

Chapter 23

Prefledging energetics of Kelp Gull (*Larus dominicanus vetula*) chicks in a warm environment

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Several studies have measured prefledging energy budgets of gull and tern chicks living in a cold environment. They showed that thermoregulation costs are the largest part of their energy expenditure. This is one of the first studies which determine, with the use of DLW, the prefledging energy budget of a gull (Kelp Gull; *Larus dominicanus vetula*) in a warm environment. The research took place on Robben Island in South Africa where the average ambient temperature during the field season was about 20°C. Behavioural observations showed that the chicks are mainly inactive without being brooded, 92% of the time during the day. This is con-

sistent with the semi precocial mode of development, the chicks are fed by their parents and don't show much activity. Of the total MEI (metabolisable energy intake) 22% was used for tissue gain and the remaining energy is used for RMR (resting metabolic rate), activity, synthesis and thermoregulation. The predictions of the energy expenditure are close to the measured values in this research. When we compare residuals with the other tern and gull studies at different latitudes we find a significant effect of latitude; an increase of about 1% in peak and total MEI per degree latitude.

Keywords: Kelp Gull, *Larus dominicanus vetula*, Robben Island, energetics, doubly-labelled water

Introduction

Gull and tern (Laridae) chicks exhibit the semi-precocial mode of development, whereby they leave the nest within a few days after hatching but are still fed by their parents at least until fledging (Starck and Ricklefs 1998). Time budget analysis of semi-precocial tern chicks has indicated that they can be at rest for up to 90% of their time (Klaassen *et al.* 1989). Therefore, chicks with this developmental mode exhibit low energetic costs for locomotion, potentially resulting in a high growth efficiency compared with precocial shorebird chicks which forage for themselves (Schekkerman and Visser 2001). However, because of their exposed life-style, semi-precocial chicks may need to allocate a substantial amount of energy to temperature regulation in order to compensate for the heat lost through their downy plumage. In young chicks, these costs are reduced by parental brooding (Klaassen 1994), whereas older chicks rely on shivering thermogenesis to maintain their body temperature (Visser and Ricklefs 1993, Hohtola and Visser 1998). At high latitudes these costs can amount to about 25% of the entire prefledging energy budget of growing chicks. It is thought that at low latitudes, chicks expend much less energy on temperature regulation (Klaassen 1994), possibly resulting in a lower level of energy requirement between hatching and

fledging, and therefore in a higher growth efficiency.

The construction of energy budgets represents an important tool for understanding the effects of developmental mode and climate on postnatal development. Of the total metabolisable energy intake (i.e., the gross energy intake minus fecal and urinary energy loss) of larid chicks, only about 25% is used for the synthesis of tissue (Drent *et al.* 1992, Klaassen *et al.* 1992, Klaassen 1994, Weathers 1996). The remainder is dissipated as heat, as a by-product of tissue synthesis or due to the maintenance of physiological functions when at rest at thermoneutrality, heat increment of feeding, locomotion or temperature regulation (Ricklefs 1974).

In the past, the question of latitudinal adaptation in larid postnatal development has mainly been addressed by constructing energy budgets for six species in temperate-zone, arctic, and high arctic habitats. Until now, an energy budget for growth has been constructed for only two (sub) tropical species (Common Tern [*Sterna hirundo*] and Sooty Tern [*Sterna fuscata*], Ricklefs and White 1981). Clearly, species with (sub)tropical breeding distributions are under-represented in the existing dataset. Therefore, using the Doubly Labelled Water (DLW) method and growth measurements, we constructed the energy budget of the Kelp Gull *Larus dominicanus vetula* in South Africa, where the

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temperatures are high relative to other localities where the energetics of gulls and terns have been investigated. In this way, comparisons can be made to provide more insight the adaptations and differences between birds breeding different latitudes.

Materials and Methods

Study species

The Kelp Gull inhabits temperate-zone and circumpolar areas in the southern hemisphere. The *vetula* subspecies is resident and common in southern Africa (Crawford *et al.* (1982), Crawford (1997), Underhill *et al.* (2001) and Calf *et al.* (2003)). Adults primarily forage at sea where they feed on fish and fish offal, but they also feed along the coast on beaches and sandy shores (Crawford 1997). Kelp gulls breed in colonies, and complete clutches typically contain 2–3 eggs which are incubated for about 28 days. Chicks are fed by both parents. After hatching chicks stay in the nest for the first few days; thereafter they are mobile.

Study area and weather measurements

Measurements were obtained at two colonies on Robben Island, South Africa (33°47'S, 18°21'E), every 3–4 days between October 2003 and January 2004. Both colonies were situated at a distance of about 100 m from the coastline. Ambient temperatures were obtained from a weather station close to the coastline, and were stored in a data logger at 10-min intervals.

Growth rate

Upon discovery, nests and their eggs were marked and subsequently inspected every 2–3 days, with increased frequency prior to the expected hatching date. After hatching each chick was weighed with a Pesola spring balance (to the nearest 0.1 g) and given unique yellow markings with picric acid. The hatching day was designated as Day 0. Each chick was weighed repeatedly between hatching and fledging, or until death.

We only used growth data of chicks which fledged successfully. For each individual, different calculation procedures (SPSS 14.0) were tested to describe the growth rate: (1) the logistic growth curve with a fitted asymptote, (2) the Gompertz growth curve with a fitted asymptote (Ricklefs 1973). The model with the best fit was used to construct the general growth curve, which was also used to construct the energy budget for successful growth.

Behavioural observations

Behavioural observations of chicks were performed between November 10 and January 15. Observations took place at all times of day between 5:45 am and 20:00 pm in bouts of approximately two hours. We categorized behavioural activity following Klaassen *et al.* (1989) and Klaassen (1994): parental brooding, standing, sitting and lying in the vegetation, preening, begging, eating, locomotion, social aggressive interactions. Additionally, we scored the duration of the time that the chicks were protected from solar radiation by the parents. When exhibiting this behaviour, parents spread their wings above the chicks when standing near them without making any other physical contact. No rain fell during the observations. One to four chicks from different nests were observed simultaneously.

DLW measurements

We applied the Doubly-labelled water (DLW) method to measure the daily energy expenditure in 16 free-living chicks. On capture, chicks were weighed with a Pesola spring balance (see above) and subsequently injected intraperitoneally with a doubly labeled water mixture (²H enrichment 32%, and ¹⁸O enrichment 63%) applying a dose (D, g) using the equation:

$$D = 0.13 + 0.0008 M \quad (1)$$

where M represents the chick's body mass (g). From each chick, after an equilibration period of 1h, 4–6 capillaries were filled with 10–15µl blood (henceforth referred to as "initial blood sample") from the brachial vein. Capillaries were flame-sealed immediately. Chicks were returned to the place where they had been captured. Chicks were recaptured 23.83h later, on average (range 23.12–24.50h), to be re-weighed and to collect a second blood sample ("final sample") using the same procedure. Blood samples were also collected from four randomly chosen chicks to assess the natural abundances of ²H and ¹⁸O in their body water pools. For further details regarding the analytical procedures applied, see Visser and Schekkerman (1999). The average enrichments of the natural abundance samples were observed to be 159.1 (SD = 3.43) ppm, and 2004.1 (SD = 2.70) ppm, respectively.

The amount of body water was calculated for each chick using the "plateau method", based on the population specific background level, the dose, and the individual-specific ¹⁸O enrichment of the initial blood sample (Speakman 1997, Visser *et al.* 2000). Rates of CO₂ production were calculated with Speakman's equation 7.17 (1997). Validation studies on growing precocial and semi-precocial chicks have revealed this to be the most appropriate model (Klaassen *et al.* 1989, Visser and Schekkerman 1999, Visser *et al.* 2000). As the last step, daily rates of CO₂ production were converted to daily energy expenditure (DEE, kJ/d) using a factor of 27.3 kJ/l based on a protein-rich diet (Gessaman and Nagy 1988).

Energy budget

The energy budget of growing chicks consists of two components: the amount of energy spent (as measured with the DLW method), and the amount of tissue energy accumulated. Daily energy expenditure comprises all routes of energy loss to fuel different types of behaviour (including locomotion), temperature regulation, heat increment of feeding, and the bio-synthesis related heat loss (Drent *et al.* 1992). Of the gross energy intake of a bird, only a fraction is metabolisable energy (MEI, kJ/d). MEI can be used for both anabolic (energy accumulated in body tissue, E_{tis}, kJ/d) and catabolic purposes (DEE, Klaassen *et al.* 1989, Gabrielsen *et al.* 1992):

$$MEI = DEE + E_{tis} \quad (2)$$

The energy used for tissue growth E_{tis} can be calculated with the growth rate of the chicks and the mass-specific energy content of the tissue. The DEE consists of the resting metabolism (RMR), the biosynthesis-related heat loss (E_{syn}, kJ/d), costs of thermoregulation (E_{tr}, kJ/d) and activity costs (E_{act}, kJ/d):

$$DEE = RMR + E_{syn} + E_{tr} + E_{act} \quad (3)$$

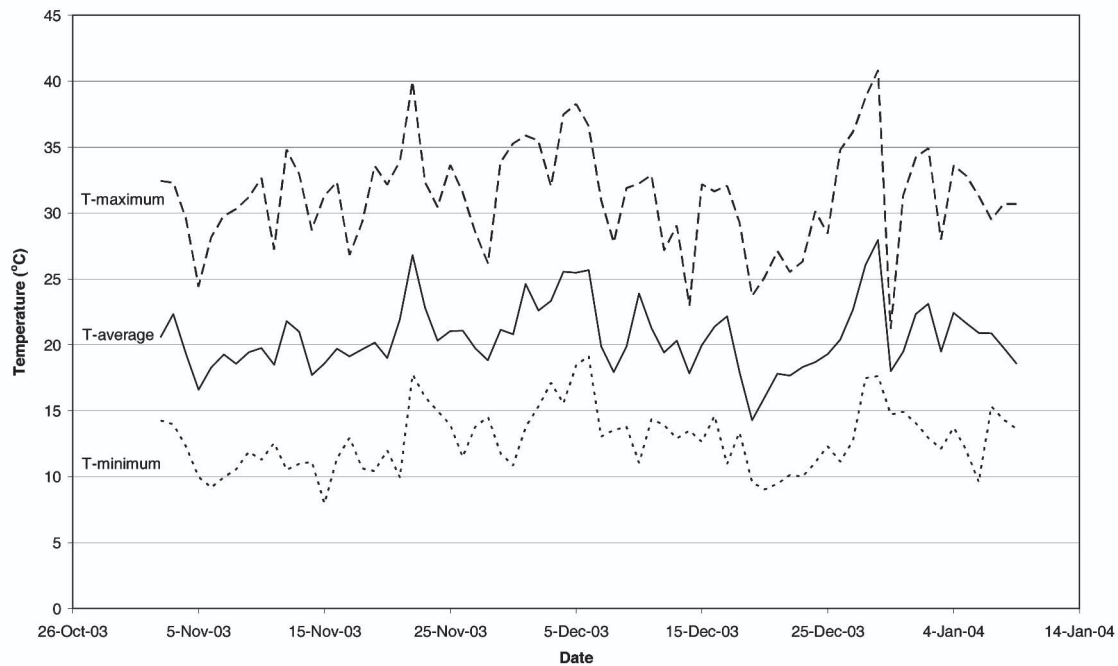


Figure 1: Development of maximum, average, and minimum operative temperatures as measured with a black sphere in the Kelp Gull colony

None of these components are calculated or determined separately. Nonetheless the equation provides insight in different avenues of heat loss, which affect the chicks' energy requirements.

Results

Weather

In Fig. 1 we display the maximum, average and minimum operative temperatures in the colony. Average maximum and minimum temperatures were 31.3 °C (SD = 3.95), and 12.8 °C (SD = 2.44), respectively.

Reproductive success

A total of 88 nests were found. The average laying date of the first egg of each nest was 2 November ($N = 88$, $SD = 20.0$) and the average hatching date was 21 November ($N = 56$, $SD = 18.7$). The duration of the incubation period was about 28 days. The fact that the difference between the average laying and hatching dates was less than this (19 days) is explained by the increased level of egg predation towards the end of the incubation period. The successfully developing chicks ($N = 19$) fledged after 38 days.

Growth rate

A total 104 chicks hatched from 65 successful nests (i.e., 1.6 chicks per nest on average). Nineteen of these chicks could repeatedly be captured until fledging, enabling us to construct individual-specific growth curves for chicks which fledged successfully (Fig. 2). Of the different models applied, the Gompertz growth curve with a fitted asymptote yielded the best fits (individual R^2 values ranged between 0.98 and 1.00, $N = 19$). The average asymptotic body mass was found to be 1 084g ($SD = 246.9$ g), the average growth rate constant was $0.081d^{-1}$ ($SD = 0.02 d^{-1}$), and the average time to the point of inflection was 13.7d ($SD = 2.7$ d). At day 38 the mass at fledging (M_f) was calculated to be 970g.

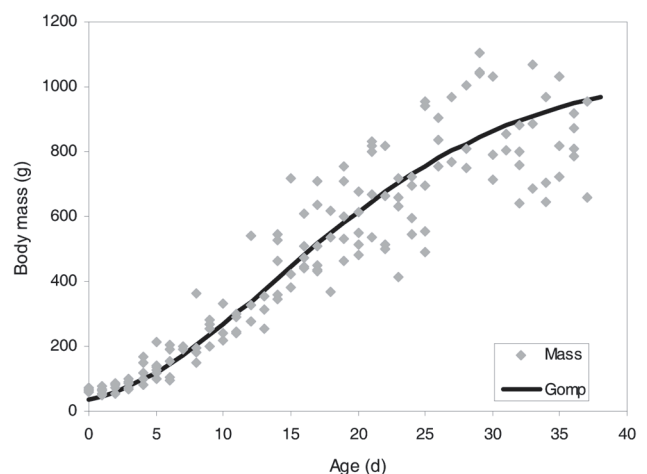


Figure 2: Development of body mass of chicks which fledged successfully ($N = 19$). The curve represents the Gompertz growth curve which gave the best fit: $M = 1084 \exp(-\exp(-0.081(t - 13.7)))$, where M and t represent the body mass (g), and age (d), respectively

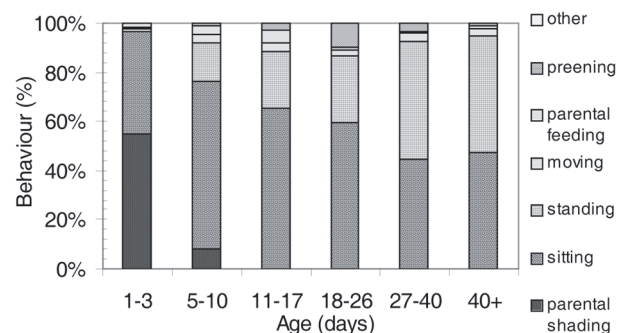


Figure 3: Behavioural development of Kelp Gull chicks as a function of age

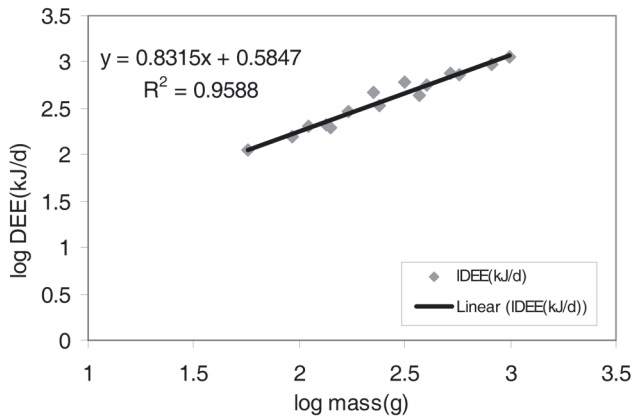


Figure 4: The relationship between body mass and daily energy expenditure in Kelp Gull chicks. The line represents the linear regression relating $\log(\text{DEE})$ to $\log(\text{mass})$

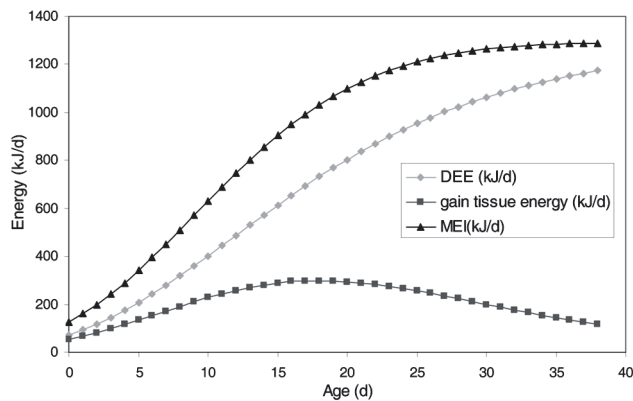


Figure 5: The energy budget for growing Kelp Gull chicks. The metabolisable energy intake is the sum of the energy used for gain in tissue energy and the daily energy expenditure, and is the daily amount of energy chicks require to fledge successfully after 38 days

Behavioural observations

Total observation time of the chicks was about 80 h (Fig. 3). Parental shading was particularly observed in 1–3d chicks, which on average were shaded 55% of the time. This percentage decreased rapidly with age (Fig. 3). Chicks spent on average 42% of their time sitting in the vegetation, and only 1.1% of their time standing. Feeding time comprised on average only 1.7%. Preening behaviour showed a peak between 18 and 26 days of age, when they spent about 10% of their time engaged in this activity. This coincided with the rapid growth of feather sheaths. On average, chicks spent 92% of their time being inactive (parental shading, standing and sitting), which is consistent with the expectations for semi-precocial development.

Daily energy expenditure

The relationship between $\log \text{DEE}$ (kJ/d) and \log body mass (M , g) is depicted in Fig. 4, and can be described by:

$$\log_{10}(\text{DEE}) = 0.832 \cdot \log_{10}(M) + 0.585$$

($R^2 = 0.96$, standard error of the slope 0.048, $P < 0.01$) (4)

which can be rewritten as:

$$\text{DEE} = 3.846 M^{0.832} \quad (5)$$

Energy budget

In Fig. 5 the different components of the energy budget are depicted. The upper line is the MEI, which represents the sum of the DEE and tissue energy (equation 2), and equals the total daily amount of energy the chicks need to receive to successfully fledge after 38 days. The DEE component of the budget has been derived from equation 5, and the growth curve. The total gain in tissue energy (E_{tis} , kJ/d) is calculated from the mass-specific energy density (ED , kJ/g), based on Drent *et al.* (1992) for Laridae:

$$ED = 4.18 + 4.61 \cdot (M/A) \quad (6)$$

where M is the mass (g) of the chick, and A the asymptotic body mass (1 084g). The total energy content of the body at a specific time point is the product of ED and M . The daily change in the total energy content represents E_{tis} .

The highest MEI (Peak-DME, kJ/d) value was calculated to be 1 289kJ/d at 38 days. The sum of the daily MEI values (Total-MEI, kJ) between hatching and fledging was calculated to be 35 375kJ, which represents the total amount of metabolisable energy needed for successfully raising a chick. The total gain of tissue energy during growth was calculated to be 7 781kJ, which represented 22% of the Total-MEI. Thus, in Kelp Gull chicks a total of 78% of the Total-MEI was dissipated as heat.

Discussion

Behavioural observations

Kelp Gull chicks were inactive for about 92% of their time. Parental shading was frequently observed in young chicks up to 10 days of age. In older chicks, this behaviour was no longer observed. From this age chicks may be capable of regulating their own body temperature at ambient temperatures above 30 °C. Chicks of both Arctic (*Sterna paradisaea*) and Common Terns (*Sterna hirundo*) were reported to be inactive for about 87% of their time (being brooded by their parents to prevent cooling of the body, and at rest; Klaassen 1994). The brooding component of the time budgets for chicks of both of these species were observed up to the age of 10 days.

Growth rate and energy budget

The observed Gompertz growth rate constant of 0.081/d, was 60% higher than predicted for a general bird species, but Laridae as a group are reported to exhibit high growth rate residuals (Starck and Ricklefs 1998).

The Peak-DME, and Total-MEI values for the Kelp Gull were found to be 1 289kJ/d and 35 375kJ, respectively. Weathers (1992) reviewed the literature regarding the energy budgets during growth, and he derived predictive equations based on 30 mainly altricial bird species with an asymptotic body mass range of 9.7–3700g:

$$\text{Peak-DME} = 11.69 M_f^{0.9082} T_f^{-0.428} \quad (7)$$

where M_f represents the mass at fledging and T_f The fledging period (for the Kelp Gull 970g and 38d, respectively). The estimated Peak-DME for Kelp Gull is 1 279kJ/d. Our measured value of 1 289kJ/d with is 0.8% above prediction.

The Total-MEI (kJ) represents total amount of food the parents have to provide to their chicks to enable them to fledge successfully. According to Weathers (1992) this value can be predicted for a bird species by the equation:

Table 1: Energy budget parameters for larid species in relation to latitude. Sources: 1 C. Eising and G.H. Visser unpub. data; 2 Gabrielsen *et al.* (1992); 3 this study; 4, 5, 6, and 7 Klaassen (1994); 8 and 9: Ricklefs and White (1981).

Species	Latitude(°N/S)	Fledging time (days)	Fledging mass (g)	Peak MEI (kJ/day)	Total MEI (kJ)	R _{peak} %	R _{total} %
1. Black-headed gull	53N	30	225	395	9 120	5.9	21.4
2. Kittiwake	79N	35	399	852	18 400	45.0	34.8
3. Kelp Gull	34S	38	970	1 289	35 375	0.8	16.0
4. Antarctic tern	62S	27	131	398	7 150	66.6	62.7
5. Arctic tern	53N	22	105	233	3 996	9.3	27.0
6. Arctic tern	79N	22	112	277	4 628	22.5	39.1
7. Common tern	53N	25	112	239	4 852	11.6	33.2
8. Common tern	25N	30	110	199	4 412	2.1	8.1
9. Sooty tern	25N	60	198	135	6 882	-45.3	-37.5

$$\text{Total-MEI} = 6.65 M_{fl}^{0.852} T_{fl}^{0.71} \quad (8)$$

which yields a predicted value of 30 425kJ. Our observed value is 16% above the predicted value.

We found that 22% of the Total-MEI was used for the gain in tissue energy. This is slightly below the average value of 27% reported by Drent *et al.* (1992), based on a review of 14 gull and tern species.

To better interpret our energy budget data for the Kelp Gull, we assembled data from the literature for different larid species on T_{fl} , M_{fl} , Peak-DME, Total-MEI, and latitude (Table 1).

Residuals for Peak-DME and Total-MEI (R_{peak} , and R_{total} , respectively, %) were calculated as:

$$R_{peak} = 100 \cdot (\text{observed Peak-DME} - \text{predicted Peak-DME}) / \text{predicted Peak-DME} \quad (9)$$

$$R_{total} = 100 \cdot (\text{observed Total-MEI} - \text{predicted Total-MEI}) / \text{predicted Total-MEI} \quad (10)$$

where the predicted values were derived from Weathers (1992). The relationship between R_{peak} and latitude L (degrees N or S) is displayed in Fig. 6, and can be described by:

$$R_{peak} = -44.3 + 1.12 (SE = 0.40) \cdot L \quad (11)$$

($R^2 = 0.47$, $P = 0.024$), which means that R_{peak} increases by 1.12% per degree latitude.

The relationship for R_{total} and latitude is also displayed in Fig. 6, and can be described by:

$$R_{total} = -28.4 + 0.99 (SE = 0.34) \cdot L \quad (12)$$

($R^2 = 0.48$, $P = 0.022$), which means that R_{total} increases by 0.99% per degree latitude. This confirms earlier predictions of Drent *et al.* (1992) and Klaassen (1994) that in larid species the costs of rearing offspring become higher at higher latitudes. As chick activity does not increase with latitude (see preceding paragraph), it is most likely that these increased costs at high latitudes are caused by elevated thermoregulatory costs.

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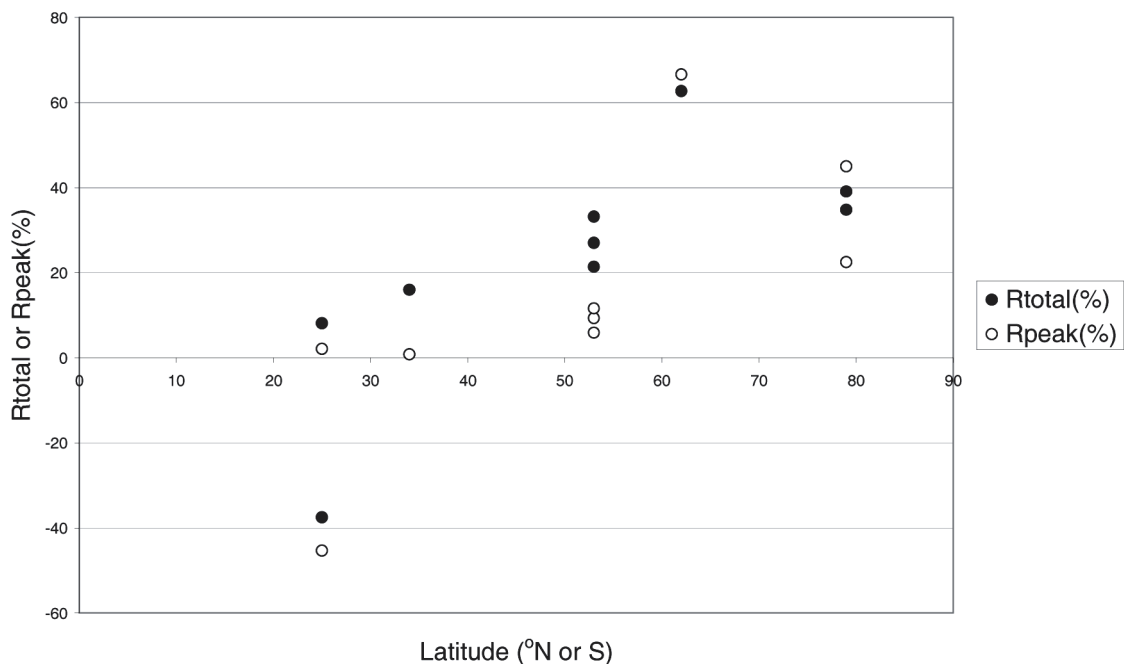


Figure 6: Relationships between latitude and the Relative Peak-DME (R_{peak} , %, open symbols), and Relative Total-MEI (R_{total} , %, solid symbols) for different larid species. See Table 1

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