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

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Running headline: General model for Euphausiid respiration

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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 modelling.

Key-words

Euphausia superba; *Euphausia pacifica*; *Meganyctiphanes norvegica*; factorial multiple regression; artificial neural network; general additive model; respiration data sets;

Highlights

- We present an Artificial Neural Network (ANN) model on Euphausiid respiration rate.
- ANN includes effects of latitude *LAT*, day of the year *DoY*, and daylight hours *DLh*.
- General additive models (GAM) with *DLh* and *DoY* were test in *Euphausia superba*.
- GAM indicates low metabolic activity in mid-June and high at the end of December.

Abbreviations

O_2: oxygen; DVM: diel vertical migration; *LAT*: latitude; *LON*: longitude; *D*: sampling water depth; *DoY*: day of year (1 to 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

1. Introduction

Knowledge of metabolic rates under different environmental conditions and from latitudinal and seasonally differing scenarios is central information in comparative modelling 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 1960's as indicators for aerobic energy turnover. Recently Ikeda (2012) presented a stepwise 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. 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 analyse 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 analyse 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 data base 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 subsection *2.2. Data transformation & pre-analysis*), leaving us with 2479 data sets relating to 23 species (Fig. 2, 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 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 12h (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 12h;
- 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* (J J^{-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 (Fig. 2, 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 describe the existing relationships despite linearizing transformations (see above) and are quite sensitive to intercorrelation between independent parameters (Draper and Smith, 1981). 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

(*Meganyctiphanes*, *Nematoscelis*, *Thysanoessa*). Accordingly, the MLR model had eight input parameters:

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

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 ("centred 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

$$H_1 = \tanh(b_0 + b_1 \times 1/T + b_2 \times \log(D) + b_3 \times \log(M) + \ldots b_8 \times \mathrm{genus.C})$$
$$H_2 = \tanh(c_0 + c_1 \times 1/T + c_2 \times \log(D) + c_3 \times \log(M) + \ldots c_8 \times \mathrm{genus.C})$$
$$H_3 = \tanh(d_0 + d_1 \times 1/T + d_2 \times \log(D) + d_3 \times \log(M) + \ldots d_8 \times \mathrm{genus.C})$$

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 hanseni* 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).

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

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)

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

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

or $f(X) = a_2 + b_6 \text{ x } \sin(2\pi \text{ x } (DoY/365 - a_3))$

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 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 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 sinusoideal 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* <8h, the seasonal pattern in *M. norvegica* metabolic activity remains inconclusive.

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. *Meganyctiphanes* and *Thysanoessa* are mainly present beyond 50°N, while *Nematoscelis* are found around 40° in 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 (1985) 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°S, where measurements are available for only one species, *Euphausia 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 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 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 modelling attempts. The highest data coverage for the GAM model was available for the Antarctic krill *Euphausia superba*, which helped to simulate and put numbers to the strong seasonal metabolic adjustments observed in this species.

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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.

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

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

$$H_2 = \tanh(c_0 + c_1 \times 1/T + c_2 \times \log(D) + c_3 \times \log(M) + \ldots c_8 \times \mathrm{genus.C})$$

$$H_3 = \tanh(d_0 + d_1 \times 1/T + d_2 \times \log(D) + d_3 \times \log(M) + \ldots d_8 \times \mathrm{genus.C})$$

	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
$b_1 =$	27854.45	57230.88	14617.81	-9652.23	16404.96
$b_2 =$	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	-12644.40
$c_2 =$	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	-0.09131	-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
$d_1 =$	28677.77	25377.93	-7718.31	4158.86	-23008.00
$d_2 =$	-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				

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

Table 3. Multiple Linear Regression (MLR) of *Euphausia pacifica* and *Meganyctiphanes 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

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

$a = -0.3437$ $b_2 = -0.4294$ $b_3 = -0.1664$ $b_4 = -5019.8520$ $b_5 = 0.3757$

$N = 497$ $r^2 = 0.494$

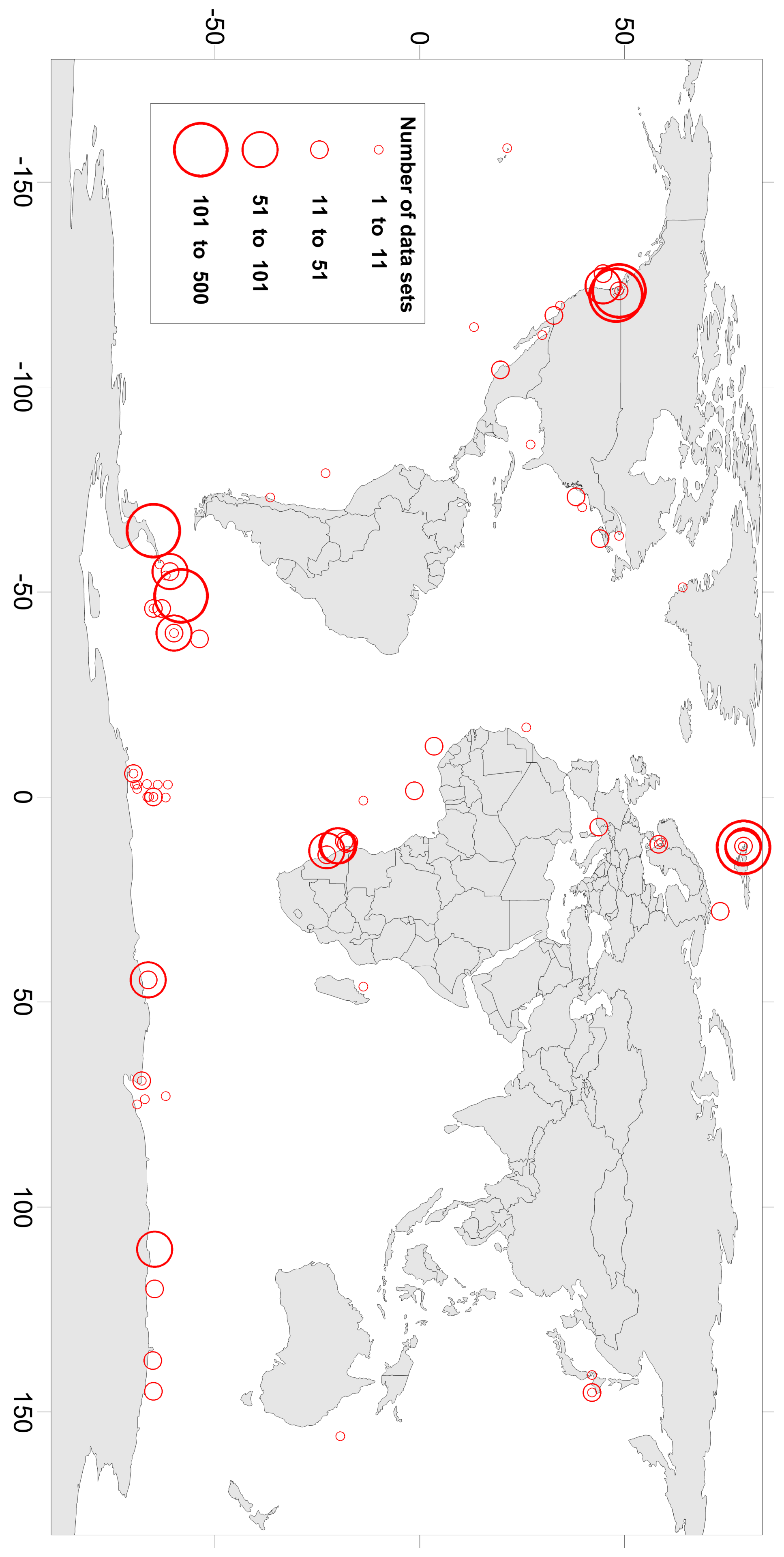
M. norvegica

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

$a = 8.4833$ $b_1 = -2763.9620$ $b_2 = -0.1103$ $b_3 = -0.5963$

$N = 132$ $r^2 = 0.526$

Fig. 1



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101 to 500
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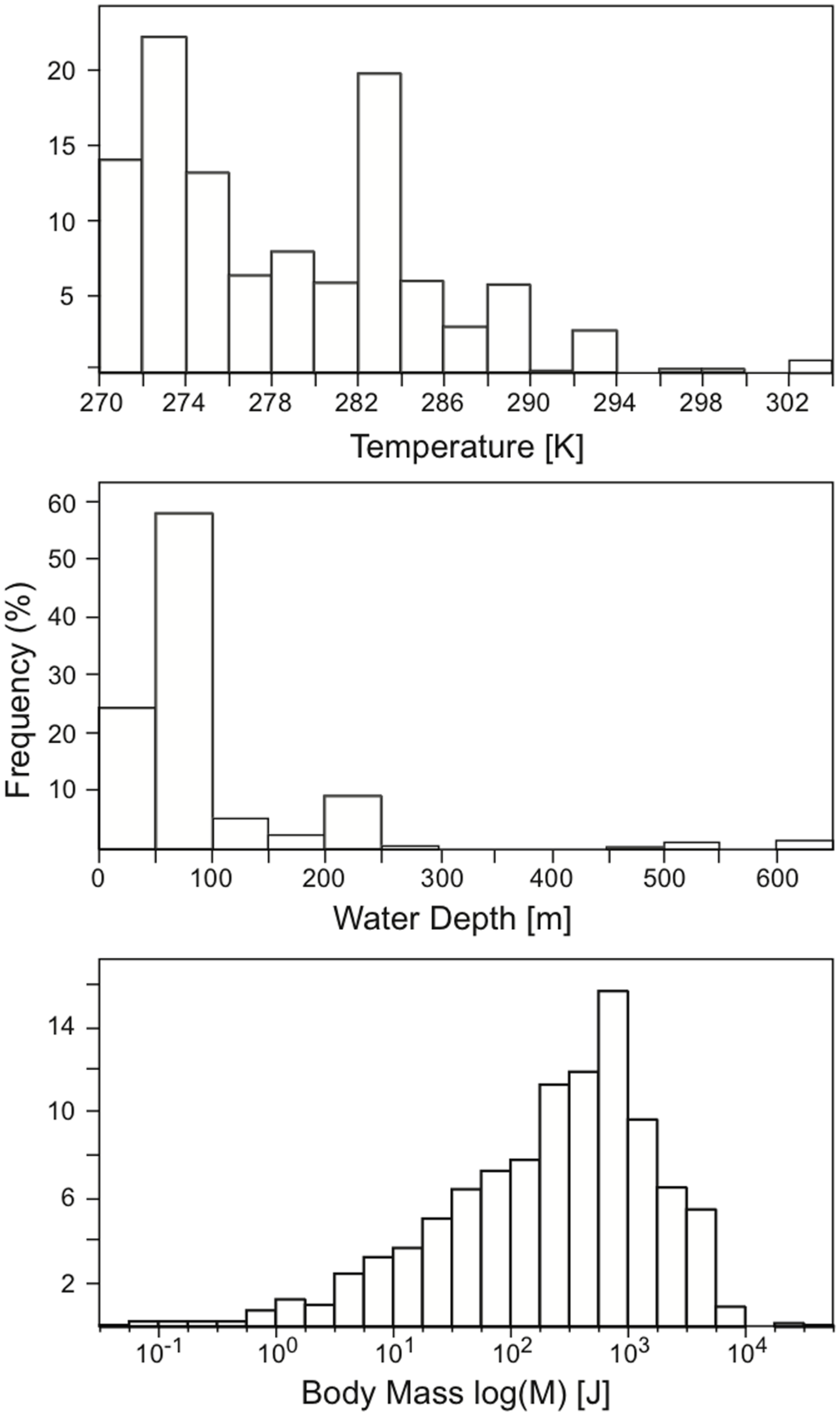
-50
0
50
100
150

Fig. 2



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Frequency (%)
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30
20
10
0
100
200
300
400
500
600
Water Depth [m]
14
10
6
2
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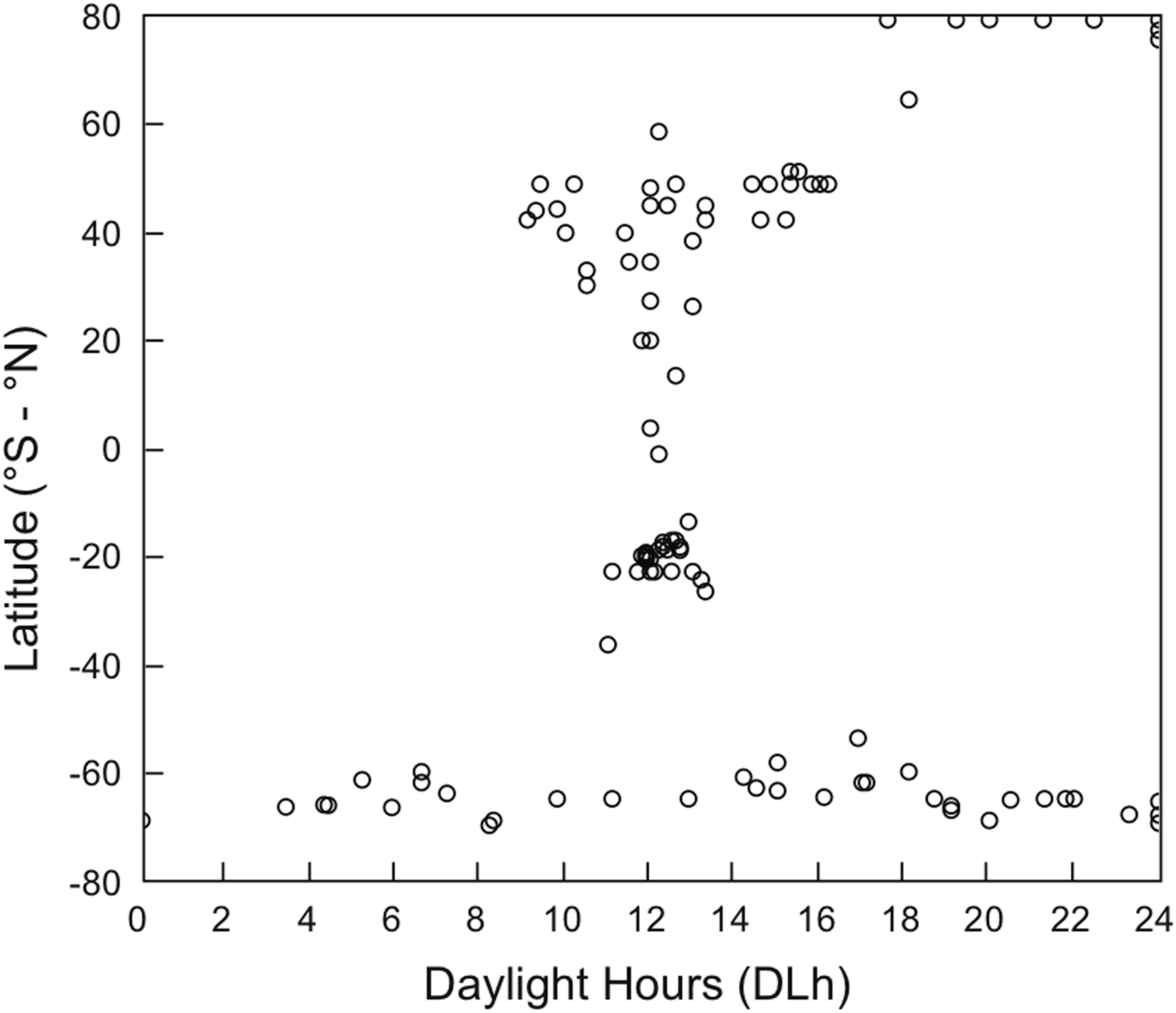
10^{0}
10^{1}
10^{2}
10^{3}
10^{4}
Body Mass log(M) [J]

Fig. 3



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-60
-80
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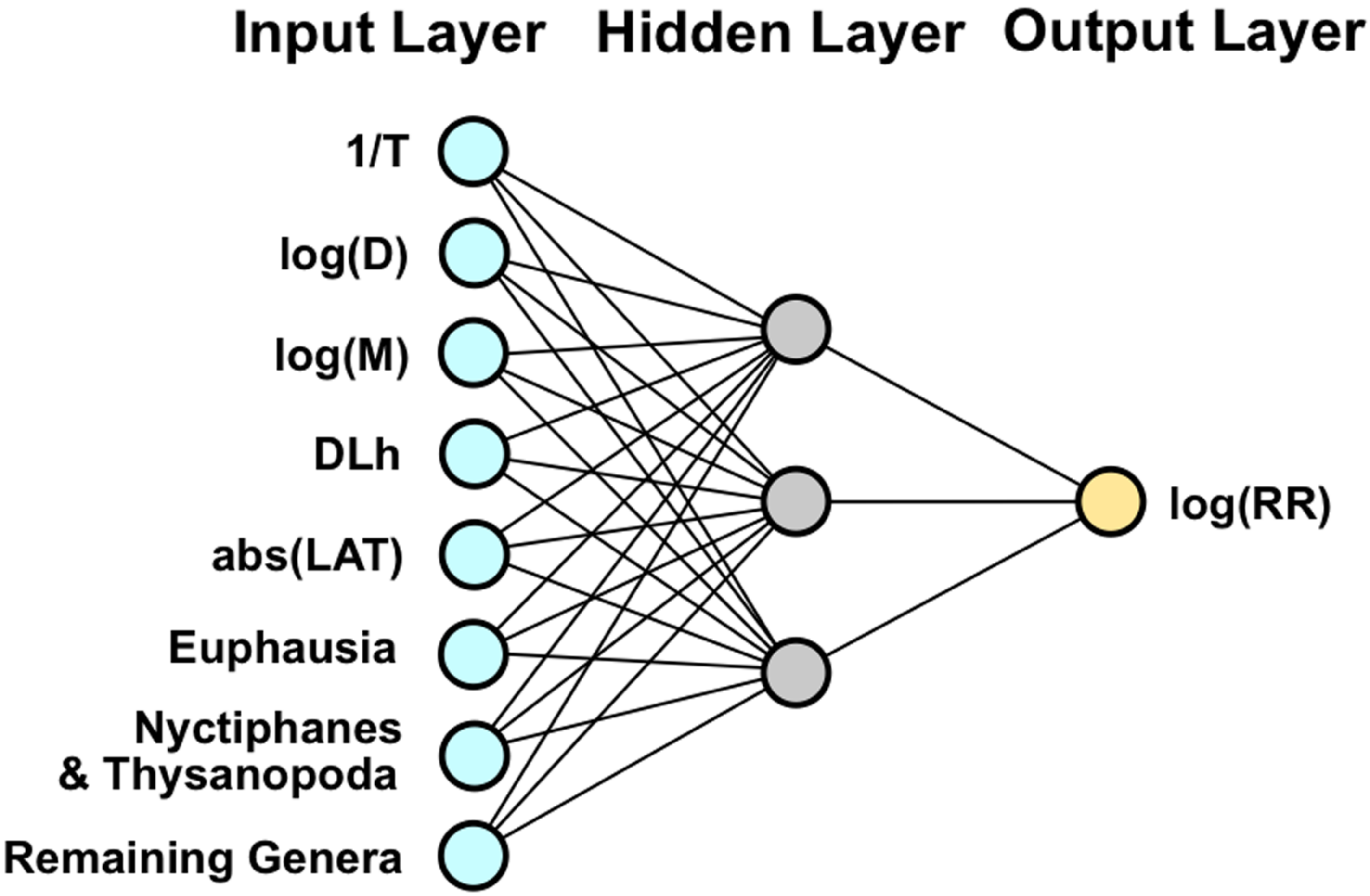
14
16
18
20
22
24
Daylight Hours (DLh)

Fig. 4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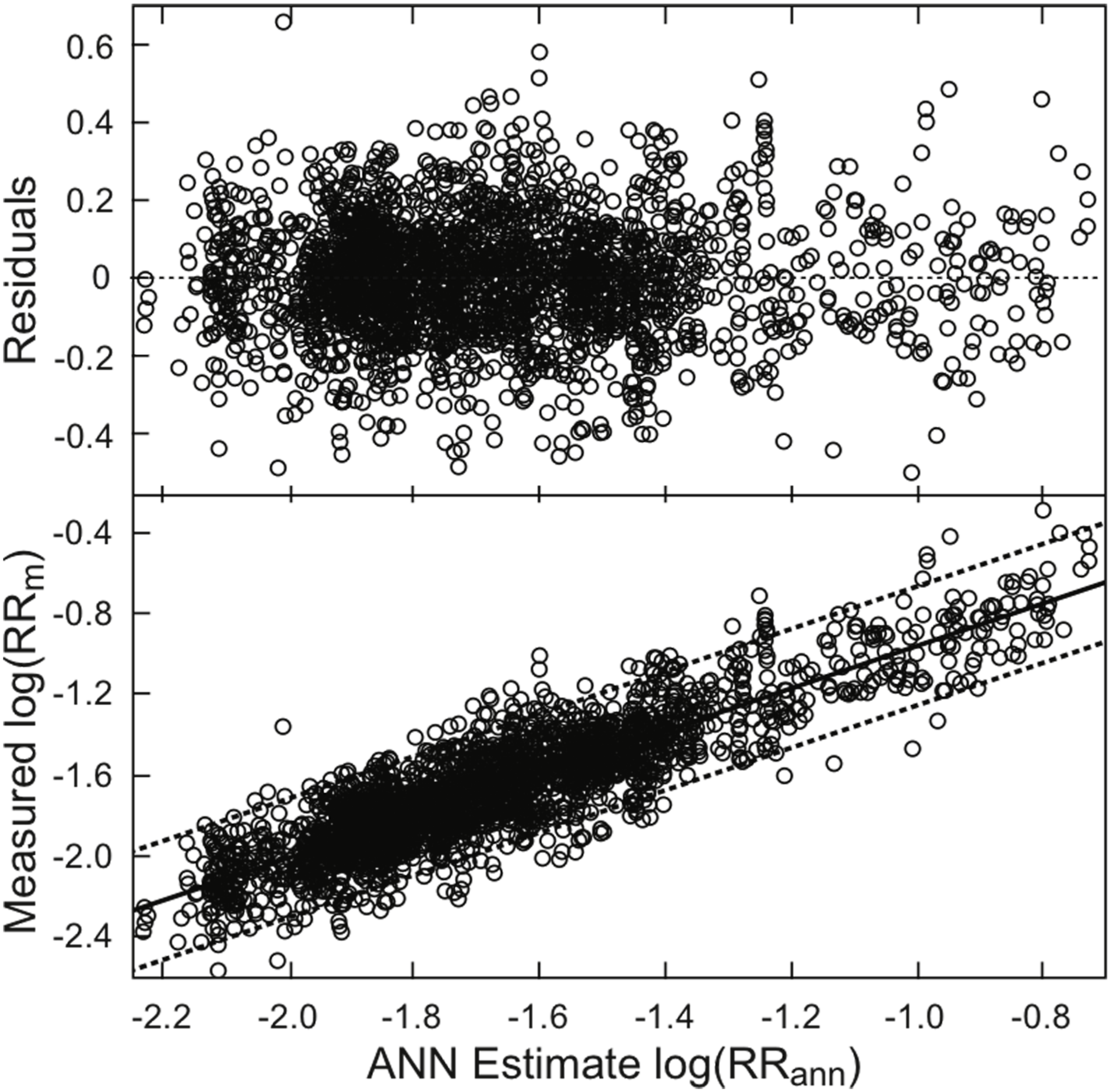
Hidden Layer
Output Layer
1/T
log(D)
log(M)
DLh
abs(LAT)
Euphausia
Nyctiphanes
& Thysanopoda
Remaining Genera
log(RR)

Fig. 5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0.4
0.2
0
-0.2
-0.4
Measured log(RR_m)
-0.4
-0.8
-1.2
-1.6
-2.0
-2.4
-2.2
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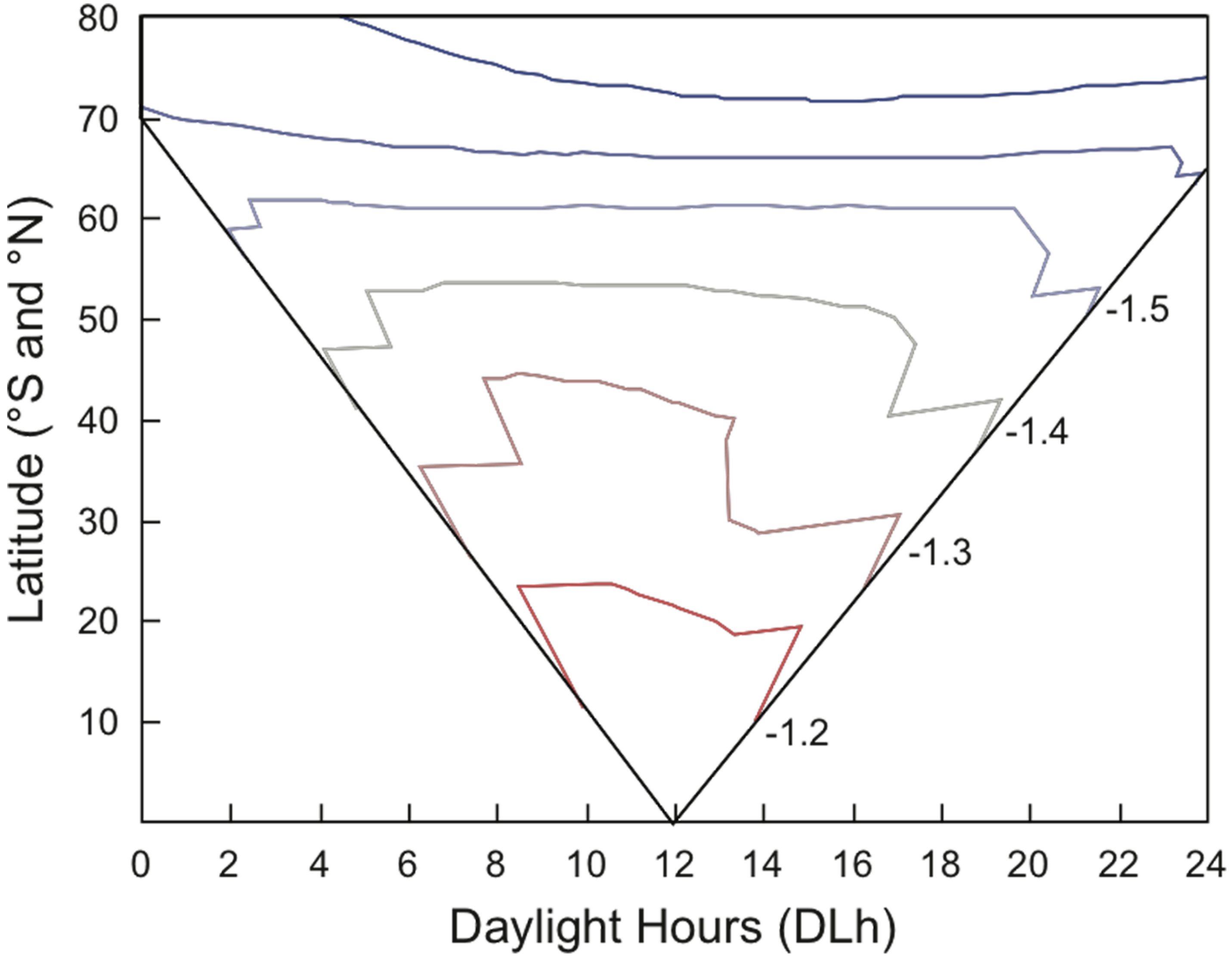
-1.6
-1.4
-1.2
-1.0
-0.8
ANN Estimate log(RR_{ann})

Fig. 6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10
Latitude (°S and °N)
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2
4
6
8
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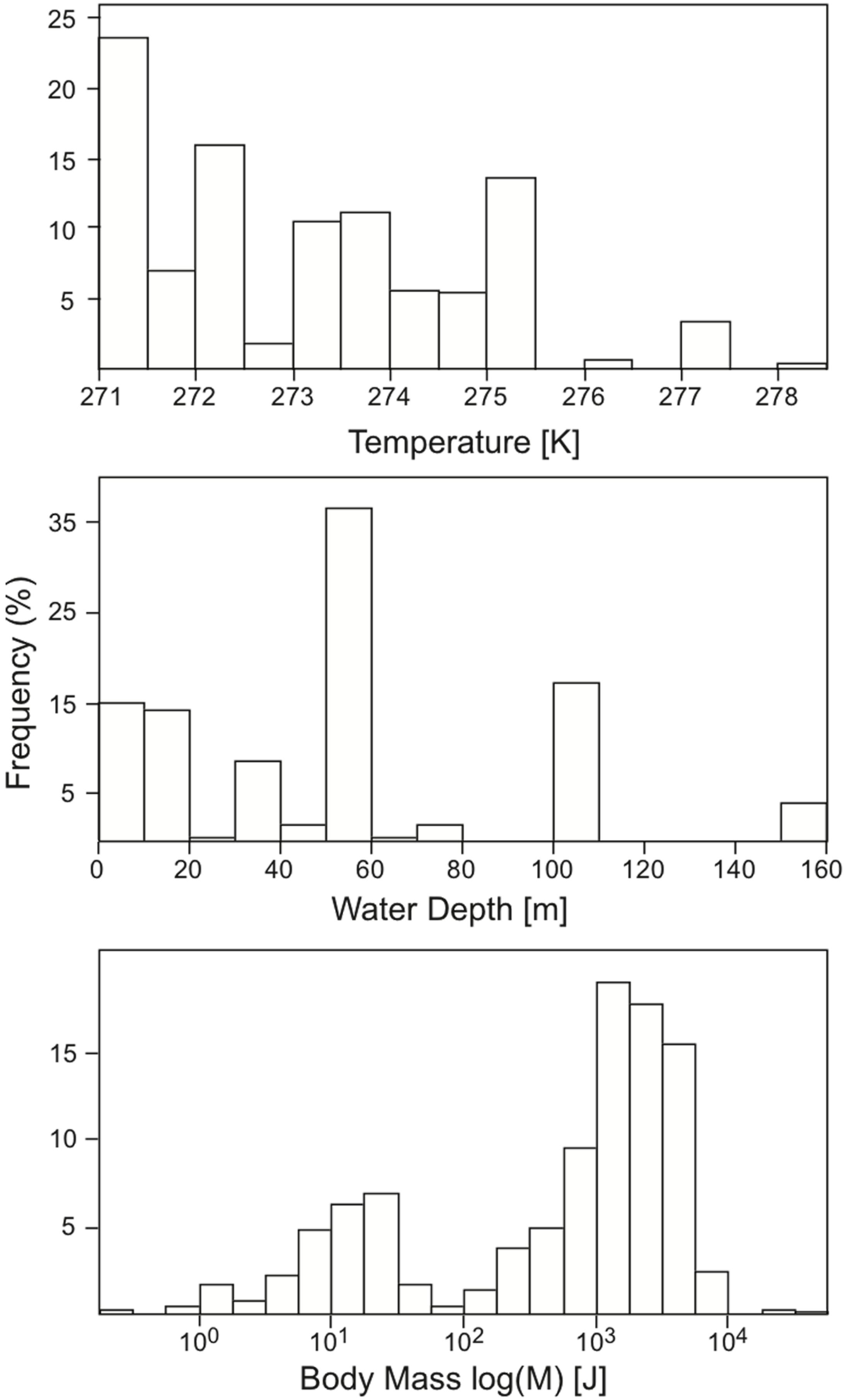
16
18
20
22
24
Daylight Hours (DLh)
-1.5
-1.4
-1.3
-1.2

Fig. 7



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5
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272
273
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275
276
277
278
Temperature [K]
Frequency (%)
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5
0
20
40
60
80
100
120
140
160
Water Depth [m]
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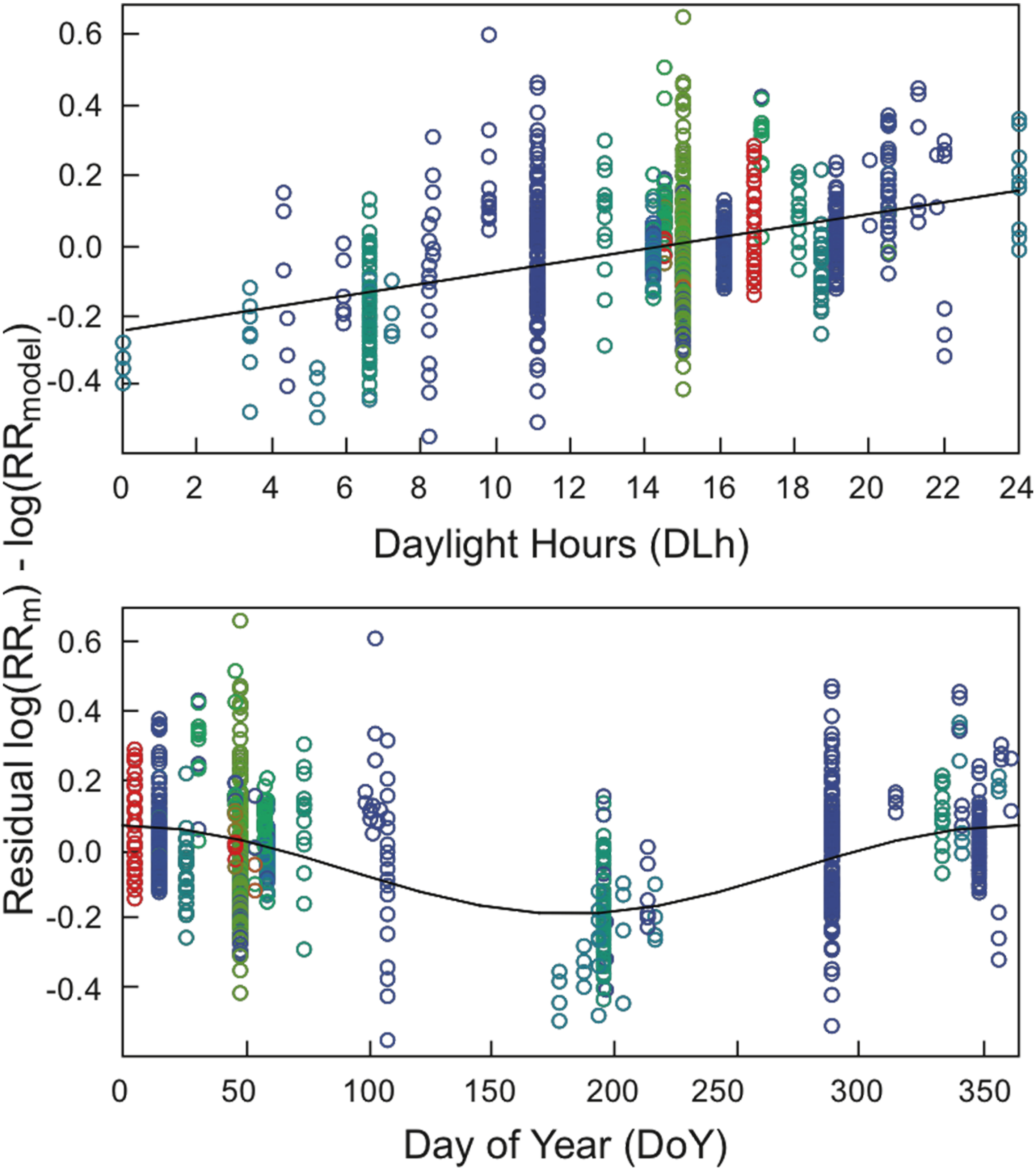
10
5
10^0
10^1
10^2
10^3
10^4
Body Mass log(M) [J]

Fig. 8



0.6
0.4
0.2
0.0
-0.2
-0.4
0
2
4
6
8
10
12
14
16
18
20
22
24
Daylight Hours (DLh)
Residual $\log(RR_m)$ - $\log(RR_{model})$
0.6
0.4
0.2
0.0
-0.2
-0.4
0
50
100
150
200
250
300
350
Day of Year (DoY)

Fig. 9

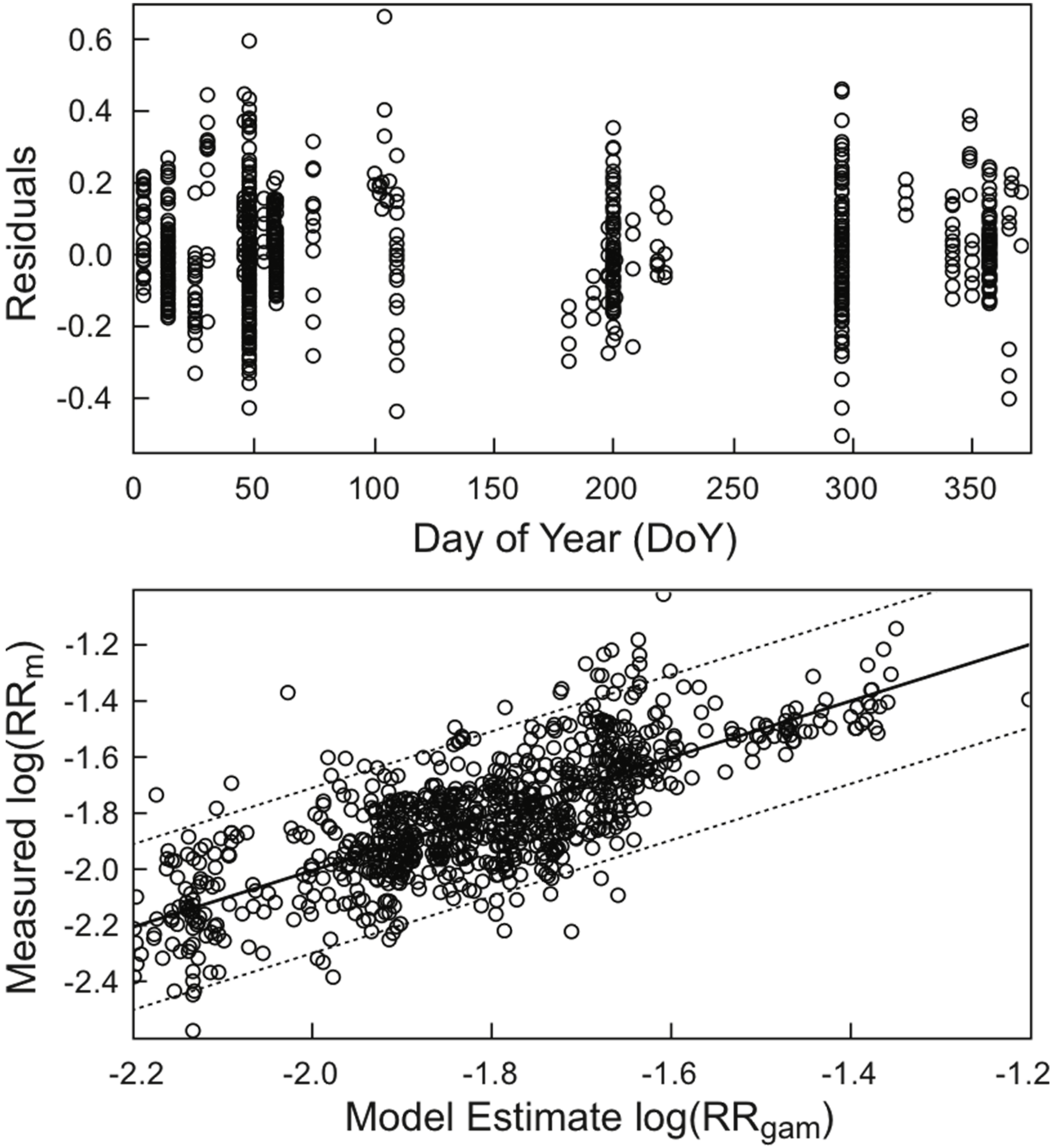
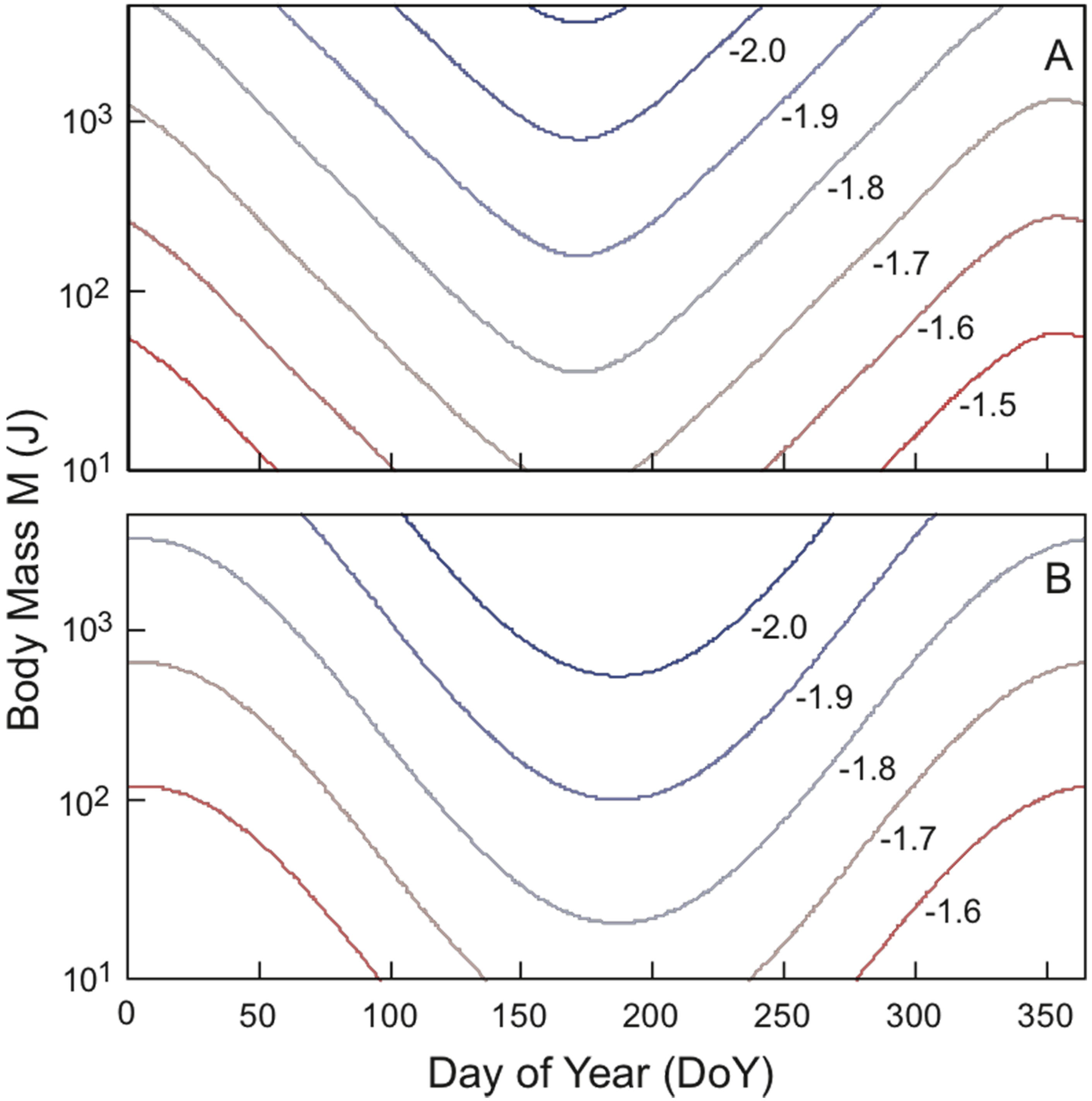
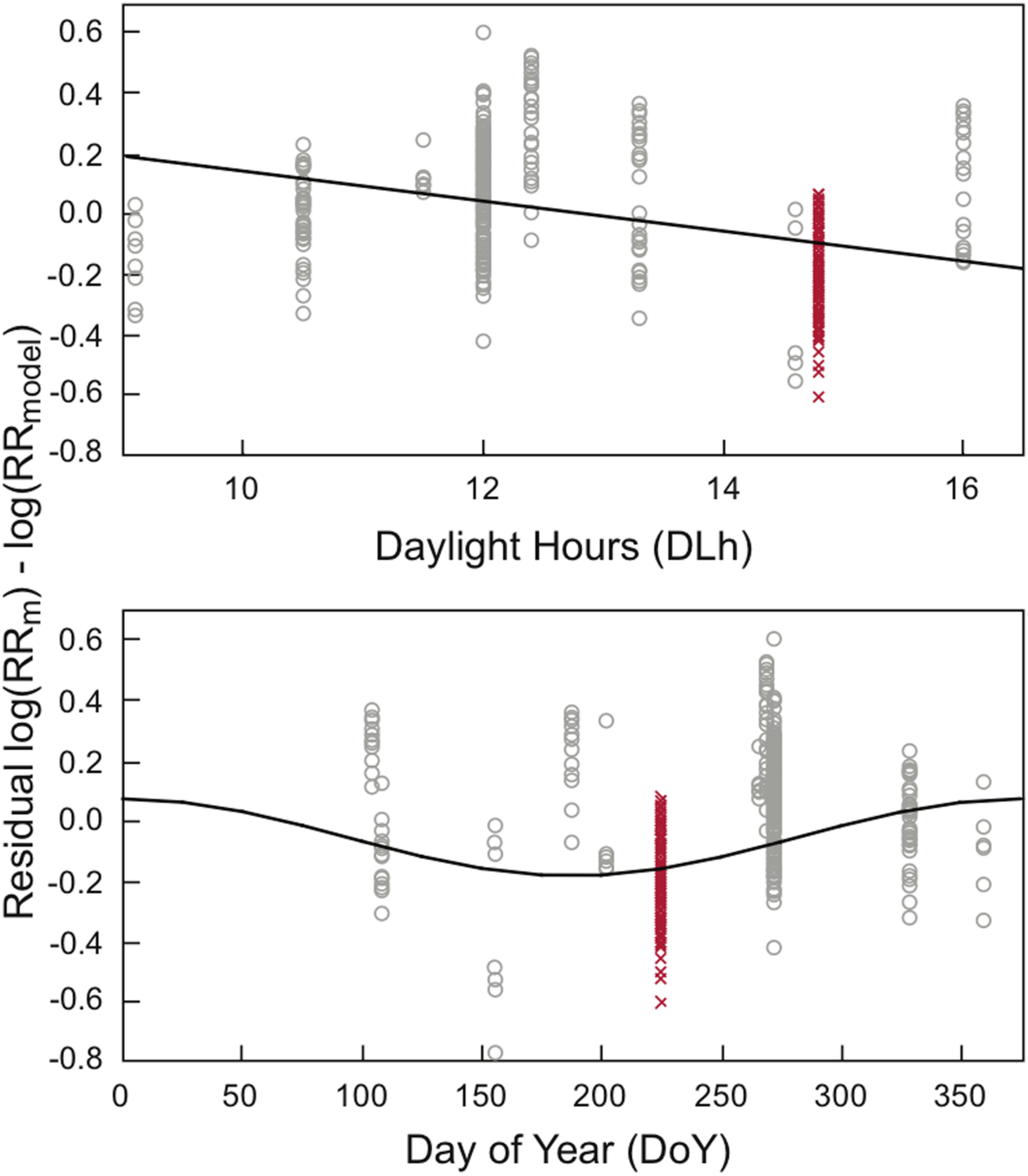

Residuals
0.6
0.4
0.2
0.0
-0.2
-0.4
0
50
100
150
200
250
300
350
Day of Year (DoY)
Measured log(RR_m)
-1.2
-1.4
-1.6
-1.8
-2.0
-2.2
-2.4
-2.2
-2.0
-1.8
-1.6
-1.4
-1.2
Model Estimate log(RR_{gam})

Fig. 10



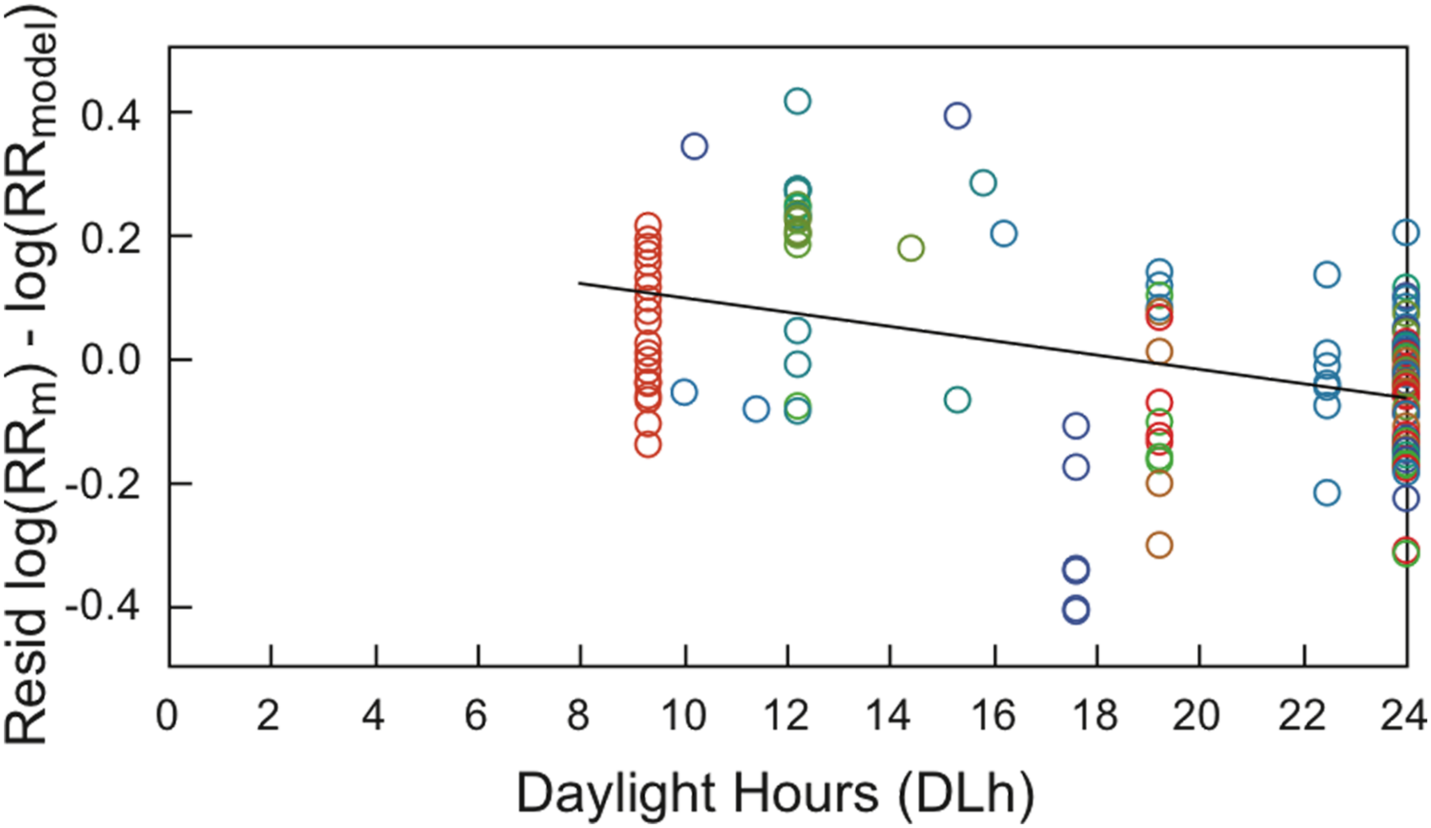
A
B
-2.0
-1.9
-1.8
-1.7
-1.6
-1.5
-2.0
-1.9
-1.8
-1.7
-1.6
Body Mass M (J)
10^3
10^2
10^1
10^3
10^2
10^1
0
50
100
150
200
250
300
350
Day of Year (DoY)

Fig. 11



Residual log(RR$_m$) - log(RR$_{model}$)
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
10
12
14
16
Daylight Hours (DLh)
0
50
100
150
200
250
300
350
Day of Year (DoY)

Fig. 12



Resid log(RR$_m$) - log(RR$_{model}$)
0.4
0.2
0.0
-0.2
-0.4
0
2
4
6
8
10
12
14
16
18
20
22
24
Daylight Hours (DLh)