*Evolutionary Ecology Research*, 2006, **8**: 455–470

# Geographic covariation between metabolic rate and life-history traits

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## ABSTRACT

**Question:** Is there a clinal covariation between life-history traits and metabolic rate?

**Hypothesis:** Reproductive output will negatively covary with metabolic rate along an intraspecific latitudinal gradient.

**Methods:** In a common garden design we studied metabolic rate in five populations of the common terrestrial isopod, *Porcellio laevis*, over a range of 15° of latitude in Chile. We also measured life-history variables in the same populations.

**Conclusions:** Female body mass, female size at first reproduction, egg and juvenile size, and reproductive output were negatively correlated with mean annual air temperature and positively correlated with latitude. In contrast, metabolic rate and egg number were positively correlated with temperature and negatively correlated with latitude. Individuals inhabiting cooler climates (i.e. southern populations) tended to have lower metabolic rates. We found a significant, negative phenotypic correlation between metabolism and reproductive output for all studied populations, in a gradual and consistent direction along the latitudinal gradient.

*Keywords*: latitudinal variation, metabolism, physiology–life history covariation, reproductive output, trade-offs.

## INTRODUCTION

Geographically widespread species must cope with environmental differences among habitats. This ability can, in principle, be achieved by genetic differentiation and/or phenotypic flexibility (Blanckenhorn, 1997). Life-history traits are considered indirect measurements of fitness (Stearns, 1992). In both endotherms and ectotherms, intraspecific variations in life-history traits are pervasive along latitudinal clines (Mousseau and Roff, 1989; Negovetic and Jokela, 2001). Studies of the physiological basis of life-history trade-offs have been a central topic in evolutionary ecology (Townsend and Calow, 1981; Stearns, 1992; Roff, 2001; Zera and Harshman, 2001). Physiological variation in the life history of an individual can have profound implications for fitness (Ricklefs and Wikelski, 2002). Theoretically, the costs of maintenance may have important effects on the quantity of energy available for activity and reproduction (Calow,

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1977; Sibly and Calow, 1986; Weiner, 1992; Angilletta, 2001). Nevertheless, evidence of these covariations is currently sparse (Spicer and Gaston, 1999; Ricklefs and Wikelski, 2002; Wikelski *et al.*, 2003; but see Ayres and Scriber, 1994, for examples in swallowtail butterflies; Angilleta, 2001, for lizards; and Pörtner *et al.*, 2001, for cod).

Life-history theory has developed around the idea that a suite of traits has been modified by natural selection to cope with particular ecological conditions (Stearns, 1992; see also Fox and Czesak, 2000; Lardies and Castilla, 2001; Ricklefs and Wikelski, 2002). Nevertheless, geographic variation in life-history traits may be also related, to some extent, by individual differences in metabolic rates ($\dot{V}O_2$) among populations as well as by differences in habitat qualities. Thus, it is feasible to use energetic approaches to evaluate life-history variation along a temperature gradient by comparing populations experiencing different temperatures and habitats along a latitudinal cline. Furthermore, $\dot{V}O_2$ is central in the network of physiological traits that covary with life-history traits, and additionally may mediate trade-offs (Wikelski *et al.*, 2003) and ecological processes at a high level of biological integration (Brown *et al.*, 2004). Thus, we tested the following hypothesis: reproductive output (i.e. total dry mass of eggs) will be linked and negatively correlated with metabolic rates along an intraspecific latitudinal gradient among populations of the terrestrial woodlouse *Porcellio laevis* inhabiting different habitats in southern South America.

## MATERIALS AND METHODS

### Animals and study site

*Porcellio laevis* is widely distributed in Chile (Leistikow and Wägele, 1999). Woodlice were collected during the austral summer of 2002, at five localities in northern-central Chile situated along a latitudinal gradient: Arica (18°30′S), Iquique (20°10′S), Antofagasta (23°38′S), La Serena (29°55′S) and Santiago (33°23′S). Woodlice from each site were collected by hand from under stones, pieces of wood and soil litter. Specimens were placed in containers with vegetable soil and carrot slices, and transported to the laboratory. A subsample of ovigerous females was placed in individually labelled vials and fixed in diluted alcohol (50%) for further analyses of life-history traits. Climatological data for the different localities are presented in Table 1.

### Life-history traits

Using a compound microscope (MEIJI EMZ-TR) equipped with a calibrated ocular micrometer, we measured the total length of each fixed ovigerous female. From each female we removed a sample of 30 eggs to determine embryonic stage. Eggs were divided into three developmental stages following Lardies *et al.* (2004a). To calculate egg volume, we randomly separated 15 eggs from each female. For each egg we measured length ($L$) and width ($W$), and calculated egg volume using the equation for the volume ($V$) of a spheroid ($V = \pi LW^2/6$). We calculated mean egg volumes for each female, and then multiplied the average volume per egg by the total number of eggs to estimate the clutch volume. The magnitude of increase in egg volume during embryonic development was computed. To determine the dry weight of the brood, the egg mass of each female was washed four times using distilled water, and then dried at 60°C. The dry weight of each egg mass was recorded using an analytical balance (±0.01 mg) (CHYO JK-180). We also measured the dry body mass of adult females, which were also dried.

**Table 1.** Climatological data for the five study sites

| | Arica (18°30′S) | Iquique (20°10′S) | Antofagasta (23°38′S) | La Serena (29°55′S) | Santiago (33°23′S) | Years of observation | Source |
|---|---|---|---|---|---|---|---|
| Temperature (°C) | 18.9 (15.3, 22.9) | 18.7 (15.1, 22.2) | 17.0 (13.3, 20.1) | 14.8 (11.2, 18.9) | 13.9 (7.7, 22.1) | 35 | Di Castri and Hajek (1976), FAO (1985) |
| Relative humidity (%) | 74 | 78 | 78 | 84 | 87 | 35 | Di Castri and Hajek (1976), FAO (1985) |
| Precipitation (mm) | 0 | 2 | 2 | 127 | 356 | 65 | Di Castri and Hajek (1976), FAO (1985) |
| Total radiation ($cal/cm^2 \times day^{-1}$) | 422 | 424 | 423 | 340 | 310 | 20 | FAO (1985) |
| Climate | Desert | Desert | Desert | Semi-arid | Mediterranean | | Di Castri and Hajek (1976) |

*Note*: The latitude of each locality is indicated in parentheses. Temperature is presented as the annual average, with annual average minimum and maximum temperatures in parentheses.

To detect differences in biomass (clutch invested per female) among populations, we calculated the reproductive output (RO) as RO = (total mass of egg batch/female mass without eggs) (see Clarke *et al.*, 1991). We measured the total length of manca (i.e. the first instars of an isopod) as manca size, the distance between the mid-dorsal anterior margin of the carapace and the distal margin of the pleotelson. Manca size was measured for a subsample of 10 mancas from each female, which were fixed in 50% alcohol immediately after emerging from the marsupium. All eggs and mancas were counted under a compound microscope.

## Maintenance, acclimation and metabolic rate

All females without eggs were acclimated in large plastic containers whose base was covered with a layer of plaster of Paris at 18 ± 1°C and a light/dark regime of 12 : 12 h. We periodically added water to provide moisture. Food was supplied weekly in the form of mashed rabbit food pellets (Lardies *et al.*, 2004a). After 3 weeks, $\dot{V}O_2$ was measured at 18°C, which is near their preferential temperature (Castañeda *et al.*, 2004) and represents an adequate 'portrait' of metabolic rate among populations (Lardies *et al.*, 2004b, 2004c). Rates of oxygen consumption were determined using a 'closed system' (Vleck, 1987) consisting of disposable 10 ml hermetic syringes fitted with three-way valves (see Chappell, 1983; Ashby, 1997; Chown *et al.*, 1997; Nespolo *et al.*, 2003). Animals were weighed to the nearest milligram and then placed individually within syringes. The syringes were then sealed and placed in a temperature-controlled incubator for the duration of the measurement interval (~ 3 h). Three blank syringes served as controls. For measurements of $\dot{V}O_2$, air was injected from this syringe into a Tygon tube (1.5 m long), connected to an oxygen analyser. The air passed through small granules of Baralyme and Drierite to absorb carbon dioxide and water respectively, which were contained in each syringe in a compartment isolated from the woodlice. At the end of the measurement interval, oxygen concentrations were determined using a Fox Field Oxygen Analysis System (Sable System International, Nevada, USA) supplied with barometric pressure compensation. Output from the oxygen analyser was recorded by a computer equipped with the DATACAN program (www.sablesys.com). This system was neither intended to measure the instantaneous rate of metabolism, nor resolve discontinuous gas exchange (Chappell and Rogowitz, 2000), since each measurement is an average of oxygen consumption over several hours. However, technical errors associated with this measurement method are small (Anderson *et al.*, 1989).

## Statistical analyses

Statistical analyses were performed using STATISTICA 6.0 (Statistica, 2001). Linear regressions were performed between total length and egg number for acclimation temperature. To test for differences in egg volume, both at the intra-population level (between different developmental stages) and at the inter-population level (between similar stages), we used a one-way analysis of variance (ANOVA). The same analysis was used to estimate differences in female total length and reproductive output between the five sites at differing latitudes. To evaluate differences in egg number and clutch volume between localities we used analysis of covariance (ANCOVA), with female body length as the covariate (Sokal and Rohlf, 1997). When differences in the means were significant, a Tukey HSD test was performed (Sokal and Rohlf, 1997). Before the analyses of variance, we checked assumptions of normality

and homoscedasticity of the raw data using Kolgomorov-Smirnov and Cochran C tests respectively. To test for differences in $\dot{V}O_2$, our experimental design included two predictor variables: one categorical variable (locality) and one continuous variable (body mass); the dependent variable was $\dot{V}O_2$. To test for the effects of locality on $\dot{V}O_2$, we performed ANCOVA with body mass as the covariate. Again all assumptions were checked. When no parallelism was observed, we performed a separate slopes model ANCOVA (Nespolo *et al.*, 2003). Linear regressions were performed between body mass and $\dot{V}O_2$ for each population. Pearson product–moment correlations ($r_p$) were conducted between egg volume and egg number (per unit female weight), and average female reproductive output and mass-corrected $\dot{V}O_2$ were computed for each population.

## RESULTS

### Life-history traits

Average body length and size at first reproduction in females were greater in individuals from high latitudes (Santiago), and decreased towards low-latitude populations (Arica) (one-way ANOVA: $F_{4,433} = 78.05$, $P < 0.0001$; see Table 2). The same trend was also observed for female body mass (one-way ANOVA: $F_{4,395} = 13.92$, $P < 0.0001$; Table 2). We found a significant linear relationship between total length and egg number for all populations (Table 3). After removing the effects of body mass, we found differences in egg production between populations, where egg number was higher in the low-latitude population (ANCOVA: $F_{4,422} = 31.25$, $P < 0.0001$). This pattern received further support when comparing the number of eggs produced per unit of female body mass: different values were noted between sites (one-way ANOVA: $F_{4,422} = 85.06$, $P < 0.0001$), ranging from 8.8 eggs in Arica to 3.1 eggs in Santiago (see Fig. 1), with a gradual decrease towards high latitudes (linear regression: $y = 16.379 - 0.3894x$; $r^2 = 0.94$, $P < 0.0001$). To avoid errors in the estimation of egg number, these comparisons were conducted only for females with stage I eggs (i.e. recently produced eggs). Average clutch volume between geographically distinct populations was significantly different (ANCOVA: $F_{4,422} = 98.99$, $P < 0.0001$; Table 2), with the smallest clutch volumes in individuals from low latitudes and the largest ones in individuals from high latitudes (Table 2).

At the intra-population level, egg volume was different between developmental stages within all populations (one-way ANOVA: Arica: $F_{2,97} = 21.44$, $P < 0.0001$; Iquique: $F_{2,86} = 16.69$, $P < 0.0001$; Antofagasta: $F_{2,86} = 78.39$, $P < 0.0001$; La Serena: $F_{2,94} = 51.11$, $P < 0.0001$; Santiago: $F_{2,97} = 63.41$, $P < 0.0001$). Among populations, the volume of recently extruded eggs was also significantly different (one-way ANOVA: $F_{4,215} = 112.44$, $P < 0.0001$), increasing towards high latitudes in a significant, linear fashion ($y = 0.0072 + 3.888x$; $r^2 = 0.95$, $P < 0.0001$; see Fig. 1).

A negative phenotypic correlation ($r_p = -0.40$, $P < 0.05$) was observed between egg volume and egg number per unit female body mass towards decreasing latitudes. We observed a larger increase in egg volume (from stage I to III) in the high-latitude populations (e.g. 133.91% in Santiago) than in the low-latitude populations (e.g. 87.26% in Arica) (one-way ANOVA: $F_{4,318} = 82.11$, $P < 0.0001$; Table 4). Manca size was greater in the high-latitude populations, decreasing towards the low-latitude populations (one-way ANOVA: $F_{4,1152} = 100.02$, $P < 0.0001$) (Fig. 2). Finally, reproductive output increased gradually from low- towards high-latitude populations ($y = -0.069 + 7.170x$; $r^2 = 0.97$, $P < 0.0001$; Fig. 3),

**Table 2.** Total length (TL), female body mass ($m_b$) and clutch volume (CLV) of ovigerous *Porcellio laevis* females collected at five different localities (mean, standard deviation and number of females)

| | Arica (18°30′S) | | | Iquique (20°11′S) | | | Antofagasta (23°38′S) | | | La Serena (29°55′S) | | | Santiago (33°23′S) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | TL (mm) | $m_b$ (mg) | CLV ($mm^3$) | TL (mm) | $m_b$ (mg) | CLV ($mm^3$) | TL (mm) | $m_b$ (mg) | CLV ($mm^3$) | TL (mm) | $m_b$ (mg) | CLV ($mm^3$) | TL (mm) | $m_b$ (mg) | CLV ($mm^3$) |
| Mean | 9.82 | 53.35 | 4.33 | 10.05 | 73.78 | 5.14 | 12.45 | 80.35 | 5.88 | 14.55 | 94.64 | 6.42 | 14.92 | 98.52 | 7.92 |
| S.D. | 1.11 | 3.54 | 1.03 | 1.32 | 4.43 | 1.35 | 0.82 | 3.99 | 1.04 | 0.94 | 4.66 | 1.27 | 0.55 | 3.57 | 3.10 |
| *n* | 100 | 100 | 100 | 64 | 64 | 64 | 79 | 79 | 79 | 78 | 78 | 78 | 99 | 99 | 99 |

**Table 3.** Linear regression equations for the estimation of egg number (EN = dependent variable) and metabolic rate ($\dot{V}O_2$ = dependent variable; mean ± standard error) for each population (P = independent variable), representing the number of data points for females with freshly produced eggs (stage I)

| Locality | Regression | Standard error of estimate | $r^2$ | $P$ | $n$ |
|---|---|---|---|---|---|
| Arica | EN = (4.07 ± 0.81)P – (12.32 ± 2.04) | 0.071 | 0.55 | <0.001 | 38 |
| | $\dot{V}O_2$ = (0.32 ± 0.016)P + (4.93 ± 0.92) | 0.045 | 0.79 | <0.001 | 99 |
| Iquique | EN = (4.43 ± 1.02)P – (17.00 ± 3.15) | 0.081 | 0.38 | <0.05 | 24 |
| | $\dot{V}O_2$ = (0.26 ± 0.025)P + (2.24 ± 2.04) | 0.025 | 0.62 | <0.001 | 63 |
| Antofagasta | EN = (5.88 ± 2.42)P – (31.41 ± 3.92) | 0.052 | 0.61 | <0.001 | 27 |
| | $\dot{V}O_2$ = (0.24 ± 0.018)P + (5.41 ± 1.63) | 0.060 | 0.72 | <0.001 | 78 |
| La Serena | EN = (5.12 ± 0.93)P – (33.25 ± 4.37) | 0.066 | 0.54 | <0.001 | 31 |
| | $\dot{V}O_2$ = (0.17 ± 0.014)P + (1.46 ± 1.57) | 0.072 | 0.71 | <0.01 | 57 |
| Santiago | EN = (7.93 ± 1.61)P – (38.49 ± 4.52) | 0.049 | 0.70 | <0.001 | 42 |
| | $\dot{V}O_2$ = (0.10 ± 0.007)P + (5.06 ± 0.61) | 0.057 | 0.68 | <0.001 | 98 |

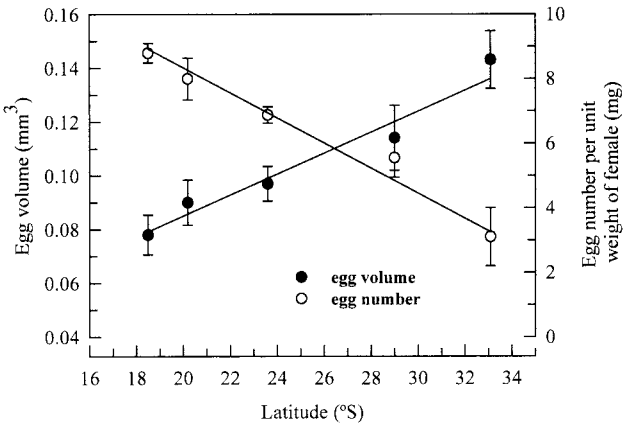


**Fig. 1.** Mean egg volume (EV; solid circles) of freshly extruded *Porcellio laevis* eggs (stage I), and egg number (EN; open circles) per unit weight of females (mean ± standard deviation; based on milligrams of dry weight), for populations collected in Arica, Iquique, Antofagasta, La Serena and Santiago (P). The dotted and solid lines indicate significant linear regressions (EV = 0.0072 + 3.888P; EN = 16.379 – 0.3894P) between EV-P and EN-P respectively (see Results for statistics). The correlation coefficient between egg number and egg volume is $r_p = -0.58$.

with significant differences in output between populations (one-way ANOVA: $F_{4,615} = 87.81$, $P < 0.0001$).

## Metabolic rate

As expected, $\dot{V}O_2$ was significantly correlated with body mass (Table 3), and $\dot{V}O_2$ was affected by latitude (ANCOVA, separate slopes model: $F_{4,394} = 107.80$, $P < 0.0001$). We

**Table 4.** Increases in egg volume in ovigerous females for five populations of *Porcellio laevis* differing in latitude (see Materials and methods), during the incubation period (stages I–III) ($n$ = number of individuals)

| Embryonic stage | Arica (18°30′S) | Iquique (20°11′S) | Antofagasta (23°38′S) | La Serena (29°55′S) | Santiago (33°23′S) |
|---|---|---|---|---|---|
| Stage I–II | 30.74 ($n = 38$) | 36.65 ($n = 24$) | 38.91 ($n = 27$) | 45.53 ($n = 31$) | 55.18 ($n = 42$) |
| Stage II–III | 56.52 ($n = 35$) | 51.10 ($n = 38$) | 58.53 ($n = 24$) | 63.28 ($n = 33$) | 78.73 ($n = 35$) |
| Total | 87.26 | 87.75 | 97.44 | 108.81 | 133.91 |

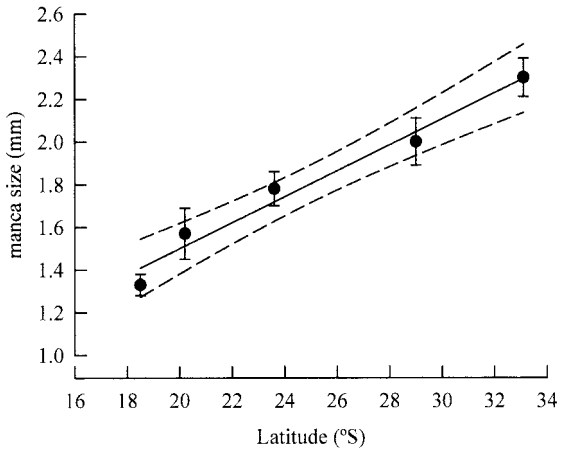


**Fig. 2.** Manca size (MS) (mean ± standard deviation) for the five populations (P) of *Porcellio laevis* located along a latitudinal cline. The solid line represents the regression between variables and is represented by MS = 0.4133 + 0.0513P ($r^2 = 0.93$, $P < 0.0001$). The dotted lines indicate the 95% confidence interval of the regression.

observed a gradual increase in $\dot{V}O_2$ from high- to low-latitudes ($y = 35.753 - 0.632x$; $r^2 = 0.59$, $P < 0.0001$; Fig. 3). Finally, we observed a negative phenotypic correlation ($r_p = -0.35$, $P < 0.05$) between reproductive output and mass-corrected $\dot{V}O_2$ for all populations (Fig. 3).

## DISCUSSION

### Geographic variations in life-history traits

Female *P. laevis* increase in body size towards high latitudes. This pattern is of particular importance given that body size is correlated with physiological, behavioural and ecological traits (see Peters, 1983; Brody and Lawlor, 1984; Blanckenhorn, 2000; Fox and Czesak, 2000; Robinson and Partridge, 2001). This pattern also agrees with that observed in some ectotherms, which tend to be larger in colder environments (Atkinson and Sibly, 1997; Robinson and Partridge, 2001; Blanckenhorn and Demont, 2004).

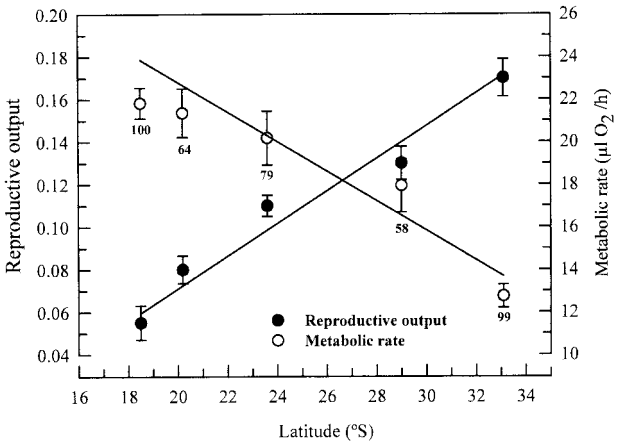


**Fig. 3.** Reproductive output (mean ± standard deviation; based on dry weight) and metabolic rate (weighted mean ± standard deviation; at 18°C) for the five populations of *P. laevis* along a latitudinal gradient in Chile (see Results for statistics). The correlation coefficient between traits is $r_p = -0.51$. Numerals below the bars indicates the number of females for which the number of instars was counted.

Optimal resource-allocation models may explain the temperature–size rule. However, Kozlowski *et al.* (2004) suggested that it is possible to find a combination of parameters for which the temperature–size rule does not hold. Latitudinal clines in body size with an established genetic basis have been reported in several ectotherms (Imasheva *et al.*, 1994; Chown and Gaston, 1999; Billerbeck *et al.*, 2000; Huey *et al.*, 2000; Robinson and Partridge, 2001; Fischer and Fiedler, 2002). Many ecological variables are likely to be selective agents, with temperature being a key one (Fischer and Fiedler, 2002; but see Blanckenhorn and Demont, 2004). We observed that body mass was significantly correlated with latitude (Lardies *et al.*, 2004c). Taken together, these correlations suggest a process of size-selection on body mass with thermal environment. Our results support various geographic rules (e.g. Spicer and Gaston, 1999; Blanckenhorn and Demont, 2004) including Bergmann's rule (Atkinson and Sibly, 1997).

Latitudinal variation in the life-history traits of *P. laevis* could, in part, be caused by differences in environmental temperature. On the other hand, clines in life-history traits may be managed by differences in size. Therefore, when we analysed correlations between size and life-history traits, we used size as the covariate in our analyses to ensure that the traits were indeed significantly different at a given size. Egg production in female *P. laevis* from the northern zone begins at smaller sizes than for females from high-latitude localities (Jones and Simons, 1983; Lardies and Wehrtmann, 2001; Fischer and Fiedler, 2002). Temperature has also been recognized as a factor stimulating growth and early ovarian development (Nelson *et al.*, 1988a, 1988b). Nevertheless, another factor that may explain the observed variation in size is the nutritional state of females (David *et al.*, 2001).

When considering egg production in equally sized ovigerous females of *P. laevis*, the number of eggs per weight of ovigerous female increased from high to low latitudes (Lonsdale and Levinton, 1985; France, 1992; Fox and Czesak, 2000). These differences can be explained by the fact that egg size is negatively correlated with egg number in many species. Indeed, in the present study, northern populations produced a large quantity of small eggs, while intermediate- and high-latitude populations produced a smaller quantity of large eggs

(Lonsdale and Levinton, 1985; Wägele, 1987; Fleming and Gross, 1990; Wilhelm and Schindler, 2000). Assuming that the same amount of energy is invested in egg production at all latitudes, theory predicts that a female can produce a large quantity of small eggs or a smaller quantity of large eggs. This trade-off is known to occur in many invertebrates (Lawlor, 1976; Clarke *et al.*, 1991; France, 1992; Giangrande *et al.*, 1994; Wehrtmann and Kattner, 1998; Lardies and Wehrtmann, 2001). However, our results show that reproductive output increased with latitude; hence the same amount of energy was probably not invested by all females, although the trade-off between egg number and egg size remained.

As a consequence of incorporation of water during embryonic development, egg volume in *P. laevis* increases, remaining within the range of variation reported for other crustaceans in Chilean coastal habitats (Lardies and Wehrtmann, 2001). The greater increase in egg volume in southern localities may be related to greater fluctuations in climatic variables (Belk *et al.*, 1990; Fox and Czesak, 2000). In habitats subjected to high seasonality, rainfall appears to be the most important factor affecting the reproduction and development of woodlice (Warburg, 1993) as well as the increase in egg volume (Wright and Surbida, 2001).

We believe that the low variability in environmental factors in the low-latitude zone, in comparison with the intermediate- to high-latitude populations of *P. laevis*, may allow for the production of smaller eggs, with a smaller increase in volume throughout embryonic development. Helden and Hassall (1998) reported a similar relationship for terrestrial isopods, concluding that differences in egg size reflect real differences in per embryo maternal investment. On the other hand, juvenile size at release and/or egg size is related to the fitness of individual offspring in many arthropods (Capinera, 1979; Fox and Czesak, 2000), including terrestrial isopods (Lawlor, 1976; Brody and Lawlor, 1984). In nature, a smaller initial size in terrestrial isopods could result in higher juvenile mortality for at least two reasons. First, smaller young may have lower energy reserves, and consequently be more sensitive to periodic food shortages. Second, mancas remain small for a longer time, and consequently are exposed to higher predation risk (Warburg, 1987). Also, temperature and humidity can significantly affect juvenile survival in terrestrial isopods (Sutton and Holdich, 1984).

## Metabolic rate

Inter-population variation in metabolic rate has been reported in most groups of invertebrates (see Spicer and Gaston, 1999). Our principal conclusion is that individuals inhabiting colder climates tend to have lower metabolic rates [but see Tsuji (1988) for inverse acclimation in lizards]. While in our study female body mass increased significantly with latitude (see Table 2), the difference in mass-independent $\dot{V}O_2$ persisted. At the intraspecific level, increases in $\dot{V}O_2$ have been reported for low-latitude populations of several invertebrate species (Schultz *et al.*, 1992; Berrigan, 1997; Berrigan and Partridge, 1997; Dittman, 1997). In the present study, differences in $\dot{V}O_2$ could have simply been due to phenotypic flexibility. Given that in terrestrial isopods realized rates of acclimation to temperature are especially fast (Willmer *et al.*, 2000, p. 222), it is likely that observed differences in $\dot{V}O_2$ are the end-product of local adaptation, and are probably a heritable characteristic. The low gene flow reported for terrestrial isopods (Gentile and Sbordoni, 1998), together with the variable environmental conditions that operate along a latitudinal gradient, support the idea that differences in $\dot{V}O_2$ reflect local adaptation or drift. Our results support the idea that low maintenance costs are principally determined by low environmental temperatures along the gradient. In contrast, others have interpreted higher $\dot{V}O_2$ values to be advantageous in arthropods. This hypothesis is that of

metabolic cold adaptation (see Chown and Gaston, 1999; Addo-Bediako *et al.*, 2002; Lardies *et al.*, 2004b). Nevertheless, in iteroparous organisms that have life-cycles longer than one year, and are active throughout the year, higher $\dot{V}O_2$ values are not necessarily an advantage, since individuals can grow until the next reproductive season and increase reproductive success. In this sense, we agree with Clarke (1991), who pointed out that metabolic cold adaptation represents a fitness cost to organisms, and is unlikely to evolve (but see Tsuji, 1988).

## Covariation between reproductive output and metabolic rate

Implicit in the covariation between reproductive output and maintenance cost is that between-population variations in $\dot{V}O_2$ result in higher fitness in individuals of different populations. Evidence for covariations between these traits is sparse (Ricklefs and Wikelski, 2002). Few studies have examined between-population variation in physiological and life-history traits. Ayres and Scriber (1994) found that a tiger swallowtail population from Alaska had an estimated fitness three times greater than that of individuals from Michigan. Angilletta (2001) demonstrated that differences in maintenance metabolism between populations of the widespread lizard, *Sceloporus undulatus*, contributed to greater reproductive output in South Carolina than in New Jersey. Nevertheless, in a recent study, Sears (2005) found that sagebrush lizards from a high-altitude population grew faster than two populations at lower altitudes. Sears reported that the difference in daily resting metabolic expenditure was greater in low- than in high-altitude populations, which could explain differences in patterns of growth in nature.

Data in the literature suggest that the reproductive output of polar species is lower than that of species inhabiting temperate zones (Clarke, 1987). Assuming that intraspecific patterns resemble interspecific ones, the pattern observed for *P. laevis* is at odds with this, since reproductive output increased towards higher latitudes. However, our results are in line with studies of marine crustaceans, which reported an increase in reproductive output associated with an increase in latitude (Lardies and Wehrtmann, 2001). Furthermore, we observed that reproductive output in *P. laevis* increased towards high latitudes. Thus, females invest about 5% of their body mass in egg production at low latitudes compared with 18% at high latitudes. We also observed a gradual increment in clutch volume towards higher latitudes with a concomitant increase in reproductive output. This suggests that individuals at high temperatures allocate more energy to rapid growth and high metabolic rates, and invest less energy in reproduction (see Lardies, 2003). In contrast, the slow growth and low $\dot{V}O_2$ of species inhabiting low-temperature habitats (Brey and Clarke, 1993) allow for greater energy investment in egg production, since eggs contain larger internal reserves (Lardies and Wehrtmann, 2001). In other words, at low latitudes individuals increase maintenance costs and thereby reduce investment in growth and/or reproduction. Nevertheless, latitude-induced patterns in maintenance costs have received little attention. Our results suggest that across the wide distribution of *P. laevis*, there is covariation between reproductive output and metabolic costs, resulting in lifetime reproductive effort being invariant with latitude (see Clarke, 1987, 2003). Alternatively, it could be that females at high latitude simply delay reproduction while storing more energy. This would also allow for an assessment of development time, which is very important for adaptation to season length, as opposed to temperature (i.e. latitude) *per se* (Blackenhorn and Demont, 2004).

Woodlice at low latitudes experience a warmer environment and have higher maintenance costs than populations at higher latitudes. Such variation in metabolism has implications

for understanding the proximate causes of geographic variation in life history, because maintenance metabolism directly affects production efficiency (Calow and Townsend, 1981). However, the greater reproductive output at higher latitudes may be caused by a higher rate of assimilation, a lower rate of energy expenditure, or a combination of both. In this sense, we propose that high energy expenditure in maintenance may affect life-history traits and their variability. Indeed, maintenance metabolism was negatively correlated ($r_p = -0.51$) with reproductive output. Nevertheless, Angilletta (2001) proposed that multiple physiological factors (energy assimilation and metabolic rate among others) interact to influence variation in life-history traits.

In summary, our main findings are that female size, offspring size and the proportion of biomass allocated to eggs increase with latitude, but the rate of metabolism and the number of eggs decrease. Consequently, maintenance metabolism correlates negatively with the proportion of biomass allocated to eggs and, most probably, with female and offspring size along the latitudinal gradient. We are aware, however, of inferring causality in such correlative data. Nevertheless, based on data for other taxa, we believe that organismal physiology that has adapted locally to environmental variation is primarily affected, resulting in variation in life-history traits. Finally, because in this study we were not able to differentiate between environmental effects and genetic adaptation, future studies must rear and maintain animals from the beginning in a common-garden environment.

## ACKNOWLEDGEMENTS

We are grateful to J.C. Opazo and M. Soto-Gamboa for field support. This research was funded by FONDECYT 3040042 to M.A.L. and by FONDAP 1501-0001 (Program 1) to F.B. This study complies with current Chilean legislation regarding the collection and treatment of invertebrates.

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