

# AN ASSESSMENT OF THE MERITS OF LENGTH AND WEIGHT MEASUREMENTS OF ANTARCTIC KRILL *EUPHAUSIA SUPERBA*

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**ABSTRACT.** Published relationships of various length measurements as predictors of wet or dry weight in Antarctic krill *Euphausia superba* Dana are standardized with new data on the relationships of three length measurements to wet and dry weight as functions of sex, maturity stage and moult stage. The range of coefficients and exponents for these relationships are examined and an example given to indicate the potential such variation has for introducing error into estimates of biomass based on acoustic data. An alternative approach is examined in which length and additional biological data are assessed in terms of decreases in the residual variance of relationships. We have identified key sources of variability where relatively small increases in the effort of analysis result in large improvements in the precision of prediction. Surprisingly, the stage of the moult cycle of the animal has little effect upon length-weight relationships. The use of categories of sex and maturity stage, however, has a marked effect upon the residual variance. Again surprisingly, the simple division of krill into male and female categories is of little practical use in improving the precision of any prediction of weight. However, the separation of gravid females, either from male or non-gravid female krill or from adult male and other krill does result in a marked improvement in the precision of prediction. Example equations are provided.

## INTRODUCTION

Although many studies of Antarctic krill *Euphausia superba* Dana include reports of length measurement, the length of krill is often only of indirect interest: in these cases it is merely an intermediate step in the estimation of more important variables. In fisheries studies, for example, estimates of krill abundance and population dynamics (in the form of total biomass and production) are often expressed as wet weight, although derived from length data. In analyses of energetics, length is usually converted to dry weight, which may itself eventually be converted to weight of carbon or calorific value. Length data have also been used as an intermediate in the derivation of growth curves (Mackintosh, 1972; Mauchline, 1980; Rosenberg and

others, 1986), age classes (Siegel, 1986a) and as a predictor of potential swimming speed of krill (Kils, 1981a).

The measurement of length has been a prime tool in krill research for essentially operational reasons; it is easy and rapid to measure (although see Watkins and others, 1985, for an example of a simple, significant, systematic error) and can be related to several required variables by simple equations. It has often been used where the accurate direct measurement of the required variable was not feasible (e.g. weight at sea) or where direct measurements, either on board ship or at the home laboratory, would have been too labour-intensive for the analysis of large numbers of animals. The long history and broad international scope of krill research has led to the use of a bewildering variety of different measures of length (Mauchline, 1981; this paper, Fig. 1) and a large number of proposed relationships between them (Siegel, 1982a; Miller, 1983). Even an internationally co-ordinated attempt at standardization of length measurements for *E. superba* (Mauchline, 1981) omitted the standard measurement used by the *Discovery* expeditions. This measurement was adopted by British researchers specifically to facilitate direct comparison and is also used routinely by German and Polish workers (Siegel, 1982a).

The increasingly complex nature of the problems being addressed in krill research has led to a shift away from simple field analyses of length-frequency distributions. In addition to more complex field studies, detailed examination of preserved specimens and laboratory experiments on live krill have been undertaken. These studies utilize additional measures of length other than total length, for example uropod length for laboratory growth studies and carapace length for the analysis of the diets of krill predators. Recent work on the estimation of age of krill (Ettershank, 1984) has also indicated that the analysis of multiple morphometric measurements of *E. superba* may be a useful tool.

Morphological differences between the sexes of *E. superba* have been recognized as having an effect on the precision of the use of length as a predictor of mass. This is especially so for carapace length (Siegel, 1982a; Miller, 1983) but few published length-weight relationships take sex and maturity stage fully into account. Furthermore, despite much recent interest in the moult cycle of krill (Buchholz, 1982, 1985; Morris and Keck, 1984), no published work has acknowledged the potential importance of moult stage in morphometric relationships.

In this paper we have used data from a study of swarming in krill (Watkins and others, 1986) which required the analysis of a number of biological and morphometric parameters for each krill. The data set from this study provided a comprehensive set of equations relating both length-to-length and length-to-weight measurements for sex and a wide range of maturity stages and moult stages of *E. superba*. However, rather than simply contribute even more equations to the already large and confused literature, we have identified major sources of variation in the morphometric relationships and provided criteria for assessing which measurements to use for a particular application. Before such an exercise could be undertaken we felt it necessary to standardize all the existing morphometric literature for *E. superba*; this paper is therefore presented in two parts. The first examines simple morphometric relationships both in the literature and from this study; the second presents an assessment of the merits of various combinations of different length and weight measurements.

## DEFINITIONS

*Sex and maturity stage*

*Euphausia superba* can be classified by sex and, within each sex, by maturity stage (Makarov and Denys, 1981). For our data we have used an hierarchical alphanumeric code where the first letter indicates sex, the second the developmental stage and the number the maturity stage (Table I).

Table I. Codes and definitions for sex and maturity stages of *Euphausia superba*

Code	Definition	Makarov and Denys (1981)
J	Juvenile	J1
M	Male	M
MS	Male sub-adult	MII A
MS1	Male sub-adult stage 1	MII A (1)
MS2	Male sub-adult stage 2	MII A (2)
MS3	Male sub-adult stage 3	MII A (3)
MA1	Male adult stage 1	MIII A
MA2	Male adult stage 2	MIII B
F	Female	F
FS	Female sub-adult	FII B
FA1	Female adult stage 1	FIII A
FA2	Female adult stage 2	FIII B
FA3	Female adult stage 3	FIII C
FA4	Female adult stage 4	FIII D
FA5	Female adult stage 5	FIII E

*Moult stage*

Buchholz (1982) described 17 stages of the moult cycle which we have reduced to five broad categories. Category A is the immediate post-moult phase while BC is the phase of cuticle consolidation (late post-moult). For frozen specimens we have departed from Buchholz (1982) and included the first pre-moult stage (DO) with BC because it is often impossible to distinguish these stages. Early pre-moult (D1) is, however, clearly distinguishable as are the pre-moult (D2) and late pre-moult (D3) categories. The group D3 is equivalent to the stage D3-4 used by Buchholz (1982).

*Preservation*

The same length-to-length conversion equations were applied (see Appendices) irrespective of the preservation technique used. Formalin preservation has a negligible effect on the length of the krill in comparison with the accuracy of most measurements; Lockyer (1973) stated that shrinkage due to formalin preservation was approximately 1%. Miller (1983) also observed no significant change in length-to-length relationships before and after preservation. Where available, the preservation technique used has been noted in the Appendices.

*Regression equations*

Throughout this paper the predictive linear regression model was used in preference to the geometric mean regression model because we are concerned with,

for example, the prediction of weight from length, rather than the descriptive models underlying population relationships between weight and length (for a further discussion of this point see Ricker, 1973; Laws and Archie, 1981; Sprugel, 1983; Bird and Prairie, 1985; Jensen, 1986). Length-to-length and weight-to-weight relationships were examined on a linear basis whereas length-to-weight relationships were based on  $\log_{10}$ -transformed lengths and weights.

Length-weight raw data were pooled for some sexes where no significant differences were detected between the component stages, for example, MS1, MS2 and MS3 were grouped together in a new category, male sub-adult (MS). Where there were significant differences between length-weight regressions for the various sexes, data were not pooled unless comparison with published equations was required, for example all male krill, all female krill and all krill.

## MATERIALS AND METHODS

### *Sampling*

Krill were obtained from a small area to the south-west of Elephant Island (approximately 61° 30' S, 56° 30' W) between 24 February and 9 March 1985 using a large Longhurst-Hardy Plankton Recorder (Bone, 1986). A detailed description of the sampling location and techniques was provided by Watkins and others (1986).

### *Krill analysis*

Freshly collected krill were frozen at  $-60^{\circ}\text{C}$  individually in compartmented plastic trays. Upon return to the UK more than 3000 krill were weighed frozen (precision  $\pm 0.1$  mg) and the total length ((AT) anterior eye to tip of telson) measured to the nearest millimetre below. A portion of the sixth abdominal segment and the uropods and telson were removed from the frozen animal and kept separately at  $-60^{\circ}\text{C}$  for moult staging. This was done using a modification of the Buchholz (1982) technique tailored specifically to deep frozen specimens. The total length of the uropod (S7) was determined microscopically (precision  $\pm 0.1$  mm) during the moult staging process. The remainder of each specimen was then sexed and maturity staged according to Makarov and Denys (1981) and the carapace length (S4) measured using a binocular microscope (precision  $\pm 0.1$  mm). Both parts of the krill were then freeze dried separately for at least 24 h before being weighed (precision  $\pm 0.1$  mg).

## THE TRADITIONAL APPROACH TO MORPHOMETRIC RELATIONSHIPS

Studies of the morphometry of *Euphausia superba* have generally examined the single relationships between weight and length irrespective of sex and maturity stage. In a limited number of cases, different relationships for each sex were given while in other instances separate relationships were given for each haul, although the reason for this was often not clear. In this section we have drawn together as many published relationships as possible and presented them in a standard form which allows direct comparison both between them and with our own extensive data set.

### *Length-length relationships*

The precise definitions, codes and a visual representation of the various length measurements of krill are presented in Fig. 1. To simplify the comparison of

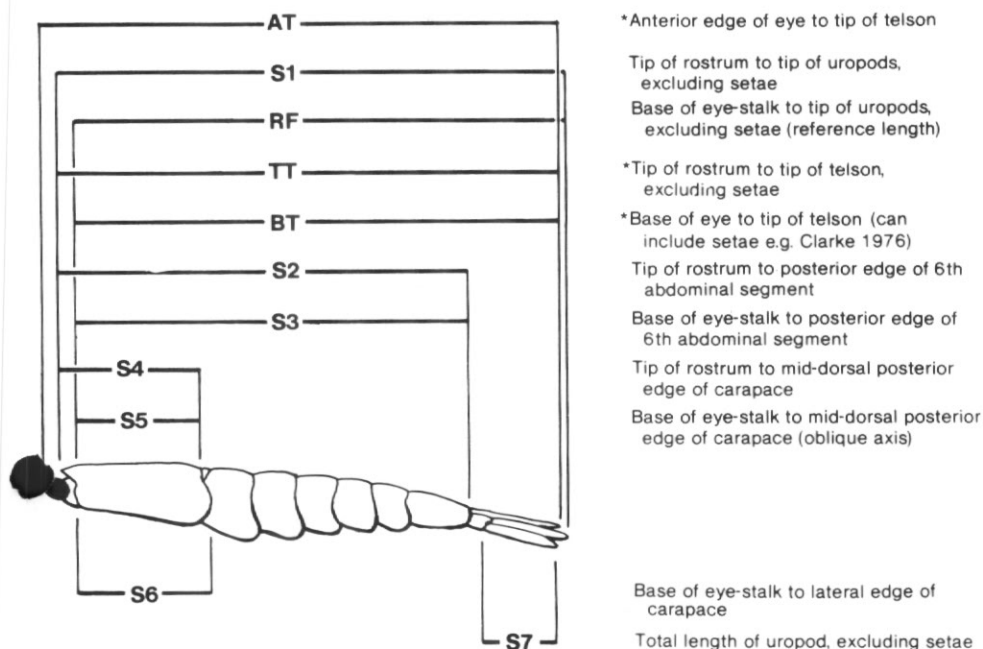


Fig. 1. Definitions and codes for various length measurements of *Euphausia superba*.

published length-weight equations (where the effects of both different coefficients and exponents must be envisaged) the predicted weight for a selected length has also been calculated. In order to convert this selected length (45 mm, AT, anterior eye to tip of telson) to other equivalent lengths, the appropriate equation for each sex and maturity stage (Appendix 1) or the equations given by Miller (1983) were used. The latter gave lengths of 45, 44, 43, 38, 15 and 7 mm for measurements S1, TT, RF, S2, S4 and S7 respectively. Where required, the conversion of length S2 (tip of rostrum to posterior edge of sixth abdominal segment) to S1 (tip of rostrum to tip of uropods) was used as an intermediate step. It was assumed that BT (base of eye to tip of telson) was equivalent to AT minus the diameter of the eye. The eye diameter was obtained using the equation:

$$AT = 12.48 + 14.92 \times \text{eye diameter}$$

(Siegel, 1986a;  $n = 915$ ,  $r^2 = 0.79$ ).

This gave an eye diameter of 2 mm (to the nearest mm) for the chosen length. It was assumed that the difference between AT and TT (tip of rostrum to tip of telson) was equivalent to the eye diameter. The reference measurement, RF (base of eye to tip of uropods) was assumed to be equivalent to TT minus half the eye diameter, even though observations on larger krill indicated that the uropods extended well beyond the telson in some animals.

In view of the number of different types of length measurements for *Euphausia superba* (Mauchline, 1981; Fig. 1), two authors (Siegel, 1982a; Miller, 1983) analysed samples of krill with the specific aim of producing conversion equations. In other studies, for example this paper, the measurement of more than one length for each krill has provided data for such conversion equations as a by-product. All available published length-length conversion equations have been standardized and are

summarized in Appendix 1 with new data from this study. Length-length conversion equations are presented for the various combinations of total length (AT), carapace length (S4) and uropod length (S7) as a function of sex. No equivalent equations for each moult stage or group of moult stages are provided as there are no comparative data and such conversions were not utilized.

There are a number of common features in all length-length relationships. In general, those studies that have set out to provide equations for converting from one length measurement to another have used relatively small numbers of krill covering a considerable size range; they have thus produced high correlation coefficients. In contrast, those studies that separated the sexes and maturity stages involved reduced size ranges with consequent smaller coefficients of correlation for each group. The data in Appendix 1 show, however, that it is important to distinguish both sex and maturity stage because of the large differences in predicted values for animals of the same length but of different sex. This is particularly noticeable when using carapace length (S4) to predict total length. In this case, use of our equations for male (M), female (F) and all krill pooled (ALL) and a carapace length of 15 mm gives predicted total lengths (AT, see Appendix 1) of 50, 44 and 47 mm respectively.

#### *Length-weight relationships*

To facilitate comparison, published length-weight relationships were transformed from the linear equation of the form:

$$\log W = \log a + b \log L,$$

to the power equation of the form:

$$W = aL^b,$$

where  $W$  = weight (g),  $L$  = length (mm) and the coefficient  $a$  has been multiplied by  $10^6$  for convenience of presentation.

All available length-wet weight relationships for *E. superba* were incorporated with new data for the full range of sex and maturity stages (Appendix 2). The ranges of both coefficient (a) and exponent (b) were large as was the range of predicted weight for the chosen standard length. For example, when predicting wet weight from total length (AT), the coefficients (a) ranged from 0.83 to 35.48 while the exponents (b) varied between 2.59 and 3.58; predicted wet weight for a krill of 45 mm AT (measured not derived) ranged from 0.56 to 0.87 g. As with conversions from one length measurement to another, it is important to differentiate between sexes and maturity stages, particularly when using carapace length (S4) as the predictor. In this case, and again using our equations, a carapace length of 15 mm would predict a wet weight of 0.71 g for females and 1.05 g for males, or 0.88 g if sex were ignored (Appendix 2).

In the case of predicting dry weight from total length (AT), the coefficients ranged from 0.07 to 20.42 and the exponents from 2.36 to 3.80 (Appendix 3). Predicted dry weights for krill of total length 45 mm varied from 0.12 to 0.21 g. As with wet weight, sex and maturity stage greatly affected predicted dry weights for M, F and ALL krill, giving weights of 0.23, 0.17 and 0.21 g respectively for an animal with carapace length of 15 mm.

In contrast to length-weight relationships that include sex and maturity stage, there are no published data that differentiate between moult stages. Whilst we may expect changes in wet weight, dry weight and length during the moult cycle it was not clear whether this would be reflected in length-weight relationships. This study shows that

Table II. Equations relating total length (AT in mm) and weight in *Euphausia superba* as a function of moult stage, with predicted weight for the standard length

Moult category	Coefficient ( $\times 10^6$ )	Exponent	n	$r^2$	Range	Predicted weight (g) for standard length of 45 mm
<i>(a) Wet weight</i>						
A	3.63	3.21	690	0.77	35-58	0.736
BC	3.02	3.25	633	0.77	37-57	0.713
D1	2.29	3.33	548	0.81	36-57	0.733
D2	3.72	3.21	531	0.76	39-58	0.754
D3	4.90	3.13	499	0.85	31-55	0.732
ALL	3.39	3.23	2901	0.81	31-58	0.741
<i>(b) Dry weight</i>						
A	1.51	3.05	679	0.62	35-58	0.167
BC	0.68	3.26	629	0.66	37-57	0.167
D1	0.56	3.31	543	0.66	36-57	0.166
D2	1.95	3.00	524	0.53	39-58	0.178
D3	2.46	2.93	496	0.74	31-55	0.172
ALL	1.00	3.16	2871	0.66	31-58	0.168

there is very little variation between either coefficients or exponents for both wet weight (Table IIa) and dry weight (Table IIb) over the five moult stages.

#### Weight-weight relationships

The collection of both wet- and dry-weight data for individual krill allowed the derivation of equations to predict dry weight from wet weight for *E. superba* for sex, maturity stage and moult stage (Table IIIa). Published weight-weight relationships have been collated in Table IIIb. To simplify comparison, an approximate overall proportion of water in krill has been calculated from these data by utilizing the slope of the relationship. The proportion of water estimated from our data ranges from 66 to 81% for the various maturity stages with no obvious discernible pattern. The proportion of water over the moult cycle (with krill grouped by moult stage only) showed less variation, ranging from 75 to 79% (Table IV).

#### DISCUSSION

Length-weight relationships have been used for a variety of purposes in the study of *Euphausia superba*. However, given the context in which they are often used, there has been little critical appraisal of their validity. We have shown that general relationships that ignore sex and maturity are inappropriate and likely to lead to large errors in prediction because of the different morphologies of subadults and adults, and of males and females. Even when sex and maturity are taken into account there is still a further potential for error if the relationships are used to extrapolate beyond the range of the original data. Such extrapolations are not only statistically invalid but may also be biologically inappropriate. It is also important to use an equation of the correct statistical derivation, that is a predictive regression rather than a geometric mean regression. The latter is appropriate for estimating the underlying population relationship between length and weight or for examining fundamentals of shape in krill. The former is correctly used if weight is predicted from length, but it is an inappropriate descriptor of krill populations.



Table III. Equations deriving dry weight ( $W_d$ , g) from wet weight ( $W_w$ , g) with the proportion of water in *Euphausia superba*.

(a) Sex, maturity and moult stage (this study)

Sex and maturity stage	Conversion formula	n	r <sup>2</sup>	Water (%)
MS1	$W_d = 0.275W_w - 0.017$	106	0.92	73
MS2	$W_d = 0.289W_w - 0.032$	159	0.89	71
MS3	$W_d = 0.340W_w - 0.081$	108	0.93	66
MA1	$W_d = 0.218W_w - 0.002$	383	0.80	78
MA2	$W_d = 0.195W_w - 0.014$	1117	0.80	81
M	$W_d = 0.198W_w - 0.018$	1873	0.75	80
FS	$W_d = 0.195W_w - 0.014$	77	0.91	81
FA1	$W_d = 0.251W_w - 0.013$	110	0.84	75
FA2	$W_d = 0.244W_w - 0.010$	292	0.82	76
FA3	$W_d = 0.257W_w - 0.003$	396	0.90	74
FA4	$W_d = 0.275W_w - 0.014$	472	0.95	73
FA5	$W_d = 0.224W_w - 0.010$	64	0.74	78
F	$W_d = 0.281W_w - 0.026$	1411	0.94	72
ALL	$W_d = 0.236W_w - 0.004$	3284	0.79	76
<i>Moult stage</i>				
A	$W_d = 0.226W_w - 0.001$	683	0.79	77
BC	$W_d = 0.232W_w - 0.001$	630	0.80	77
D1	$W_d = 0.246W_w - 0.009$	544	0.81	75
D2	$W_d = 0.242W_w - 0.002$	530	0.75	76
D3	$W_d = 0.214W_w - 0.012$	499	0.80	79

(b) Published data

Conversion formula	n	Water (%)	Source and comment
$W_d = 0.21W_w - 2.27$	47	79	Clarke, 1976
$W_d = 0.26W_w$	—	74	Chekunova and Rynkova, 1974
$W_d = 0.216W_w$	—	78	Ikeda and Mitchell, 1982
	20	81	50 mg dry wt
	17	79	50–100 mg
	26	77	100–200 mg
	7	76	200–300 mg
	7	75	300 mg
	—	80	Ikeda and Dixon, 1982a, field
	—	79	— fed
	—	75	— fed
	—	81	— starved
	5	80	Ikeda and Bruce, 1986, 50 mg
	10	80	50–100 mg
	22	79	100–200 mg
	11	78	200–300 mg
	6	76	300 mg
	—	84	Siegel, 1982b, derived from data,
	—	77	mean, min and max respectively
	—	89 (56)	(low-accuracy raw data gave very low % water)
$W_d (\%) = 16.3 AT^{0.02}$		84	Kils 1981a derives dry weight from length (range 75–90%)



Table IV. Mean weights (g) and estimated total biomass (metric tonnes) of *Euphausia superba* around South Georgia derived from different length-weight relationships applied to a single acoustic data set. Krill length data comprised 4217 krill measured, mean length 28 mm, range 22-48 mm

Length-weight relationship		Mean weight (g)	Total biomass (metric tonnes)	Source
Intercept $\times 10^6$	Exponent			
1.8	3.34	0.167	194 340	Sahrhage, 1977/8
1.93	3.33	0.173	201 167	Siegel, 1986b
1.28	3.45	0.176	203 675	Siegel, 1986a
3.37	3.18	0.177	207 375	Lockyer, 1973
0.93	3.55	0.183	210 737	Anon, 1986
1.58	3.40	0.182	210 749	Kils, 1981a
1.8	3.38	0.193	223 748	Jadzewski and others, 1978
1.77	3.39	0.196	227 913	McHardy in Lockyer, 1973
3.85	3.20	0.217	254 126	This paper

The accurate estimation of krill abundance is a major requirement for the understanding of the Antarctic marine ecosystem (Anon, 1977) and length-weight relationships are an essential step in such an estimation from echosurveys (Hampton, 1983; Anon, 1986). Differences between length-weight equations, therefore, have an effect on abundance estimates. The magnitude of this effect can be illustrated simply by applying the general length-weight equations (ALL) extracted from Appendix 2 to an echosurvey around South Georgia: these abundance estimates vary from 200 000 to 250 000 tonnes (Table IV). This range, or potential for error, is in addition to other sources of variation and uncertainty associated primarily with survey design, sampling intensity and the accuracy of target strength estimates (Anon, 1986). Length-weight equations introduce an additional source of error which can be minimized: the second part of this paper addresses the problem of increasing the reliability of length-weight equations in the most cost-effective way.

#### A NEW APPROACH TO MORPHOMETRIC RELATIONSHIPS

An examination of length-weight and weight-weight relationships in *Euphausia superba* was undertaken to identify key sources of variability where relatively small increases in the effort of analysis would result in large improvements in the precision prediction. It was realized that, in many instances, the effort required to obtain more accurate weight estimates via length measurements would exceed that of obtaining weight data directly. Whilst the latter course would be more labour intensive, it may prove more desirable than utilizing length data and unreliable morphometric relationships. Therefore we have attempted to simplify the collection of raw data by the use of a number of simplifying assumptions based upon both biological and practical foundations.

#### *Simplifying assumptions*

Here we examine the basic factors used to distinguish sex and maturity stages (Makarov and Denys, 1981) and moult stage (Buchholz, 1982) and propose groupings of stages within which the differentiating characteristics are unlikely to affect morphometric relationships.

The differentiation between the subadult male stages (MS1, MS2, MS3) is based upon the structure of the petasma located on the first pleopod (this requires a microscopic examination) and we have assumed that this is unlikely to have an effect upon length-weight relationships. Our previous analyses have also shown that grouping these stages was statistically valid (Appendix 2, 3) for at least two (AT, S7) of the three length measurements used in this study. Similarly, adult male stages (MA1, MA2) are differentiated on the absence or presence of spermatophores and we again assumed this has no effect on morphometrics, despite a small but statistically significant difference between these two stages. The distinguishing feature of subadult females is the partial development of the thelycum and the factors used to differentiate the early adult female stages (FA1, FA2) are the presence of spermatophores while a later stage (FA3) is characterized by the presence of visible eggs in the thorax. Despite our inability to combine any of these stages on purely statistical grounds we have proposed groupings based both on convenience for field operations and an absence of obvious morphometric changes as a result of these differences. The classification of gravid females (FA4) depends upon the presence of a markedly swollen thorax and this clearly affects morphometrics, as does the presence of a large number of mature eggs affect weight. Spent females (FA5) are classified on the basis of the emptiness of the ovary in a still swollen thoracic cavity and it was unclear whether this would affect morphometrics; some groupings, therefore, retained this classification.

These considerations lead to two possible approaches to grouping sex and maturity stages (Fig. 2). The first approach is based solely on differences between the sexes (Fig. 2;  $\alpha$ ,  $\beta$ ) while the second combines krill of similar developmental stages or morphologies irrespective of sex (Fig. 2; A, B, C). A grouping in which ALL krill are combined irrespective of sex or developmental stage is the final step for both approaches.

The five moult categories can be grouped into two physiologically important phases: the intermediate moult stages (BC, D1, D2) and the stages immediately before and after ecdysis (D3, A; see Fig. 3). The latter stages of the moult cycle (D3, ecdysis and A) are those where rapid changes occur that may affect morphometrics. In contrast, the intermediate moult stages are characterized by smaller and slower changes in, for example, weight.

#### *Length-weight regression analyses*

Multiple linear regression equations for weight in relation to the three lengths, (AT, S4, S7) individually, in pairs and combined, were fitted to the raw data grouped according to Figs 2 and 3. The goodness of fit of the regression models was compared by examining the percentage of the variance explained. Differences between regression models were classified as significant only if the increase in explained variance was 1%. It is common practice to use the variance explained by a regression as the criterion for comparing different regression models. However, it is the residual variance which provides an estimate of the precision of any prediction (Snedecor and Cochran, 1980). Thus, for example, a regression model which explains 90% of the variance does not, at first sight, appear to be a major improvement over a model which explains 80% of the variance. However, the residual variance of the former is only 10%, or half that of the latter. This constitutes a twofold improvement in precision (variance) or a 1.4-fold ( $\sqrt{2}$ ) reduction in the standard error of a predicted value. Throughout this paper therefore, we shall use the residual percentage variance for comparing our length-weight regression models.

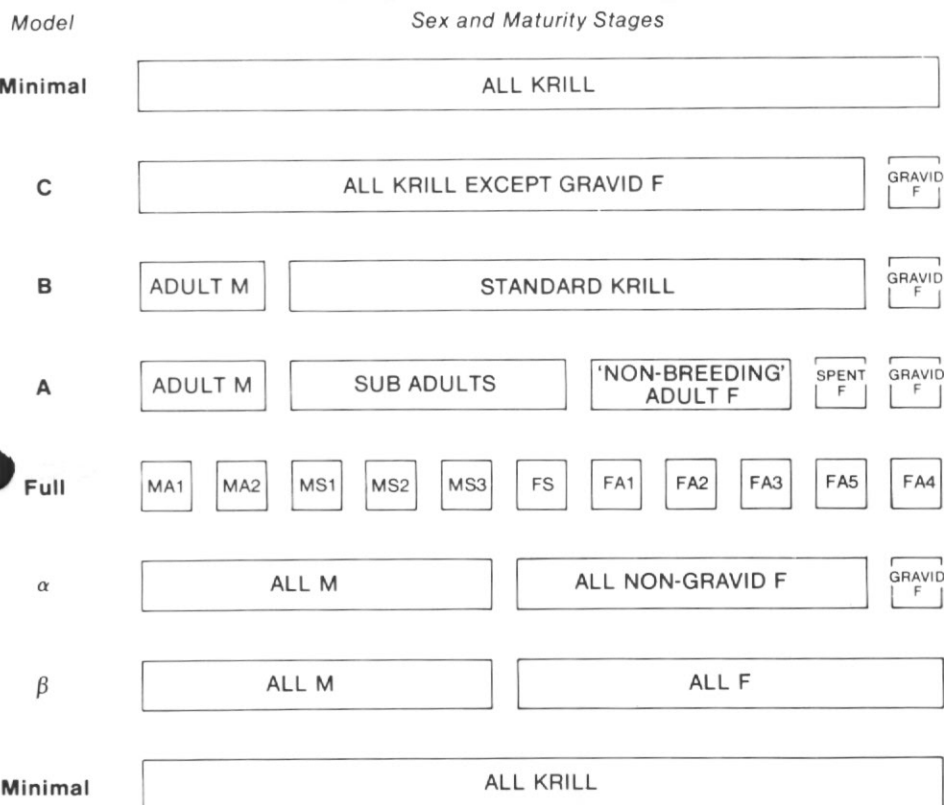


Fig. 2. Sex and maturity stage groupings used in modelling length-weight relationships of *Euphausia superba*.

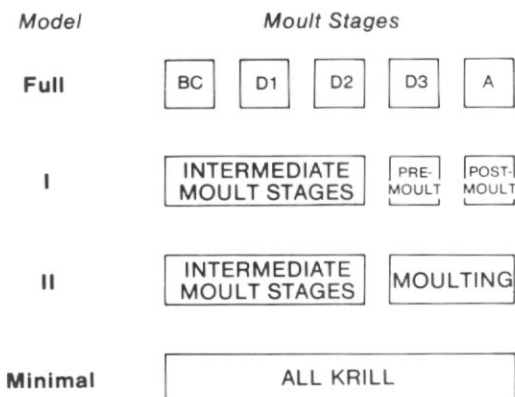


Fig. 3. Moult stage groupings used in modelling length-weight relationships of *Euphausia superba*.

## RESULTS

*Preliminary analysis*

In order to separate the effects of sex and moult stages a preliminary analysis was undertaken which examined regression models for the most detailed classifications of sex and moult together, sex in the absence of moult stage data, moult in the absence of sex data and neither sex nor moult. This analysis is presented for both wet weight (Table Va) and dry weight (Table Vb). The most complex model (sex, moult, total length, carapace length, uropod length) had a residual variance of only 9.4% in comparison to 17.6% for the model comprising total+carapace+uropod lengths and neglecting sex and moult. Virtually all of this difference can be attributed to the effect of sex because moult account for only 0.2% of the variance in the presence of the sex classification and 0.1% in its absence (Table Va). For subsequent analyses, therefore, we have excluded moult as a significant factor affecting length-weight relationships.

Table V. Residual variance (%) in the four extreme regression models of length-to-weight relationship  
*Euphausia superba*

Model	Sex and moult	Sex - no moult	Moult - no sex	Neither sex nor moult
<i>(a) Wet weight</i>				
Length measurements				
Total + carapace + uropod	9.4	9.6	17.6	17.6
Total + carapace	10.2	10.3	18.7	18.6
Total + uropod	10.8	10.9	18.1	18.0
Total	11.8	11.9	18.9	18.7
Carapace + uropod	13.4	13.7	28.7	29.1
Carapace	17.2	17.8	68.2	69.8
Uropod	23.2	24.3	38.3	40.1
<i>(b) Dry weight</i>				
Length measurements				
Total + carapace + uropod	14.7	16.3	25.3	26.0
Total + carapace	15.4	16.5	25.4	26.1
Total + uropod	16.9	18.0	32.9	33.5
Total	17.6	18.4	33.4	34.1
Carapace + uropod	18.0	19.7	32.5	33.8
Carapace	20.4	21.7	48.8	50.4
Uropod	29.4	31.8	59.4	63.7

It is interesting to note that the measurement of total length alone results in a smaller residual variance than carapace or uropod length or both together (Table V). In addition, carapace length alone is an extremely poor predictor of weight in the absence of a sex classification. Furthermore, dry weight regression models have, in general, a greater residual variance than models for wet weight but it is not clear why this should occur.

Total length is by far the most common measurement of krill, although we have also examined carapace and uropod length as these are often used in laboratory studies. Table V shows that the addition of carapace and uropod length data reduces the residual variance by only some 2%. Because both these measurements require microscopic examination the cost of collecting such data far outweighs any benefit. We shall therefore concentrate primarily on total length.

*Detailed analysis of the effect of sex and maturity stage*

Even when using total length as the only predictor of wet or dry weight, the residual variance for a model which excludes sex is still approximately twice that for one in which a detailed sex and maturity stage analysis is made (Table VI). It has been common practice to separate krill according to sex only and provide length-weight regression for males and females separately. However, simply separating sexes does not provide more precise predictions (Table VI, total length, Model  $\beta$  and no sex grouping). In contrast, separating gravid females from all other krill irrespective of sex (model C) does provide an improvement albeit small. Subsequent separation of males from non-gravid females provides a further small increase in precision (Model  $\alpha$ ). Thus the simple classification of 'males', 'gravid females' and 'other females' results in an improvement in precision of approximately half that gained by the full separation into all sex and maturity stages. An alternative classification which separates 'adult males' and 'gravid females' from all other 'standard krill' (Model B) reduces the residual variance very nearly to that of the full classification with minimal increase in effort. An intermediate step in which spent females were also separated resulted in no significant decrease in the residual variance. Further separation (Model A) produces no significant increase in precision (Table VI).

Table VI. Residual variance (%) of regression models of length-to-weight relationships for *Euphausia superba* ignoring moult stage

	Model						No sex grouping
	Full	A	B	C	$\alpha$	$\beta$	
<i>(a) Wet weight</i>							
Length measurements							
Total + carapace + uropod	9.6	10.6	11.3	13.5	11.8	14.9	17.6
Total + carapace	10.3	11.3	12.0	15.1	13.1	16.2	18.6
Total + uropod	10.9	12.3	12.6	14.0	13.3	17.4	18.0
Total	11.9	13.2	13.4	16.0	14.7	18.6	18.7
Carapace + uropod	13.7	15.1	16.6	24.4	18.5	21.9	29.1
Carapace	17.8	19.2	32.6	68.0	31.4	34.5	69.8
Uropod	24.3	28.0	39.0	29.8	29.8	39.1	40.1
<i>(b) Dry weight</i>							
Length measurements							
Total + carapace + uropod	16.3	18.9	20.5	20.6	19.6	24.6	26.0
Total + carapace	16.5	19.2	20.6	21.0	19.9	25.2	26.1
Total + uropod	18.0	21.7	22.3	23.1	22.7	29.1	33.5
Total	18.4	22.1	22.5	23.1	22.9	29.5	34.1
Carapace + uropod	19.7	22.3	25.5	28.2	23.5	28.9	33.8
Carapace	21.7	24.1	29.0	72.4	48.0	27.6	50.4
Uropod	31.8	38.5	39.5	41.4	40.5	53.9	63.7

Where it is necessary to use carapace length as a measurement, for example, in the analysis of stomach samples of krill predators when whole animals are not available, the prediction of wet weight or dry weight is unreliable in the absence of information on sex (Table VI). On other occasions, dry weight may need to be predicted from wet weight. In this case, although we present no data, moult again has little effect, while sex is important, with a single division into male and female providing increased precision.

## DISCUSSION

This study has presented a new approach to the analysis of length-weight relationships which allows the value of different length measurements and biological classifications to be assessed quantitatively. A surprising aspect is the relatively small contribution of moult stage towards explaining variance; this despite the large changes in length, wet and dry weight which occur over the moult cycle in other crustaceans (Adelung, 1971). Such changes undoubtedly occur in *E. superba* but they are obviously small in their effect upon length-weight relationships in comparison to other variables such as sex.

The most important result of our study is that it is possible to obtain major improvements in the precision of predicted weights by using a single length measurement in conjunction with a simple classification by sex and reproductive state. Even though these provide improved predictions there can be no doubt that direct measurements of weight are best. There are, however, many circumstances where direct weighing is neither feasible nor cost-effective and weight must be predicted from length. In these circumstances, effort should be directed to the most reliable combination of length measurement and classification of sex.

The practical consequences of this assessment are that total length is a very good predictor of weight and that the additional use of carapace and/or uropod length provides no useful improvement in precision. Furthermore, although it is relatively easy to divide krill into male and female categories, such a division is of little practical use in improving the precision of predictions. However, the separation of gravid

Table VII. Predictive regression equations for wet weight (g) and dry weight (g) from total length (AT, mm) for *Euphausia superba* separated into categories according to model  $\alpha$  and B (see Fig. 2). Size ranges for male, non-gravid female, gravid female, adult male and standard krill are 34-57, 31-56, 41-59, 39-57, 31-57 respectively

	$a \times 10^6$	$b$	$n$	$r^2$	$SE$ of $a$ $\times 10^6$	$SE$ of $b$	Coefficient of variation of (%)
Wet weight							
Model $\alpha$							
Male	6.13	3.0776	1882	0.81	0.22	0.0348	10.7
Gravid female	9.75	2.9809	477	0.82	0.51	0.0633	10.0
Non-gravid female	10.88	2.9077	940	0.81	0.38	0.0461	12.1
Model B							
Adult male	17.29	2.8152	1511	0.74	0.45	0.0426	9.8
Gravid female	9.75	2.9809	477	0.82	0.51	0.0633	10.0
Standard	9.60	2.9403	1311	0.84	0.28	0.0356	11.4
Dry weight							
Model $\alpha$							
Male	2.38	2.9269	1861	0.73	0.16	0.0413	12.8
Gravid female	1.99	3.0438	471	0.75	0.29	0.0810	12.9
Non-gravid female	1.39	3.0737	933	0.66	0.21	0.0715	19.4
Model B							
Adult male	4.01	2.7902	1491	0.67	0.26	0.0512	11.8
Gravid female	1.99	3.0438	471	0.75	0.29	0.0810	12.9
Standard	0.93	3.1686	1303	0.71	0.14	0.0555	18.3

females, either from all other krill or preferably from male and female krill does provide a useful improvement.

The most cost-effective classification of sex and maturity stage is to use a basic visual examination to divide krill into three groups: 'adult males', 'gravid females', and 'standard krill' (others). This produces precision comparable to that obtained from a full examination of the sex and maturity stage of the animal.

It is not our intention to recommend either a standard length measurement or a sex classification, partly because we have been unable to include data on juvenile krill and partly because such standards reduce flexibility. Nevertheless, because we think there are considerable benefits to be gained by improving the precision of prediction for both wet and dry weight we include our equations for two useful classifications of sex (Table VII). The coefficients of variation for wet weight are approximately 10%, with those for dry weight being slightly greater. These can be compared to the coefficients of variation of the traditional equations for ALL krill which are 25 and 35% for wet and dry weight respectively.

#### CONCLUSIONS

Despite the apparent simplicity of the measurement of length in *Euphausia superba*, or perhaps because of it, there is a large and unco-ordinated literature on different lengths and their use for predicting weight. In this paper we have attempted to provide the basis for a re-appraisal of the literature and a method for assessing the value of both the length measurements and additional data such as sex and maturity stage or moult stage. We have shown that it is possible to significantly improve the precision of prediction with a small increase in effort at the data-acquisition stage. We have provided equations which may be used in practice but which we hope will also be used as templates for the more efficient collection of data, leading to more precise estimation of weight.

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Appendix 1. Equations for the conversion of one length measurement to another for *Euphausia superba*.

Equations are linear and of the form: derived measurement = intercept + (slope × measured length).

An indication of correlation is given by  $r^2$  (sex and maturity stages are as defined in Table I, lengths are as defined in Fig. 1)

Conversion	Sex and maturity stage	Intercept (mm)	Slope	n	$r^2$	Range (AT, mm)	Source and comment
AT from S4	MS1	11.66	2.343	105	0.74	34-52	This paper, frozen
	MS2	11.76	2.394	155	0.76	37-54	
	MS3	12.15	2.402	108	0.73	43-57	
	MA1	11.81	2.579	383	0.60	39-57	
	MA2	8.59	2.850	1113	0.59	40-56	
	M	13.70	2.430	1864	0.53	34-57	
	FS	9.34	2.420	77	0.70	31-48	
	FA1	9.39	2.375	109	0.75	37-52	
	FA2	14.52	2.033	289	0.74	37-54	
	FA3	10.46	2.263	398	0.75	40-56	
	FA4	11.52	2.206	477	0.81	41-59	
	FA5	16.28	1.915	65	0.67	39-56	
	F	12.97	2.120	1415	0.82	31-59	
	ALL	29.02	1.239	3279	0.33	31-59	
	from S7	MS1	4.62	6.947	79	0.81	
MS2		6.09	6.825	121	0.74	—	
MS3		9.31	6.316	85	0.55	—	
MA1		14.96	5.275	297	0.48	—	
MA2		17.00	4.996	872	0.48	—	
M		12.61	5.683	1454	0.61	—	
FS		7.84	6.234	65	0.60	—	
FA1		6.28	6.671	82	0.74	—	
FA2		10.75	6.015	224	0.60	—	
FA3		12.04	5.969	340	0.63	—	
FA4		9.27	6.561	417	0.65	—	
FA5		18.34	4.948	53	0.46	—	
F		6.11	6.941	1181	0.67	—	
ALL		12.21	5.817	2635	0.62	—	
S4 from S7		MS1	2.46	1.982	78	0.61	—
	MS2	0.89	2.304	123	0.70	—	
	MS3	2.33	2.060	84	0.45	—	
	MA1	6.07	1.282	298	0.32	—	
	MA2	6.20	1.234	865	0.41	—	
	M	6.60	1.205	1448	0.31	—	
	FS	1.78	2.125	65	0.50	—	
	FA1	1.22	2.347	83	0.64	—	
	FA2	2.15	2.269	223	0.44	—	
	FA3	2.95	2.251	341	0.62	—	
	FA4	1.30	2.586	417	0.61	—	
	FA5	3.58	2.162	53	0.49	—	
	F	-0.71	2.840	1182	0.60	—	
	ALL	9.35	0.927	2630	0.07	—	
	AT from RF	—	0.74	1.046	151	1.0	—
—		1.47	1.019	—	0.98	15-60	Miller (1983), formalin
from S1	—	0.13	1.030	151	1.0	—	Siegel (1982a)
—	—	0.97	1.001	—	0.99	15-60	Miller (1983)
from S2	—	0.36	1.204	151	1.0	—	Siegel (1982a), formalin
—	—	0.00	1.214	—	—	—	Poleck (1980), formalin
—	—	0.00	1.211	—	—	—	Burukovskiy (1967)
RF from S1	—	-0.51	0.983	—	1.0	—	Siegel (1982a)
from S2	—	-0.31	1.149	—	1.0	—	—
from AT	—	-1.39	0.979	—	0.98	—	Miller (1983)

## Appendix 1 (cont.)

Conversion	Sex and maturity stage	Intercept (mm)	Slope	n	r <sup>2</sup>	Range (AT, mm)	Source and comment
S1 from S2	—	0.26	1.167	—	1.0	—	Siegel (1982a) gave S1 as AT
	—	1.52	1.120	525	0.98	15–60	Miller (1983)
from S3	—	1.66	1.165	—	0.98	—	
from S4	—	2.32	2.843	—	0.90	—	
from S5	—	2.62	3.139	—	0.92	—	
from S6	—	2.46	3.157	—	0.92	—	
from S7	—	8.19	5.233	—	0.70	—	
from S4	FS	6.90	2.490	264	0.91	19–59	Miller (1983)
	FA	24.10	1.320	130	0.56	38–58	(FA4 + FA5)
	MS	3.76	2.813	276	0.89	18–60	
	MA	22.25	1.954	109	0.62	42–60	
from S7	ALL	12.02	4.191	525	0.67	—	Formalin
	—	8.19	5.233	1461	0.69	—	Fresh
S2 from S7	ALL	3.39	4.259	22	0.87	—	Poleck and Denys (1982), formalin
	—	-1.09	5.262	31	0.87	—	
S4 from AT	F	1.59	0.367	293	0.96	—	Siegel (1982a), (J, F, FA4)
	M	1.66	0.263	539	—	—	
TT from S7	—	2.65	7.360	67	0.96	—	Ikeda and Dixon (1982b), formalin, S7, exopodite
from S1	—	-0.44	0.981	—	1.0	—	Murano and others (1979), formalin
from S4	—	2.63	2.857	—	—	—	Re-expressed from original form
from S6	—	0.00	3.378	64	—	—	Clarke (1976), fresh, TT included setae re-expressed from original form
S6 from S7	—	0.00	4.878	63	—	—	S7 included setae
from CW	—	0.00	2.770	62	—	—	CW = carapace width
AT from S4	J	-1.72	3.27	50	0.95	28–48	Hill (in prep.)
	J*	-1.59	3.28	50	0.95	28–48	*carapace removed from animal, measured when flattened
	MS	4.53	2.89	50	0.90	38–58	
	MS*	3.33	2.99	50	0.91	38–58	
	MA2	14.2	2.57	50	0.42	49–57	
	MA2*	15.6	2.48	50	0.41	49–57	
	FS	15.5	2.09	50	0.57	41–52	
	FS*	14.6	2.17	50	0.68	41–52	
	FA	10.7	2.34	50	0.73	48–63	(FA2–FA5)
	FA*	13.5	2.22	50	0.72	48–63	(FA2–FA5)
	ALL	12.1	2.39	269	0.77	28–63	
	ALL*	11.6	2.44	269	0.77	28–63	
	J	2.28	2.88	154	0.84	25–48	Hill (unpublished)
	M	3.58	3.147	621	0.69	29–63	
	F	11.09	2.319	317	0.82	37–65	



## Appendix 2. (cont.)

Length measurement	Sex and maturity stage	Coefficient ( $\times 10^6$ )	Exponent	n	r <sup>2</sup>	Range (mm)	Predicted weight (g) for a 45 mm (AT) krill	Source and comment
	M	0.83	3.56	—	—	—	0.638	Siegel (1986a), formalin
		2.36	3.25	—	—	—	0.557	
	FA4	3.4	3.27	99	—	—	0.866	
	F	1.1	3.52	281	—	—	0.726	Siegel (1986a)
		1.15	3.46	—	—	—	0.604	
		2.42	3.25	—	—	—	0.571	
		0.91	3.58	—	—	3-61	0.754	
	ALL	3.37	3.18	—	—	—	0.609	Jadzewski and others (1978)
		1.8	3.38	752	—	—	0.697	
		1.8	3.34	—	—	—	0.598	Sahrhage (1977/8)
		1.58	3.40	116	0.95	25-60	0.660	Kils (1981b), fresh
		1.28	3.45	540	—	13-60	0.647	Siegel (1986a)
		1.93	3.33	—	—	30-62	0.618	Siegel (1986b)
		1.77	3.39	—	—	—	0.712	McHardy in Lockyer (1973), formalin
S1	J	5.09	3.12	745	0.94	—	0.683	Ikeda and others (1986), formalin
	MS	2.20	3.39	357	0.84	—	0.820	
	MA1	17.15	2.85	150	0.74	—	0.828	
	MA2	6.85	3.08	381	0.90	—	0.790	
	FS	0.68	3.72	229	0.74	—	0.883	
	FA1	10.07	2.98	168	0.92	—	0.795	
	FA2	12.57	2.91	144	0.89	—	0.762	
	FA3	62.23	2.52	338	0.85	—	0.862	
	FA4	22.21	2.83	288	0.87	—	0.994	
	FA5	7.98	2.94	11	0.80	—	0.542	
	ALL	4.26	3.19	385	0.99	—	0.745	
		6.82	3.09	27	0.80	—	0.817	
		15.99	2.85	13	0.88	—	0.772	
		10.94	2.85	14	0.93	—	0.528	
		1.88	3.44	300	0.85	—	0.847	
		3.56	3.27	273	0.94	—	0.842	
		2.00	3.38	18	0.93	—	0.718	
		2.10	3.45	79	0.90	—	0.982	
		2.53	3.37	268	0.98	—	0.874	
		1.12	3.57	51	0.98	—	0.825	
		0.87	3.63	356	0.94	—	0.804	
		0.67	3.71	262	0.93	—	0.838	
		3.30	3.27	75	0.80	—	0.781	
		48.14	2.35	145	0.57	—	0.350	
		2.29	3.37	15	1.00	—	0.791	
		2.27	3.36	65	0.98	—	0.755	
		6.66	3.05	73	0.88	—	0.686	
		5.23	3.11	269	0.95	—	0.676	
		2.32	3.32	25	0.97	—	0.663	
		2.36	3.37	2811	0.99	—	0.815	
		1.7	3.42	708	0.97	20-60	0.710	Miller (1986), formalin

## Appendix 2. (cont.)

<i>Length measurement</i>	<i>Sex and maturity stage</i>	<i>Coefficient (<math>\times 10^6</math>)</i>	<i>Exponent</i>	<i>n</i>	<i>r<sup>2</sup></i>	<i>Range (mm)</i>	<i>Predicted weight (g) for a 45 mm (AT) krill</i>	<i>Source and comment</i>
S2	CAL	47.0	2.12	51	0.82	—	—	Ikeda (1984), fresh, calyptopis, 45 mm weight not applicable Furcilia
	FUR	12.0	2.83	81	0.84	—	—	
	ALL	0.58	3.70	70	0.97	—	0.406	
		3.54	3.38	299	0.94	18-42	0.774	
		7.40	3.22	106	0.98	20-37	0.904	
		9.10	3.15	124	0.95	20-37	0.862	Poleck (1980), field sample 2 months in laboratory at 0 °C 2 months in laboratory at 5 °C
S7		2432	2.89	23	0.99	—	0.673	Ikeda and Dixon (1982a), formalin
BT	ADL	2.29	3.53	47	—	27-39	0.679	Clarke (1976), fresh, adolescent, BT included setae Morris (unpubl. data), fresh
		11.8	2.87	81	0.85	28-41	0.575	
TT	M	1.29	3.43	—	—	20-55	0.559	Nemoto and others (1981), fresh
		1.01	3.43	—	—	—	0.438	
		3.71	3.15	—	—	—	0.558	
		0.22	3.92	—	—	—	0.609	
		0.37	3.77	—	—	—	0.581	
		0.33	3.82	—	—	—	0.626	
		3.75	3.19	—	—	—	0.656	
		18.75	2.78	—	—	—	0.695	
		2.82	3.25	—	—	—	0.619	
		0.68	3.62	—	—	—	0.605	
		4.84	3.10	—	—	—	0.602	
		2.62	3.26	—	—	—	0.597	
		5.32	3.06	—	—	—	0.569	
		26.42	2.64	—	—	—	0.576	
		6.64	3.02	—	—	—	0.610	
		6.24	3.02	—	—	—	0.573	
	F	3.52	3.14	—	—	—	0.509	
		0.85	3.53	—	—	—	0.538	
		0.94	3.51	—	—	—	0.552	
		5.78	3.05	—	—	—	0.595	
		5.38	3.07	—	—	—	0.597	
		431.52	1.95	—	—	—	0.691	
		8.51	2.97	—	—	—	0.647	
		7.55	2.99	—	—	—	0.619	
		2.59	3.26	—	—	—	0.590	
		1.35	3.45	—	—	—	0.631	
		1.61	3.41	—	—	—	0.647	
		0.49	3.71	—	—	—	0.613	



## Appendix 2. (cont.)

Length measurement	Sex and maturity stage	Coefficient ( $\times 10^6$ )	Exponent	n	r <sup>2</sup>	Range (mm)	Predicted weight (g) for a 45 mm (AT) krill	Source and comment
		4.41	3.12	—	—	—	0.592	
		371.54	1.37	—	—	—	0.066	
		9.66	2.89	—	—	—	0.543	
		2.69	3.23	—	—	—	0.547	
	ALL	0.93	3.55	—	—	—	0.635	Anon (1986), fresh
		—	3.62	—	—	24-58	—	Chekunova and Rynkova (1974) quoted as $W_{\text{wet}} = 3.25L^{3.62}$ (mg and mm)
	M	4.2	3.17	—	—	—	0.731	Retamal and Quintana (1982), measurement not clear
	F	5.7	3.08	—	—	—	0.704	

Appendix 3. Relationships between length (mm) and dry weight (g) for *Euphausia superba* (see Appendix 2 for details)

Length measurement	Sex and maturity stage	Coefficient ( $\times 10^6$ )	Exponent	n	r <sup>2</sup>	Range (mm)	Predicted weight (g) for a 45 mm (AT) krill	Source and comment
AT	MS1	0.76	3.23	106	0.82	34-52	0.166	This paper, frozen (MS1 + MS2 + MS3)
	MS2	0.43	3.39	156	0.76	37-54	0.173	
	MS3	0.09	3.80	108	0.73	43-57	0.172	
	MS	0.47	3.36	370	0.82	34-57	0.169	
	MA1	1.35	3.08	381	0.72	39-57	0.167	
	MA2	6.46	2.67	1110	0.64	40-56	0.168	
	M	2.38	2.93	1861	0.73	34-57	0.166	
	FS	0.87	3.20	77	0.66	31-48	0.170	
	FA1	4.90	2.71	109	0.66	37-52	0.148	
	FA2	2.46	2.90	290	0.64	37-54	0.153	
	FA3	8.13	2.65	393	0.67	40-56	0.196	
	FA4	2.00	3.04	471	0.75	41-58	0.212	
	FA5	20.42	2.36	64	0.52	39-56	0.163	
	F	0.24	3.55	1404	0.69	37-58	0.178	
	S	0.62	3.29	447	0.83	34-57	0.170	
	ALL	1.06	3.15	3265	0.67	31-58	0.171	(MS + FS)
S4	MS1	316	2.37	105	0.66	—	0.171	See above for ranges
	MS2	214	2.54	158	0.62	—	0.171	
	MS3	32	3.24	107	0.71	—	0.153	
	MA1	155	2.71	379	0.58	—	0.158	
	MA2	182	2.66	1104	0.56	—	0.160	
	MA	174	2.67	1483	0.56	—	—	
	M	221	2.57	1853	0.57	—	0.157	

Appendix 3. (cont.)

Length measurement	Sex and maturity stage	Coefficient ( $\times 10^6$ )	Exponent	n	r <sup>2</sup>	Range (mm)	Predicted weight (g) for a 45 mm (AT) krill	Source and comment
	FS	50	3.05	77	0.68	—	0.183	
	FA1	245	2.37	110	0.57	—	0.150	
	FA2	389	2.20	290	0.61	—	0.150	
	FA3	457	2.21	396	0.58	—	0.189	
	FA4	182	2.59	472	0.75	—	0.209	
	FA5	776	1.95	64	0.53	—	0.152	
	F	80	2.83	1409	0.49	—	0.174	
	ALL	1163	1.91	3262	0.49	—	0.154	
S7	MS1	759	3.07	79	0.72	—	0.168	See above for ranges
	MS2	525	3.30	123	0.64	—	0.164	
	MS3	372	3.49	84	0.53	—	0.157	
	MS	500	3.32	286	0.73	—	—	No conversion for MS
	MA1	2291	2.43	295	0.43	—	0.157	
	MA2	4786	2.03	863	0.41	—	0.158	
	MA	3890	2.15	1158	0.42	—	—	No conversion for MA
	M	2468	2.40	1444	0.52	—	0.161	
	FS	339	3.53	65	0.54	—	0.185	
	FA1	2630	2.29	83	0.42	—	0.147	
	FA2	2340	2.40	223	0.41	—	0.152	
	FA3	5890	2.04	337	0.47	—	0.192	
	FA4	2880	2.53	411	0.51	—	0.210	
	FA5	6610	1.87	52	0.42	—	0.154	
	F	945	3.04	1174	0.43	—	0.178	
	S	437	3.40	349	0.75	—	—	No conversion for S (MS+FS)
	ALL	3703	2.22	2615	0.35	—	0.172	
AT	ALL	0.07	3.76	114	0.90	25-60	0.115	Kils (1981b), fresh, (48 h, 80 °C)
	—	0.1	3.80	145	—	—	0.192	Jadzewski and others (1978)
	—	—	—	—	—	—	0.139	Hirche (1983) (70 °C) log-linear equation $W(\text{mg}) = 1.082e^{(L \times 4.009)}$
RF	ALL	—	—	—	—	19-54	0.108	Kato and others (1982) log-linear equation $W(\text{mg}) = 1.208e^{(L \times 0.104)}$
TT	—	—	3.81	25	—	—	0.139	Chekunova and Rynkova (1974), fresh, equation, $W(\text{mg}) = 0.578L^{3.81}$