

Euphausiid respiration model revamped: Latitudinal and seasonal shaping effects on krill respiration rates



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ABSTRACT

Euphausiids constitute a major biomass component in shelf ecosystems and play a fundamental role in the rapid vertical transport of carbon from the ocean surface to the deeper layers during their daily vertical migration (DVM). DVM depth and migration patterns depend on oceanographic conditions with respect to temperature, light and oxygen availability at depth, factors that are highly dependent on season in most marine regions. Here we introduce a global krill respiration ANN (artificial neural network) model including the effect of latitude (*LAT*), the day of the year (*DoY*), and the number of daylight hours (*DLh*), in addition to the basal variables that determine ectothermal oxygen consumption (temperature, body mass and depth). The newly implemented parameters link space and time in terms of season and photoperiod to krill respiration. The ANN model showed a better fit ($r^2 = 0.780$) when *DLh* and *LAT* were included, indicating a decrease in respiration with increasing *LAT* and decreasing *DLh*. We therefore propose *DLh* as a potential variable to consider when building physiological models for both hemispheres. For single Euphausiid species investigated in a large range of *DLh* and *DoY*, we also tested the standard respiration rate for seasonality with Multiple Linear Regression (MLR) and General Additive model (GAM). GAM successfully integrated *DLh* ($r^2 = 0.563$) and *DoY* ($r^2 = 0.572$) effects on respiration rates of the Antarctic krill, *Euphausia superba*, yielding the minimum metabolic activity in mid-June and the maximum at the end of December. We could not detect *DLh* or *DoY* effects in the North Pacific krill *Euphausia pacifica*, and our findings for the North Atlantic krill *Meganyctiphanes norvegica* remained inconclusive because of insufficient seasonal data coverage. We strongly encourage comparative respiration measurements of worldwide Euphausiid key species at different seasons to improve accuracy in ecosystem modeling.

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1. Introduction

Knowledge of metabolic rates under different environmental conditions and from latitudinal and seasonally differing scenarios is central information in comparative modeling of trophic carbon transport and ecosystem energetic cycling. Euphausiids constitute a significant component in many marine ecosystems and often

several or even a single krill species connect primary production to apex predator trophic levels. Data on respiration rates of krill species have been collected since the 1960s as indicators for aerobic energy turnover. Recently Ikeda (2012) presented a step-wise multiple regression model (based on 39 sources of data sets composed of 24 species from various types of ecosystems) describing a significant dependence of krill respiration rates on body mass, habitat temperature, and water sampling depth. This first attempt to include water depth in a general Euphausiids respiration model indicated respiration rates to decline with water depth. The negative depth effect on krill metabolic rates was attributed to lower temperatures and diminishing oxygen concentrations at depth, affecting the Euphausiids when they migrate down at dusk (Enright, 1977). Further, Ikeda (2012) attributed the metabolic slowdown to a reduction of the energetic costs of swimming in the absence of visual predators in deep and dark oceanic layers.

Abbreviations: O₂, oxygen; DVM, diel vertical migration; *LAT*, latitude; *LON*, longitude; *D*, sampling water depth; *DoY*, day of year (1–365); *DLh*, number of daylight hours; *T*, measurement temperature (K); *M*, body mass (J); *RR*, specific respiration rate (J J⁻¹ day⁻¹); MLR, multiple regression model; ANN, artificial neural network; GAM, general additive model.

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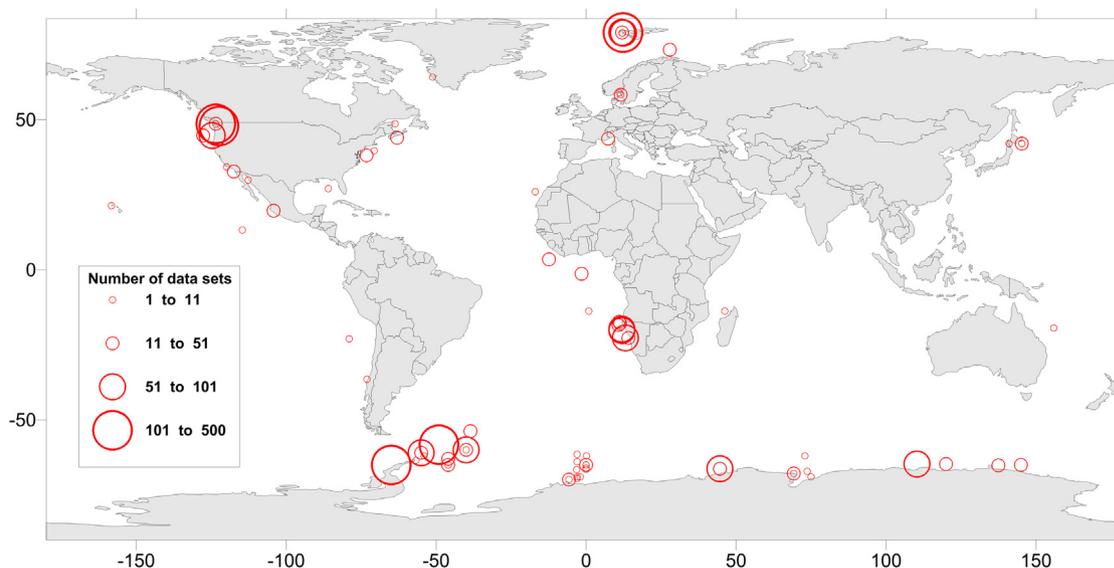


Fig. 1. Geographical visualization of Euphausiid data used in this analysis. The database consists of 2542 respiration data sets referring to 31 species collected from 51 different sources (Tremblay et al., 2014).

Identification of “depth” as a factor modulating respiration rates raises the need to understand which environmental factors determine the vertical distribution range of krill species and the time span during which they remain in the deep water layers. Indeed, important differences in timing and depth range of diel vertical migration (DVM) among seasons or under different oceanographic regimes (upwelling/downwelling) have been reported for Euphausiid species from different areas (Gaten et al., 2008; Taki, 2008; Tremblay et al., 2010; Sato et al., 2013; Werner and Buchholz, 2013; Haraldsson and Siegel, 2014). Hence we presume that, next to water depth, other factors related to season and photoperiod will affect Euphausiid respiration on a global scale and most likely at the species level, too.

Here we analyze a global respiration data compilation comprising 2479 respiration data sets from 23 species that includes the factors “latitude”, the “day of the year”, and the “number of daylight hours” as proxies for season and photoperiod. We intend to establish a corresponding general Euphausiid respiration model and to analyze seasonal patterns of respiration within single Euphausiid species.

2. Materials and methods

2.1. Initial data

Following the same criteria of data acquisition and conditioning of Brey (2010), we searched the literature for Euphausiid respiration data and added recent unpublished data provided by several colleagues. The database consists of 2542 respiration data sets referring to 31 species collected from 51 different sources (see Tremblay et al., 2014 for complete data base in PANGAEA; Fig. 1). In this excel file, the information about the setting (closed, semi-closed, or intermittent flow) and the method of measurement (chem for chemical, micro-optodes, polar for polarographic electrodes, manom for manometer, or gas for gas analyser) are also summarized. For statistical reasons, some data sets were excluded from further analysis (refer to Section 2.2), leaving us with 2479 data sets relating to 23 species (Figs. 2 and 3). In some cases, the public domain software ImageJ (<http://rsbweb.nih.gov/ij/>) was used to extract respiration data from figures.

Each data set included the following parameters:

- Sampling site latitude *LAT* and longitude *LON*;
- Sampling water depth *D* (m; in 261 cases the reported depth was <5 m, these numbers were set to $D=5$ m in order to avoid

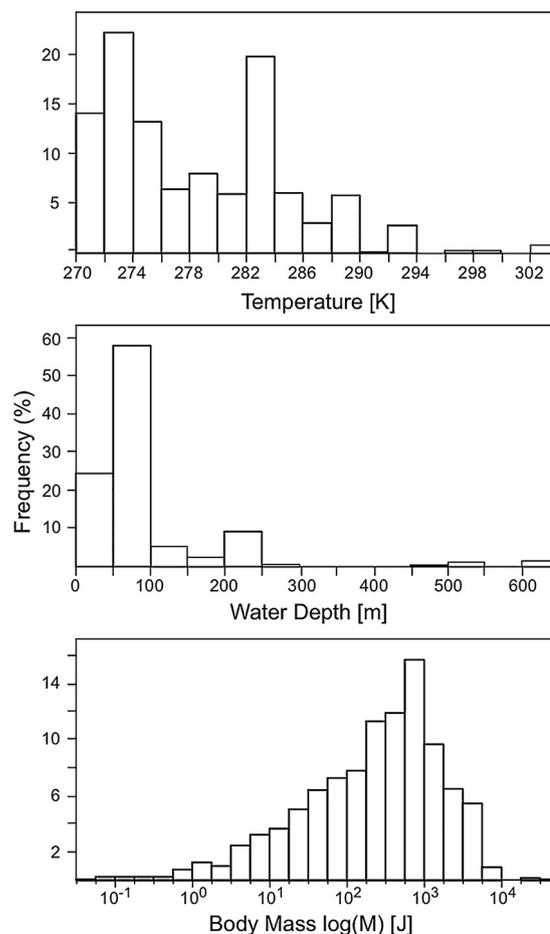


Fig. 2. Distribution of the 2479 respiration data sets with respect to water temperature (Kelvin), water depth (meters), and mean body mass (Joule).

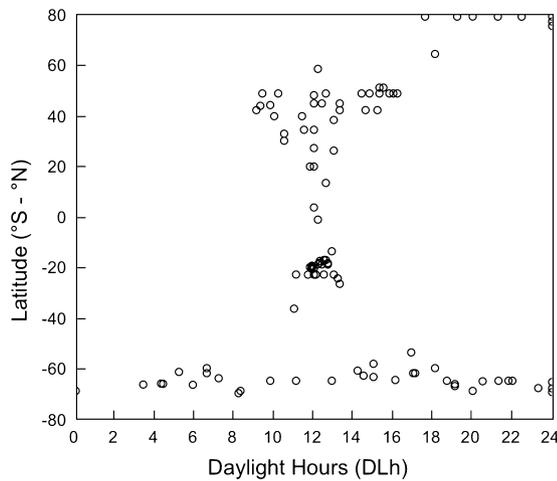


Fig. 3. Distribution of the 2479 respiration data sets with respect to daylight hours and geographical latitude.

disproportionate effects of very small depth values. In 311 cases with unknown sampling depth we set $D = 80$ m, i.e. average depth in all data sets; in a further 14 cases where divers sampled the animals we set $D = 5$ m;

- Day of the year DoY (day of year between 1 and 365); if a range of time was provided by the original source, we set $DoY =$ midday of this range. When DLh was set to 12 h (see below), DoY was set to 264 (which correspond to equinox of September 21th when the sun spends equal amount of time above and below the horizon at every location on the Earth, so night and day are about the same length), accordingly;
- Number of daylight hours DLh , calculated from LAT and DoY by the sunrise-sunset calculator (aa.usno.navy.mil/data/docs/RS_OneDay.php). A few publications summarized data over a time period of more than one year; here we set DLh to 12 h;
- Measurement temperature T (K);
- Body mass M (J), converted from original body mass units using factors provided as for Brey (2010), and other sources when necessary;
- Specific respiration rate RR ($JJ^{-1} day^{-1}$);
- Taxonomic information (species, genus, family).

2.2. Data transformation & pre-analysis

We decided to eliminate a priori four data sets with extreme water depth below 700 m. Subsequently, specific respiration rate RR , body mass M , temperature T and water depth D were transformed by approximating linear relationships between independent variables and RR according to theoretical considerations (e.g., Schmidt-Nielsen, 1984; Brown et al., 2004) and to empirical evidence (e.g. Seibel and Drazen, 2007; Brey, 2010) regarding the scaling of metabolic activity (see Brey, 2010 for a full discussion of this issue). These transformations – $\log(RR)$, $\log(M)$, $1/T$, $\log(D)$ – also facilitate a more even distribution of data and variance in the $[M, T, D]$ space. Multivariate outliers in the sample space $[\log(RR), \log(M), 1/T, \log(D)]$ were identified by Hotelling’s T^2 statistic (the square of the Mahalanobis distance; Barnett and Lewis, 1994; Prokhorov, 2001). Data sets with T^2 above the 97.5% percentile were excluded from further analysis, thus providing 2479 datasets referring to 23 species for statistical analysis (Figs. 2 and 3).

2.3. General Euphausiid respiration model

We applied fully factorial multiple regression models (MLR) as well as artificial neural network (ANN). MLRs may not appropriately

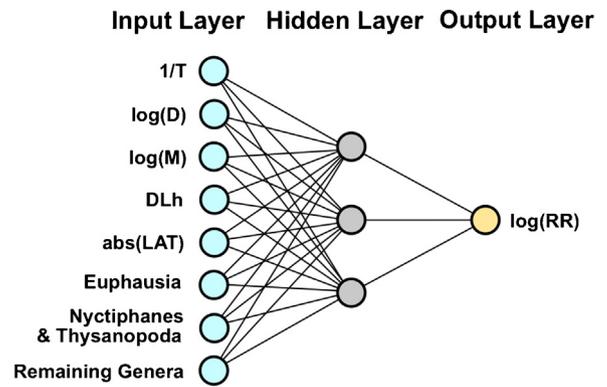


Fig. 4. Scheme of the artificial neural network (ANN) used to predict mass specific respiration rate RR in Euphausiids from five continuous parameters (temperature, water depth, body mass, daylight hours, latitude) and three taxonomic categories.

describe the existing relationships despite linearizing transformations (see above) and are quite sensitive to intercorrelation between independent parameters (Draper and Smith, 1998). This is the reason why we applied ANN of the backpropagation type (Hagan et al., 1996). ANN “learned” the relationship between dependent and independent variables from training data and was tested for its generalization capacity by comparing prediction accuracy with training (2/3) and test (1/3) data as measured by the correlation between measured RR_m and predicted RR_{ann} . An ensemble of five ANN, each trained on a bootstrapped random subsample, were pooled into a composite prediction model (see e.g., Boucher et al., 2010; Brey, 2010, 2012). Trial-runs with different sets of parameters indicated significant effects of DoY , DLh and $abs(LAT)$. We preferred DLh over DoY for model building as both parameters are strongly correlated, but DLh showed distinctly better performance. Taxonomic effects on RR were evident at the genus level and were covered by three groups, (A) *Euphausia*, (B) *Nyctiphanes* & *Thysanopoda*, (C) remaining genera (*Meganyciphanes*, *Nematoscelis*, *Thysanoessa*). Accordingly, the MLR model had eight input parameters:

$$\log(RR) = a + b_1 \times \frac{1}{T} + b_2 \times \log(D) + b_3 \times \log(M) + b_4 \times DLh + b_5 \times \text{abs}(LAT) + b_6 \times \text{genus.A} + b_7 \times \text{genus.C} + \text{interaction terms}$$

The interaction terms parameters were adjusted to mean = zero in order to render the test for the main effects independent of the test for interactions (“centered polynomials”). The ANN consisted of 8 input nodes, three hidden nodes (H), and one output node (Fig. 4). Trial runs indicated that three hidden nodes enabled the ANNs to learn properly without over-fitting. The network was parameterized as follows:

$$\log(RR) = a_0 + a_1 \times H_1 + a_2 \times H_2 + a_3 \times H_3$$

with

$$H_1 = \tan H(b_0 + b_1 \times 1/T + b_2 \times \log(D) + b_3 \times \log(M) + \dots b_8 \times \text{genus.C})$$

$$H_2 = \tan H(c_0 + c_1 \times 1/T + c_2 \times \log(D) + c_3 \times \log(M) + \dots c_8 \times \text{genus.C})$$

$$H_3 = \tan H(d_0 + d_1 \times 1/T + d_2 \times \log(D) + d_3 \times \log(M) + \dots d_8 \times \text{genus.C})$$

Note that internally the input data were normalized (mean=0, S.D.=1) and that the network parameter values were adjusted accordingly. In order to see whether or not certain input parameters enhanced ANN’s predictive power, we compared goodness of

fit of differently sized ANN by means of ANOVA of the correlation coefficients r^2 of individual ANN test and training subsets.

2.4. Seasonal respiration model for single Euphausiid species

We selected those Euphausiid species with a considerable number of data sets distributed throughout the year, i.e. *E. superba* ($N=875$), *E. pacifica* ($N=498$) and *M. norvegica* ($N=132$), for the analysis of seasonality in respiration rate. Other species showed great data sets, like *Euphausia hansenii* and *Thysanoessa inermis*, but their RR measurements were not covering a large range of DLh and DoY . In a first step, we used a fully factorial MLR to describe the effects of T , D , and M on RR (see above).

$$\log(RR) = a + b_1 \times \frac{1}{T} + b_2 \times \log(D) + b_3 \times \log(M) \\ + \text{interaction terms}$$

Subsequently, we checked the residuals of the MLR for effects of DoY and DLh on RR . We presumed that seasonal effects should manifest in a linear relationship between DLh and RR , and in a corresponding sinusoidal relationship between DoY and RR . When those relationships were present, we used general additive models (GAM; Hastie and Tibshirani, 1990) to gain a better understanding of the seasonal patterns in respiration rate. We added a term $f(X)$ to the MLR above that described the relationship between RR and DLh or DoY , respectively. The GAM equation takes the general form (MLR interaction terms neglected for clarity in this display)

$$\log(RR) = a_1 + b_1 \times \frac{1}{T} + b_2 \times \log(D) + b_3 \times \log(M) + b_4 \times f(X)$$

with $f(X) = a_2 + b_5 \times DLh$

$$\text{or } f(X) = a_2 + b_6 \times \sin\left(2\pi \times \frac{DoY}{365 - a_3}\right)$$

3. Results

3.1. General Euphausiid respiration model

The MLR approach resulted in a very complex model with seven interaction terms ($r^2=0.680$, all terms significant at $P<0.05$, model not shown). The corresponding ANN model showed a distinctly better fit ($r^2=0.780$, Table 1, Fig. 5; see spreadsheet “Respir EuphausiaceaANN.xlsx” downloadable at <http://www.thomas-brey/science/virtualhandbook>). ANN predictive performance increased significantly ($P<0.05$) with increasing number of input parameters from three ($1/T$, $\log(D)$, $\log(M)$), to five (DLh and LAT included) to eight parameters (three genus terms included). The corresponding overall correlation between mean ANN prediction RR_{ann} and measured RR_m was $r^2 = 0.732$, 0.760 , and 0.780 , respectively. ANOVA further indicated that there were no differences in goodness of fit between test and training data sets. The contour plot in Fig. 6 demonstrates the effect of DLh and of LAT on RR_{ann} .

3.2. Seasonal respiration model for single Euphausiid species

3.2.1. Euphausia superba

Of the total 2479 Euphausiid data sets, 875 sets collected from 20 sources referred to *E. superba* (Fig. 7). We detected significant effects ($P<0.001$) of DLh and DoY on RR (Fig. 8). The corresponding GAM (Table 2, Fig. 9) fitted the data distinctly better than the basic MLR ($r^2 = 0.561$ and 0.572 compared to 0.440). Furthermore, depth D did not contribute significantly to GAM predictive power and was therefore removed from the GAM equations. Fig. 9 indicates that the

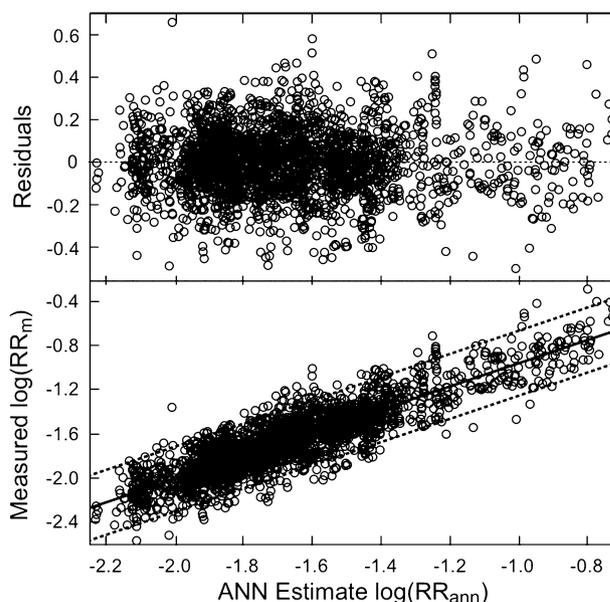


Fig. 5. Relationship between measured RR_m and ANN predicted RR_{ann} (below) and corresponding residual plot (above). See Table 1 for ANN model parameters. Stippled lines indicate 95% confidence range of predictions.

GAM term fully accounted for seasonal effects in RR . These effects were visualized in the contour plots in Fig. 10.

3.2.2. Euphausia pacifica

Of the 498 *E. pacifica* data sets (11 sources), one proved to be a consistent and distinct outlier in all models and was therefore excluded from further analysis. A fully factorial MLR analysis indicated significant effects of T , D , and M on RR as well as significant interactions between independent parameters (Table 3). There was a weak albeit significant sinusoidal relationship between the residuals of the MLR model and DoY ($r^2=0.099$, $P<0.001$), and a significant negative relationship between MLR residuals and DLh ($r^2=0.137$, $P<0.001$). We checked whether or not these relationships were artificially caused by one single source by means of excluding one source (with ≥ 10 data sets) in turn from the residual analysis. The removal of the data published by Paranjape (1967) rendered the effects of DoY and DLh insignificant (see Fig. 11). Hence

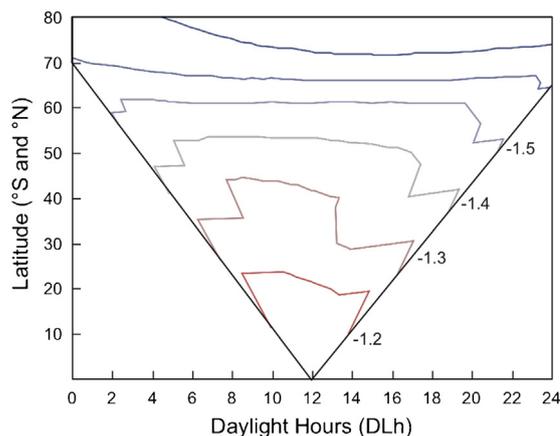


Fig. 6. Contour plot of RR_{ann} predicted by the Euphausiid global respiration model (ANN) in the daylight hours DLh versus geographical latitude LAT (north and south combined) space. DLh (as well as temperature) has been restricted to the range defined by geographical latitude. RR_{ann} represents an average for body mass 0.1, 1, 10, 100, and 1000J.

Table 1

Euphausiid global respiration model. genus. A: Euphausia, genus. B: Nyctiphanes & Thysanopoda, genus. C: remaining genera. r^2_{train} , r^2_{test} , r^2_{ann} : correlation between measured and predicted RR in training (N=1652) and test data (N=826); r^2_{ann} : correlation between measured RR and average prediction of the 5 ANN.

$$\log(RR) = a_0 + a_1 \times H_1 + a_2 \times H_2 + a_3 \times H_3$$

$$H_1 = \tan H(b_0 + b_1 \times 1/T + b_2 \times \log(D) + b_3 \times \log(M) + b_4 \times DLh + b_5 \times \text{abs}(LAT) + b_6 \times \text{genus.A} + b_7 \times \text{genus.B} + b_8 \times \text{genus.C})$$

$$H_2 = \tan H(c_0 + c_1 \times 1/T + c_2 \times \log(D) + c_3 \times \log(M) + \dots + c_8 \times \text{genus.C})$$

$$H_3 = \tan H(d_0 + d_1 \times 1/T + d_2 \times \log(D) + d_3 \times \log(M) + \dots + d_8 \times \text{genus.C})$$

	ANN1	ANN2	ANN3	ANN4	ANN5
$a_0 =$	-1.57197	-1.51099	-1.57066	-1.64152	-1.57065
$a_1 =$	0.38857	-0.21050	0.17855	0.38984	-0.45136
$a_2 =$	-1.37002	0.38061	-1.04624	-0.47103	0.21583
$a_3 =$	-0.42258	-0.19251	0.42496	-1.01710	-0.13727
$b_0 =$	-86.77930	-194.63700	-125.32500	33.20542	-47.94690
$b_1 =$	27,854.45	57,230.88	14,617.81	-9652.23	16,404.96
$b_2 =$	2.59290	-0.12465	-18.67730	2.36937	-1.00100
$b_3 =$	1.04828	-0.49462	9.78115	0.15848	0.96578
$b_4 =$	-0.39650	-0.02417	2.91508	0.19465	-0.05447
$b_5 =$	-0.12200	-0.14740	0.62981	-0.07905	-0.04532
$b_6 =$	-0.67903	0.75253	-2.30198	-3.28122	0.94072
$b_7 =$	-5.14599	-0.37181	10.78545	-0.46730	-8.10712
$b_8 =$	1.10279	-1.23824	2.61575	-2.55901	-0.08386
$c_0 =$	-9.85757	2.09214	-18.65530	35.89489	95.61789
$c_1 =$	2298.77	2022.25	4485.97	-4279.08	-12,644.40
$c_2 =$	0.82025	-1.20340	0.13205	-4.02182	-0.43695
$c_3 =$	0.36519	-1.70364	0.68528	-2.99786	-5.58249
$c_4 =$	0.00655	-0.03503	0.11844	0.01114	-1.05142
$c_5 =$	0.00417	-0.00413	-0.00873	-0.15218	-0.29912
$c_6 =$	-0.25620	0.32410	0.57758	-1.74016	5.36206
$c_7 =$	-0.41454	1.35509	0.36973	0.78609	-9.49179
$c_8 =$	0.32634	-2.09254	0.73716	-2.36783	-5.76894
$d_0 =$	-92.03570	-84.04100	32.26541	-22.47070	-110.62100
$d_1 =$	28,677.77	25,377.93	-7718.31	4158.86	-23,008.00
$d_2 =$	-2.10915	-0.20977	0.56556	2.17255	128.19910
$d_3 =$	0.12831	3.43577	0.76223	1.27308	0.39724
$d_4 =$	-0.18612	-0.35817	0.26208	0.07651	0.22187
$d_5 =$	-0.11352	-0.22685	-0.14171	0.02428	0.23487
$d_6 =$	1.00402	4.27923	-0.75113	-0.72823	-4.39197
$d_7 =$	0.95282	5.95089	-0.63204	-1.12687	-54.49430
$d_8 =$	-1.12534	-3.35537	-0.38697	-0.34093	5.77147
$r^2_{train} =$	0.756	0.746	0.740	0.744	0.746
$r^2_{test} =$	0.751	0.746	0.741	0.740	0.760
$r^2_{ann} =$	0.780				
N=	2479				

the available data did not provide sufficient evidence for a clear effect of seasonality on RR in *E. pacifica*.

3.2.3. *Meganyctiphanes norvegica*

A fully factorial MLR analysis of the 132 *M. norvegica* data sets (7 sources) indicated significant effects of T, D, and M on RR

(Table 3). There was no significant sinusoidal relationship between the residuals of the MLR model and DoY ($P=0.941$). However, MLR residuals correlated negatively with DLh (slope = -0.012, $r^2 = 0.186$, $P < 0.001$, Fig. 12). As there were no data available for DLh < 8 h, the seasonal pattern in *M. norvegica* metabolic activity remains inconclusive.

Table 2

Euphausia superba respiration models. Only significant terms ($P < 0.05$) are shown. Note the adjustment to mean = zero for log(M), 1/T and DLh.

Multiple Linear Regression (MLR)	General Additive Model (GAM) with DLh	General Additive Model (GAM) with DoY
$\log(RR) = a + b_1 \times 1/T + b_2 \times \log(D) + b_3 \times \log(M) + b_4 \times (1/T - 0.00366) \times \log(M - 2.6409) + b_5 \times (1/T - 0.00366) \times \log(D - 1.4751)$	$\log(RR) = a_1 + b_1 \times 1/T + b_2 \times \log(M) + b_3 \times (1/T - 0.00366) \times \log(M - 2.6409) + b_4 \times f(DLh)$	$\log(RR) = a_1 + b_1 \times 1/T + b_2 \times \log(M) + b_3 \times (1/T - 0.00366) \times \log(M - 2.6409) + b_4 \times f(DoY)$
$a = 14.4498$ $b_1 = -4301.6310$ $b_2 = -0.1298$ $b_3 = -0.1196$ $b_4 = -1105.8590$ $b_5 = 2804.0944$	$f(DLh) = a_2 + b_5 \times (DLh - 14.1929)$ $a_1 = 14.9328$ $a_2 = 257.2753$ $b_1 = -4501.6350$ $b_2 = -0.1688$ $b_3 = -835.8796$ $b_4 = 0.00068$ $b_5 = 33.4871$	$f(DoY) = a_2 + b_5 \times \sin(2\pi \times (DoY/365 - b_6))$ $a_1 = 11.0246$ $a_2 = 91.2073$ $b_1 = -3387.1049$ $b_2 = -0.1684$ $b_3 = -1300.6526$ $b_4 = -0.000084$ $b_5 = 185.3023$ $b_6 = 0.2650$
N=875 $r^2 = 0.440$	N=875 $r^2 = 0.563$	N=875 $r^2 = 0.572$

Table 3
Multiple Linear Regression (MLR) of *Euphausia pacifica* and *Meganctiphanes norvegica* respiration. Only significant terms ($P < 0.05$) are shown. For *E. pacifica*, MLR model uses temperature only in the interaction term $1/T \times \log(D)$, the single temperature term was not significant. Mean = zero for $\log(M)$, $1/T$, DoY , and DLh . For *M. norvegica*, MLR model uses depth only in the interaction term $\log(D) \times \log(M)$, the single depth term was not significant.

E. pacifica

$$\log(RR) = a + b_2 \times \log(D) + b_3 \times \log(M) + b_4 \times (1/T - 0.00353) \times \log(D - 1.8037) + b_5 \times \log(D - 1.8037) \times \log(M - 1.80367)$$

$a = -0.3437$ $b_2 = -0.4294$ $b_3 = -0.1664$ $b_4 = -5019.8520$ $b_5 = 0.3757$
 $N = 497$ $r^2 = 0.494$

M. norvegica

$$\log(RR) = a + b_1 \times 1/T + b_2 \times \log(M) + b_3 \times \log(D - 1.9689) \times \log(M - 2.70036)$$

$a = 8.4833$ $b_1 = -2763.9620$ $b_2 = -0.1103$ $b_3 = -0.5963$
 $N = 132$ $r^2 = 0.526$

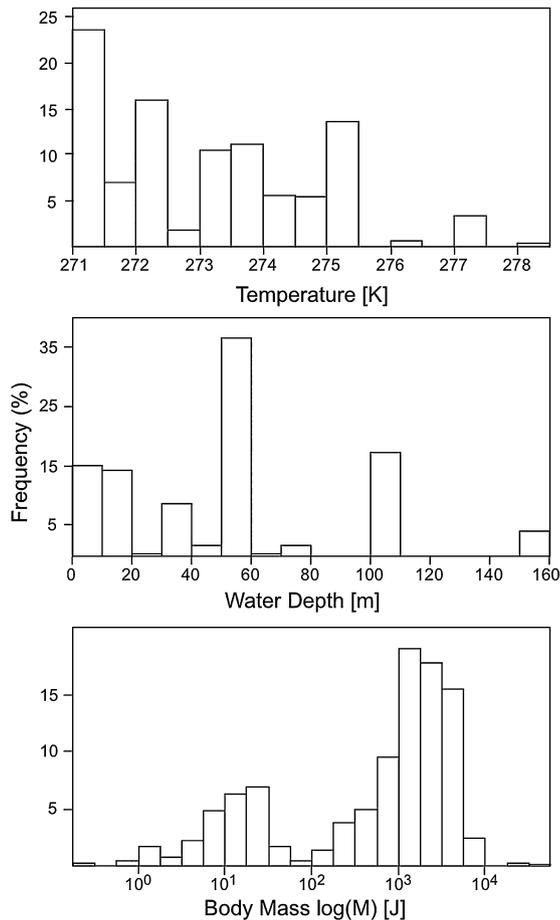


Fig. 7. *Euphausia superba*: Distribution of the 875 data sets used for model building with respect to water temperature (Kelvin), water depth (meters), and mean body mass (Joule).

4. Discussion

4.1. General Euphausiid respiration model

The ANN model confirms that geography (LAT) and seasons (DLh) should be considered in a global Euphausiid respiration model, additionally to the main parameters presented by Ikeda (2012; biomass, depth and temperature). The ANN model also highlights a taxonomic influence on the respiration rates. The good model fit ($r^2 = 0.780$) is confirmed by an acceptable residual variance, that is narrower than in a previous aquatic invertebrate respiration ANN in which Euphausiids represented only 3% of the data sets (Brey, 2010). The three taxonomic groups identified may, to some extent, relate to the geographical distribution of the corresponding genera. *Meganctiphanes* and *Thysanoessa* are mainly present beyond $50^\circ N$, while *Nematoscelis* are found around 40° in

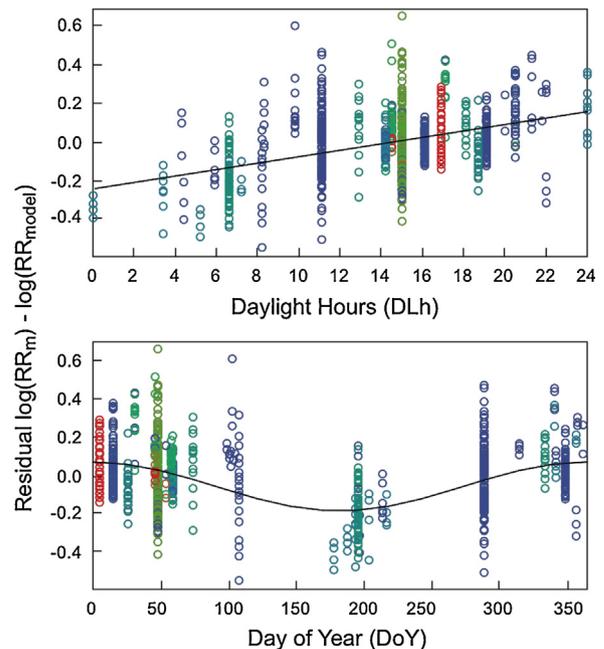


Fig. 8. *Euphausia superba*: Residuals of Multiple Linear Regression (MLR) (see Table 2 for model parameters) plotted versus Daylight hours (DLh) and Day of Year DoY . There is a significant linear relationship between residuals and DLh ($r^2 = 0.179$, $P < 0.001$) and a significant sinusoidal relationship between residuals and DoY ($r^2 = 0.176$, $P < 0.001$). Colors indicate temperature at measurement ranging from 271 K (blue) to 278 K (red).

both hemispheres. *Nyctiphanes* and *Thysanopoda* species predominate around 30° latitude in the data sources.

According to the present ANN model, Euphausiid specific respiration rate RR decreases with higher latitude and decreasing DLh . The latitudinal influence is related to both body mass and temperature changes and follows the pattern observed by Ikeda (1985a) from net zooplankton community respiration. The DLh or photoperiod length correlates with high productivity events (spring bloom) at higher latitudes, which probably cause enhanced feeding activities and higher metabolic rates. However, the influence of DLh , LAT and genus should not be over-interpreted. We cannot be sure whether we see a truly generalizable pattern of respiration, or whether this pattern represents an empirical best fit of the data, forced by the uneven geographical and seasonal distribution of species and data sources. The only latitude at which almost all day lengths (light hours) occur throughout the year is at $60^\circ S$, where measurements are available for only one species, *E. superba*.

4.2. Seasonal respiration models for single Euphausiid species

4.2.1. *Euphausia superba*

E. superba is the best and most extensively studied species both in terms of seasonal differences as well as geographically, rendering a large and comprehensive data set available for our GAM

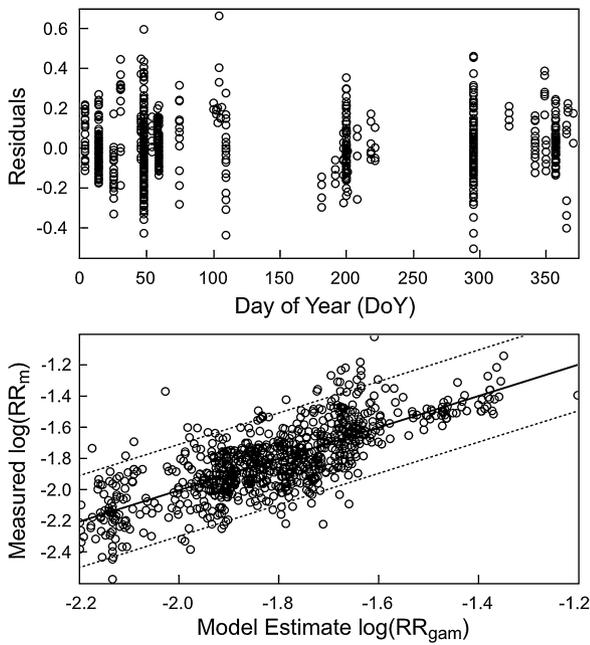


Fig. 9. *Euphausia superba*: Goodness of fit of the General Additive (GAM) model with DoY term (see Table 2 for model parameters). Plot of residuals versus DoY indicates no significant relationship ($P > 0.1$).

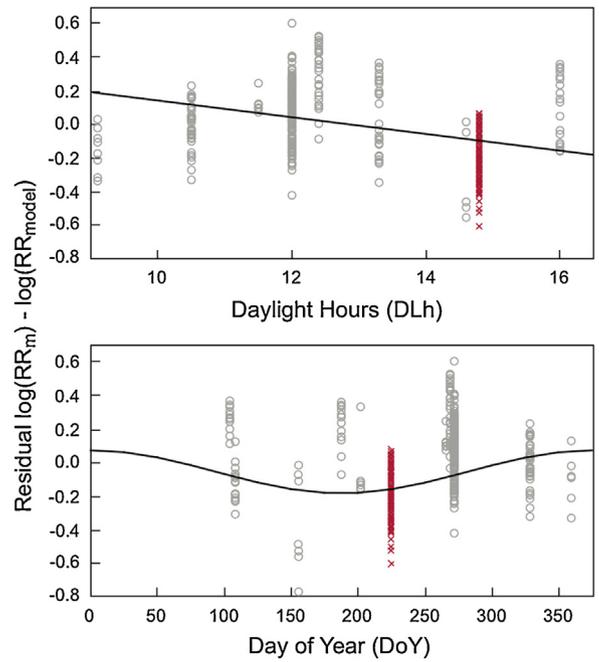


Fig. 11. *Euphausia pacifica*: Residuals of Multiple Linear Regression (MLR) (see Table 3 for model parameters) plotted versus Daylight Hours (DLh) and Day of Year DoY. The significant linear negative relationship with DLh (slope = -0.048 , $r^2 = 0.137$, $P < 0.001$) as well as the sinusoidal relationship with DoY ($r^2 = 0.099$, $P < 0.001$) becomes insignificant when the data of Paranjape (1967, cross symbols) are excluded.

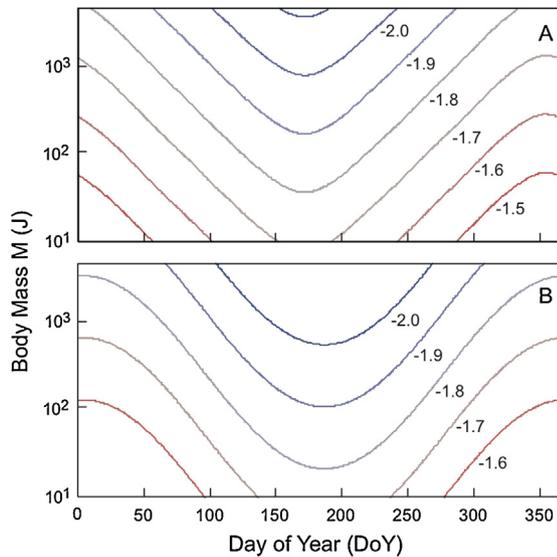


Fig. 10. *Euphausia superba*: Contour plot of RR_{gam} predicted by the General Additive (GAM) models in the day of the year DoY versus bodymass $\log(M)$ space. Model with DLh term (A) and with DoY term (B), see Table 2 for model parameters. The relationship between DoY and DLh used in (A) refers to $62^\circ S$, i.e. the average latitude in all 875 data sets.

approach. The GAM indicates DLh and DoY to be explanatory variables for RR whereas it excluded D, presumably because sampling occurred almost exclusively within the upper 80 m of the water column and therewith in a narrow depth range. Including the DLh term in the model revealed minimum metabolic activity in mid-June as opposed to a metabolic maximum at the end of December. A linear dependency of RR on photoperiod (DLh) and the seasonal sinusoidal trend with DoY was found by Meyer (2011), who reviewed investigations on seasonal metabolic activity of krill in different regions of the Southern Ocean. Our study confirms those earlier findings, but on a broad base of data from different studies looking at animals

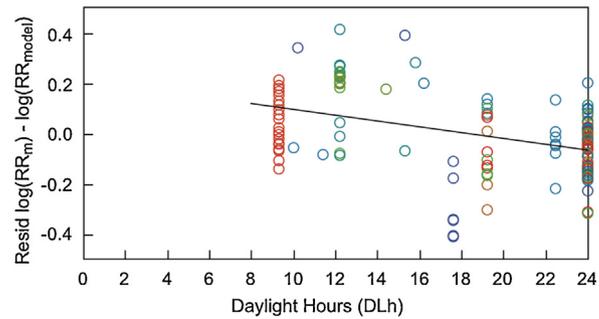


Fig. 12. *Meganyctiphanes norvegica*: Residuals of Multiple Linear Regression (MLR) (see Table 3 for model parameters) plotted versus Daylight Hours (DLh). Significant linear negative relationship with DLh (slope = -0.012 , $r^2 = 0.186$, $P < 0.001$). Colors indicate temperature at measurement ranging from 273 K (blue) to 289 K (red).

from regions across the whole Antarctic Ocean. This pattern shows evidence for a general metabolic strategy in *E. superba*, which has been investigated from the molecular (Seear et al., 2009; Teschke et al., 2011) to the organism level (Atkinson et al., 2002; Teschke et al., 2007; Gaten et al., 2008; Pape et al., 2008; Brown et al., 2013). Although, the signaling cascade that links the photoperiod cue to the target response still remains unknown, the photoperiodic cycle clearly seems to act as a major Zeitgeber for the seasonal cycle of RR, suggesting that krill has evolved an endogenous time keeping system that perceives seasonal variations in photoperiod (Meyer, 2011). Teschke et al. (2011) identified an endogenous circadian timing system in Antarctic krill and found evidence for its link to metabolic key processes on a 24 h basis, which could also be involved in the control of seasonal events. Thus, the seasonal cycle of RR in krill could be linked to an endogenous timing system, synchronized with the seasonal course of photoperiod in the environment. In a long-term experimental study lasting several years,

Brown et al. (2013) maintained *E. superba* first under simulated natural photoperiod, before they exposed part of the group to complete darkness and variable food availability and temperature over several months. These experiments showed that *E. superba* maintained similar *RR* patterns under constant darkness as under a simulated natural light regime. The authors suggested an endogenous rhythm of *RR* that was naturally “imprinted” and sustained during the one-year experimental acclimatization period under the natural light cycle. The sinusoidal pattern shown by the GAM therefore represents an applicable tool for the investigation of deviations from the “internal clock” mechanism (Kawaguchi et al., 2007; Seear et al., 2009; Brown et al., 2011; Meyer, 2011; Teschke et al., 2011) by revealing conditions that cause divergence from the theoretical annual pattern of synchronized respiration.

4.2.2. *Euphausia pacifica* and *Meganyctiphanes norvegica*

Unfortunately much less data sets are available for *E. pacifica* and *M. norvegica* than for *E. superba*. These two species are widely distributed over the north Pacific and Atlantic (from 27.50 to 65.67° N and 29.94 to 71.14° N, respectively; Brinton et al., 2003, updated 2008), and the data sets are geographically wide spread, accordingly, making difficult to detect significant seasonal patterns. In *E. pacifica*, detection of *DoY* or *DLh* effects depended exclusively on the data set of Paranjape (1967), data which were treated as outlier also in earlier studies, as the reported *RR* is conspicuously low (Ikeda et al., 2000). This is thought to reflect the permanent anoxic conditions in the deep waters of Saanich Inlet (Canada; Ikeda et al., 2000).

In *M. norvegica*, the available data indicate a negative correlation between the MLR residuals and *DLh* (Fig. 12), i.e. just the opposite of the relationship found in the Antarctic *E. superba*. However, our data base does neither represent the full range of *DLh* nor the natural temperature range experienced by *M. norvegica*. There is some evidence for seasonal patterns in respiration of this species at lower latitudes (43° N, Saborowski et al., 2002), but more data covering a wider range of the natural conditions experienced by *M. norvegica* are required for the establishment of a reliable model.

5. Conclusion

The present work confirms the effect of latitude, the day of the year of measurement, and the number of daylight hours on the respiration of Euphausiids. With this model we display the current global state of knowledge with respect to metabolic measurements available for some of the major Euphausiids, indicating where (degree of latitude) and when (time of the year) data are available or missing. Many existing data gaps with respect to both, degree of latitude and timing, call for better coverage to improve future modeling attempts. The highest data coverage for the GAM model was available for the Antarctic krill *E. superba*, which helped to simulate and put numbers to the strong seasonal metabolic adjustments observed in this species.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2014.07.031>.

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