereas that of starved larvae was 1.5% per day. Nevertheless, Thomas and Ikeda (1987) found that maintenance in food-limited conditions did not prevent krill from rematuring and reducing their *IMP* in spring. Combining these observations, it appears that there is a switch between a winter mode, in which *IMP* is slower but can respond to food variations, and a summer mode, in which *IMP* is faster but relatively inflexible. Internal processes, such as hormones, rather than ex-

ternal cues, such as food availability, probably drive the switch (Thomas and Ikeda 1987; Cuzin-Roudy et al. 2004). The capability to alter *IMP* may be important in winter, when resources are low and the costs of molting relatively high.

*Effect of incubation on GI*—We found that *GI* decreases as soon as the animal is starved in laboratory conditions. If we assume that the sum of the energy collected over the entire *IMP* determines the size of the next exoskeleton, then this decrease could be explained on energetic grounds, because the krill is being deprived of food for up to 5 d. We tested this idea with an energetic model, which calculated the energy lost through maintaining krill in filtered seawater (Table 5). We found that depriving a 40-mm krill of food for 48 h would reduce a 5% *GI* to 4.3% after 48 h and to 3.3% after 120 h. Furthermore, those animals growing the fastest would be most affected, which is in line with the results of the present study. Although the predictions of the energetic model are not exactly the same as our observations, it gives a reasonable first-order approximation of the changes in *GI* observed in the incubated animals. A tighter fit may be achieved through better parameterization, especially of metabolism, for which experimental biases have yet to be accounted for (Kils 1981). Overall, it is reasonable to assume that the induced starvation is the main cause of the observed decrease in *GI* during the *IGR* experiments and that this effect is instantaneous.

*New estimates of DGR and their implications*—Estimates of *DGR* increased by 20% once the *IMP* model and *GI* correction factors had been implemented. On average, *DGRs* rose from 0.09 mm d<sup>-1</sup> to 0.11 mm d<sup>-1</sup>. *IGR* experiments carried out by Ross et al. (2000) found average rates of around 0.08 mm d<sup>-1</sup> and maximum rates close to 0.13 mm d<sup>-1</sup>. Growth models by Ikeda (1985) and Pakhomov (1995) predicted similar values. Therefore, corrected growth estimates in the present study remain within the normal range of variability observed elsewhere. Interestingly, the average *DGRs* of some of our experiments remained very high even after correction (uncorrected: 0.31, 0.28 mm d<sup>-1</sup>; corrected: 0.32, 0.30 mm d<sup>-1</sup>, respectively). Clarke and Morris (1983)

reported a similarly high value at South Georgia ( $0.33 \text{ mm d}^{-1}$ ), but others considered the result a reflection of imprecise methods (Nicol 2000).

The findings of the present study have not always agreed with those reported previously. For instance, the  $Q_{10}$  relationship between *IMP* and temperature proposed by Buchholz (1991) and Quetin et al. (1994) did not fit the present data set, but we did find an alternative pattern in which *IMP* increased either side of an optimum temperature ( $\sim 2^\circ\text{C}$ ) in immature and mature females and changed very little in males and juveniles. The profound implications of this result merit further investigation. Gender was found to produce a twofold difference in *IMP* of similarly sized krill, with females molting at higher rates than males. Such large differences have not been reported in laboratory incubations (Buchholz et al. 1996). *GI* was found to be very responsive to environmental conditions and was reduced by even 1–2 d of starvation. Previous studies did not consider this response to be so instantaneous (Nicol et al. 1992).

In addition to making ecological observations, our main aim was to provide information that will allow future krill investigators to estimate growth parameter values from straightforward, easily obtainable measurements. Our results illustrated that it is unjustified to predict *IMP* from models based on one factor alone, for example, the temperature models of Buchholz (1991) and Quetin et al. (1994), since they are likely to produce erroneous results where body size and maturity vary. Furthermore, averaging at the level of an *IGR* experiment or series of experiments is likely to cause investigators to miss a great deal of the inter-individual variability that is fundamental to the understanding of krill growth. Our model overcomes these difficulties, since *IMP* is predicted for each individual krill as a function of a number of influential factors.

The other purpose of this work was to provide the basis for an accompanying article by Atkinson et al. (this issue) that uses our best estimates of *GI* and *DGR* and determines functional responses with temperature, food, and maturity stage. Together these studies make a significant step toward the prediction of spatial patterns in krill growth from remotely accessed or satellite-derived information.

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Received: 14 February 2005

Accepted: 7 September 2005

Amended: 27 September 2005