

Behavioral thermoregulation of the periwinkle *Nodilittorina peruviana* inhabiting the rocky intertidal of central Chile: a laboratory and field study

Termorregulación conductual del gastrópodo *Nodilittorina peruviana* en el intermareal rocoso de Chile central: un estudio de laboratorio y campo

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ABSTRACT

As an attempt to explain the distribution patterns of the periwinkle *Nodilittorina peruviana*, the aim of this study was to investigate the spatial movement of individuals in response to environmental temperature. Furthermore, the relationship between body temperature and environmental temperature as a function of body size, and the effects of environmental temperature on behavioral thermoregulation was tested. In the field, the body temperature (T_b) of *N. peruviana* showed a significant correlation with environmental temperature. However, comparisons between body and environmental temperatures revealed that T_b-values were higher than surrounding air and rocky surface temperatures. This pattern can be indicative of behavioral thermoregulation (i.e. by local migration). In fact, under laboratory conditions snails significantly avoided microhabitats with higher temperatures, showing a preferential body temperature of 14 °C. We conclude that like many other ectotherms, prosobranch gastropods are able to regulate their body temperature by the use of behavioral responses of thermoregulation, which may partially explain their pattern of spatial distribution in the rocky intertidal of central Chile.

Key words: thermal ecology, rocky intertidal, behavior, body temperature, spatial distribution, gastropods, Chile.

RESUMEN

Con el fin de explicar los patrones de distribución del gastrópodo intermareal *Nodilittorina peruviana*, el objetivo de este estudio fue investigar los patrones espaciales de movimiento de los individuos en respuesta a la temperatura ambiental. Además se estudió la relación entre la temperatura corporal y ambiental en función del tamaño del cuerpo, y el efecto de la temperatura ambiental sobre la termorregulación conductual. En situaciones de campo, la temperatura corporal (T_b) de *N. peruviana* mostró una correlación significativa con la temperatura del ambiente. Sin embargo, las comparaciones entre temperatura corporal y ambiental revelan que los valores de T_b fueron mayores que las temperatura del aire circundante y la temperatura de las superficies de las rocas. Este patrón parece indicativo de termorregulación conductual (i.e. migración local). En efecto, bajo condiciones de laboratorio, los caracoles evaden microhábitats con altas temperaturas, mostrando una temperatura corporal preferencial de 14 °C. Concluimos que como muchos ectotermos, los gastrópodos prosobranqueos son capaces de regular su temperatura corporal usando respuestas conductuales de termorregulación, lo que podría explicar en parte sus patrones de distribución en el intermareal rocoso de Chile central

Palabras clave: ecología térmica, intermareal rocoso, conducta, temperatura corporal, distribución espacial, gastrópodos, Chile.

INTRODUCCION

The study of thermoregulation has the potential of providing a bridge between the physiological processes taking place within

an organism and its ecological relationships (Tracy & Christian 1986). In order to regulate body temperature and maintain their physiological homeostasis, animals and mainly ectotherms, require environmental

thermal heterogeneity in time and space. As postulated by Tracy & Christian (1986), since space and time are ecological resources, they provide the units whereby the thermal environment can be quantified as a resource.

Spatial patterns of distribution of rocky intertidal gastropods have been traditionally explained as a consequence of: a) abiotic factors such as desiccation and wave action (e.g., Branch 1981, Little & Stirling 1985, Chelazzi et al. 1988, Hobday 1995); and b) biotic factors, associated with intra- and interspecific interactions (e.g., Wootton 1993, Menge 1995). Traditionally, the upper boundaries of distribution of high rocky intertidal species have been explained by physical factors acting during tidal emersion, whilst biological factors are thought to influence the lower distribution boundaries of intertidal animals (Underwood & Denley 1984, Paine 1994).

Here we examine the relationships between the thermoregulatory processes and thermal environment under field and laboratory conditions in the periwinkle (*Nodilittorina peruviana*) inhabiting the rocky intertidal of central Chile. Prosobranch gastropods of the family Littorinidae have been used as a model to investigate the role of biological and physical stress on distributional patterns of intertidal organisms over ecological and evolutionary time (Gendron 1977, Boulding & Van Alstyne 1993, Chapman & Underwood 1996). The most important biological factors determining littorinid distribution include: food preference, competition, and predation (Underwood & McFadyen 1983). While, the main physical factors affecting patterns of spatial distribution include: wave action, heat stress, desiccation, and availability of crevices and refuges (Atkinson & Newbury 1984, Garrity 1984, Chapman & Underwood 1994).

Investigations dealing with patterns of distribution of intertidal animals in the temperate Southern Pacific zone have

been centered on the role of biotic factors (Castilla & Paine 1987, Santelices 1990, Menge 1995). By contrast, the effects of abiotic factors have received little attention (but see Santelices et al. 1980, Cancino & Rojas 1986). In South America there have been no detailed accounts of the ecology of any littorinid species, although there have been descriptions of their general intertidal zonation and geographical distribution (Santelices 1980, Brattstrom & Johanssen 1983). *Nodilittorina peruviana* is one of the most common periwinkles of the upper intertidal zone in northern and central Chile (Santelices 1980). Santelices et al. (1986) studied seasonal patterns of distribution and abundance of *N. peruviana* in the intertidal rocky shores of central Chile, documenting a pronounced important effect of environmental temperature in the annual variation of spatial distribution of this species.

As an attempt to explain the relationships between thermoregulation (Johnston & Bennett 1996) and pattern of spatial distribution of *N. peruviana*, the aim of this study was to determine: 1) thermal preferences, 2) the relationship between body temperature, environmental temperature and body mass, and 3) spatial movements of *N. peruviana* in response to the rock-surface temperature.

MATERIAL AND METHODS

Field measurements

Field studies were conducted during winter and summer time of 1996, on rocky platforms at the high intertidal zone in Las Cruces (33° 30'S; 71° 38'W), central Chile. Detailed descriptions of the study region are in Santelices (1990). Body temperature (T_b) of *N. peruviana* through daytime, preferential body temperature (PBT, n = 30), air temperature (T_a, at 1 cm above each snail), and rock surface temperature

(Ts) were measured by using a copper-constantan thermocouple digital thermometer (± 0.1 °C). Measurements were conducted every two hours for a period of 24 hours. To guarantee the independence of measurements, each snail was recorded only once. To examine the relationship between temperature preferences and body size in this species, Tb and body weight of 30 individuals were measured at 14:00 and 18:00 h, during winter time. To avoid hand warming, animals were manipulated with the same wire of the thermocouple. Wet weight, including shell was determined by using a field electronic balance (± 0.1 mg).

Laboratory experiments

Individuals used in laboratory experiments were collected in the high rocky intertidal zone during winter time at the same site where field measurements were conducted. Animals were transported to the laboratory (aquarium) where they were acclimated for at least one day before measurements were made. To determine the effects of rock surface temperature on the spatial distribution and Tb of *N. peruviana*, two rocky microhabitats were offered to 40 individuals, under two different experimental conditions: a) condition one, where both rocky microhabitats exhibited similar Ts (14.5 °C); and b) condition two, one of the microhabitats at Ts = 40 °C, and the other microhabitat Ts = 14.5 °C. A heat source was provided by a 250 W infrared lamp. To incorporate the temporal variability associated with the behavioral response, experiments were repeated three times.

In order to determine substratum temperature preferences, multiple-choice experiments were conducted. A surface thermal gradient ranging from 10 to 30 °C was established in an experimental aquarium of 180 x 70 x 10 cm. Groups of 40 snails were located in the center of the aquarium, place at which the highest surface temperature of the experimental system was recorded. Heat was supplied through a 250 W infrared lamp

located at 40 cm above the surface of the aquarium. After two hours, both, spatial distribution of the individuals and selected Ts were recorded. This experiment was repeated five times. Due to the lack of independence among sites within the temperature gradient, the Friedman nonparametric test and then a multiple comparison test (Conover 1981, Roa 1992) was used to test for substratum temperature preferences. In order to prevent the possible influence of water loss (dissection) on the snail behavior, both laboratory experiments were carried out in a cold room with a high relative humidity and precaution was taken that a water film was always covering the experimental substrata.

RESULTS

Winter measurements of the diel variations in Tb of *N. peruviana* in the field, were positively correlated with air (Ta) and rock surface (Ts) temperatures (Pearson correlation coefficients = 0.98 and 0.81, respectively, $p < 0.001$; Fig. 1). A linear relationship between Tb and Ts was observed (Fig. 2). However, mean Tb's were significantly higher than Ts (Kruskal-Wallis test = 69.45; $p < 0.001$). On the other hand, interestingly, summer measurements of diel variations in Tb's in the field were significantly lower than Ts during day-time (Kruskal-Wallis test = 12.42; $p < 0.005$, Fig. 2), but higher than Ts during the night (Kruskal-Wallis test = 33.45; $p < 0.001$, Fig. 2).

Observed Tb- values were positively correlated with body size (Fig. 3). In fact, at 14:00 h the correlation between Tb and body mass was 0.58 ($p = 0.009$), whilst a correlation coefficient of 0.71 ($p = 0.0001$) was obtained at 18:00 h (Fig. 3). The relationships between Tb and body mass for different day times showed non-significant differences between slopes (ANCOVA: $F = 0.659$; $df = 1, 56$; $p = 0.42$); suggesting that the relationship between Tb and body mass is constant through daytime.

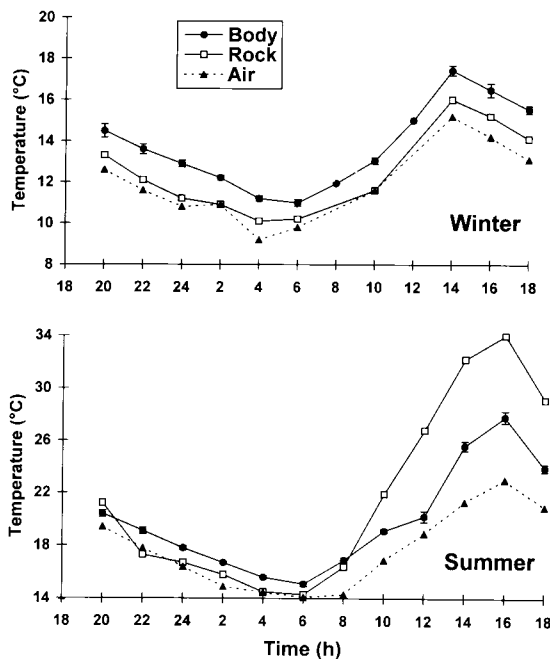


Fig. 1: Diel variations in body temperature of the snails *Nodilittorina peruviana* and their relationship with the air and surface rock temperature during winter and summer. Many standard deviation are within the points.

Variaciones diarias en la temperatura corporal del caracol *Nodilittorina peruviana* y su relación con la temperatura del aire y de la superficie de las rocas durante invierno y verano. En varios casos la desviación estándar se encuentran dentro de los puntos.

Higher T_s -values limited the spatial distribution of the intertidal snails (Fig. 4). In fact, significant differences were detected in the occupation of the microhabitat associated with differences in T_s (chi-square: 44.551, df: 1, $p < 0.001$; Fig. 4). During the experiment of temperature selection, individuals of *N. peruviana* exhibited non random T_s preferences (Friedman test: $T_2 = 2.837$, $k_1=10$, $k_2 = 40$, $p < 0.01$). In this way, the null hypothesis of no thermal preferences was rejected (Fig. 5). Multiple comparison tests revealed that PBT in this species ranged from 14 to 17 °C (Table 1).

DISCUSSION

The rocky intertidal is generally organized into different zones. One major

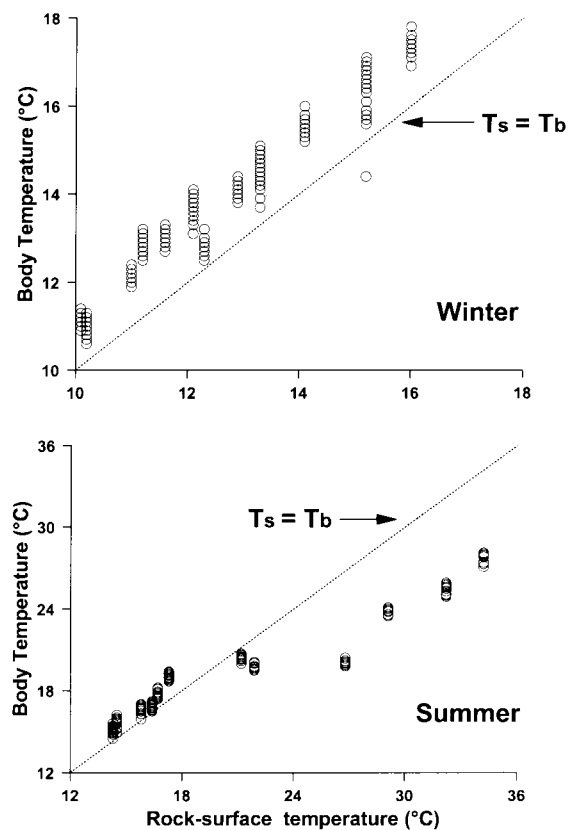


Fig. 2: Relationship between body temperature (T_b) of *Nodilittorina peruviana* and surface rock temperature (T_s) during winter and summer. Dotted line indicates isothermal conditions, $n = 360$.

Relación entre la temperatura corporal (T_b) de *Nodilittorina peruviana* y la temperatura de la superficie de las rocas (T_s) durante invierno y verano. La línea punteada indica la condición isotérmica, $n = 360$.

cause of this zonation is widely assumed to be differential responses of the intertidal organisms to gradient of abiotic (physical and chemical) conditions. Tolerance of marine intertidal organisms to temperature, salinity, and desiccation can be correlated with their position in the intertidal through time (Johnson 1975). Intertidal organisms, such as *N. peruviana*, inhabiting the highest levels of the shore, must tolerate a harsh physical environment, but are seldom subject to interspecific interactions, because few other species are found in the same area (Santelices 1990).

In the field, T_b of *N. peruviana* showed a significant relationship with environmental

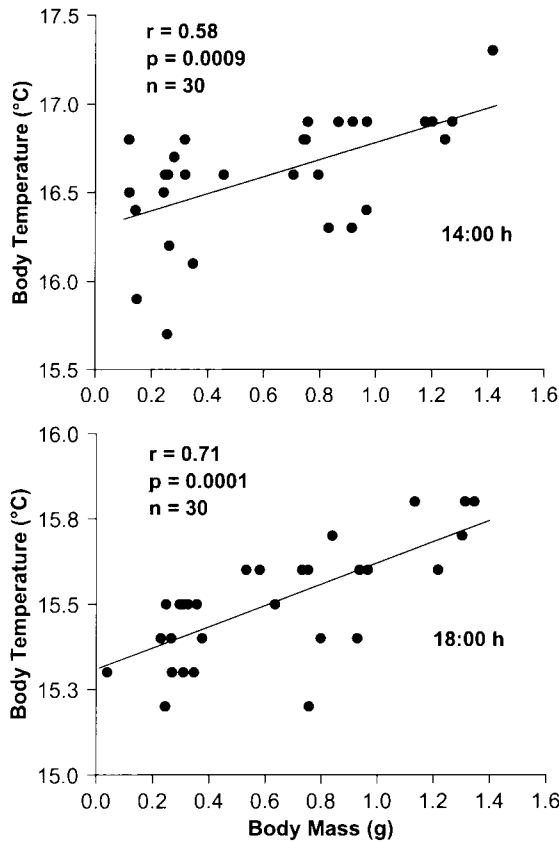


Fig. 3: Relationship between body mass and body temperature of *Nodilittorina peruviana* in the field.

Relación entre la masa corporal y la temperatura de cuerpo de *Nodilittorina peruviana* bajo condiciones de campo.

temperature. However, comparisons between body and environmental temperatures revealed that T_b -values were higher than surrounding T_a and T_s . This pattern can be indicative of behavioral thermoregulation, which is active local migration into the zone of preferential temperature. Now we offer the following explanations to the observed relationships between body temperature and environmental temperature in space and time (see Fig.1): a) during light-hours in winter, and in the absence of thermal stress, animals are probably selecting crevices and other sunny areas where conditions allow to maintain their body temperatures; b) during both winter and summer nights, the rocky surfaces exposed to solar radiation during the day are warmer than adjacent air (RE Soto

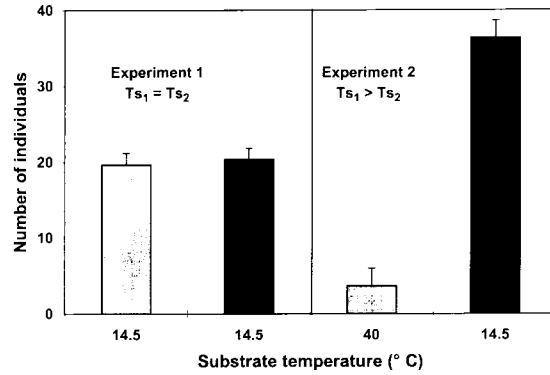


Fig. 4: Microhabitat use frequency by *Nodilittorina peruviana* under two rock surface temperature (T_s) conditions in a laboratory experiment. Experiment 1: T_s habitat a = T_s habitat b (14.5 °C); while Experiment 2: T_s habitat a (40 °C) > T_s habitat b (14.5 °C).

Frecuencia de uso de microhábitats por *Nodilittorina peruviana* bajo dos condiciones de temperatura superficiales de la roca (T_s) en un experimento de laboratorio. Experimento 1: T_s de hábitat a = T_s de hábitat b (14,5 °C); mientras que Experimento 2: T_s de hábitat a (40 °C) > T_s de hábitat b (14,5 °C).

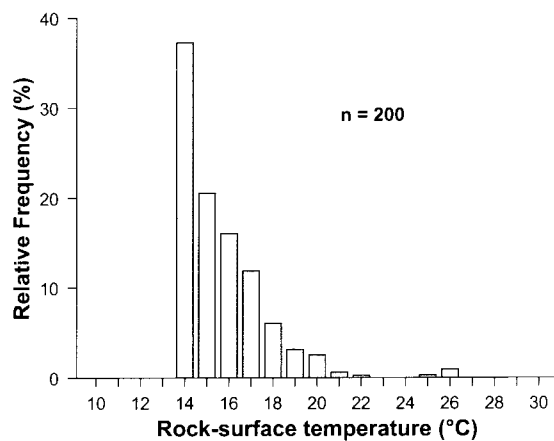


Fig. 5: Relative frequency distribution of surface rocky temperature preferences of *Nodilittorina peruviana* under laboratory conditions.

Distribución de frecuencias relativas en las preferencias por temperatura superficial de rocas por *Nodilittorina peruviana* bajo condiciones de laboratorio.

personal observations). Thus, at night, the rock surfaces reradiate (long-wave radiation) to the environment generating gradients of temperature. Consequently, at night the organisms are able to find thermal patches where thermoregulation is possible; and c) the position that an organism occupies in the

TABLE I

Test for substratum temperature preferences by *Nodilittorina peruviana* in the laboratory experiment. The Friedman multiple comparison test was used, ns = non significantly differences, ** = $p < 0.01$.

Prueba para preferencias de temperatura de sustrato por *Nodilittorina peruviana* en un experimento de laboratorio. Se usó la prueba de Friedman para comparaciones múltiples, ns = diferencias no significativas, ** = $p < 0.01$

| | | Temperature Gradient | | | | | | | | | | | | | | | | | | | |
|----|----|----------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| | | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
| 10 | ns | ns | ns | ** | ** | ns | ** | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| 11 | — | ns | ns | ** | ** | ns | ** | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| 12 | — | — | ns | ** | ** | ns | ** | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| 13 | — | — | — | ** | ** | ns | ** | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| 14 | — | — | — | — | ns | ns | ns | ns | ns | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** |
| 15 | — | — | — | — | — | ns | ns | ns | ns | ns | ** | ** | ** | ** | ** | ** | ns | ** | ** | ** | ** |
| 16 | — | — | — | — | — | — | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| 17 | — | — | — | — | — | — | — | ns | ns | ns | ns | ** | ** | ** | ** | ns | ** | ** | ** | ** | ns |
| 18 | — | — | — | — | — | — | — | — | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| 19 | — | — | — | — | — | — | — | — | — | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| 20 | — | — | — | — | — | — | — | — | — | — | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| 21 | — | — | — | — | — | — | — | — | — | — | — | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| 22 | — | — | — | — | — | — | — | — | — | — | — | — | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| 23 | — | — | — | — | — | — | — | — | — | — | — | — | — | ns | ns | ns | ns | ns | ns | ns | ns |
| 24 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | ns | ns | ns | ns | ns | ns | ns |
| 25 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | ns | ns | ns | ns | ns | ns |
| 26 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | ns | ns | ns | ns | ns |
| 27 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | ns | ns | ns | ns |
| 28 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | ns | ns |
| 29 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | ns |
| 30 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | ns |

intertidal zone is often related to its behavioral response to light, temperature or desiccation. When exposed to summer light-hours and when the amount of solar radiation is high, these mobile animals can reduce thermal stress by selecting crevices and increasing local humidity gradient through clustering. This behavioral strategy allows the animals to maintain their body temperature, that is, a T_b below stressful environmental temperatures (see Fig. 2). In short, T_b was slightly higher or equal to T_s and T_a at night but lower than T_s during daytime, which strongly suggest behavioral thermoregulation.

Furthermore, the positive relationship between T_b and body mass indicates that large snails are able to maintain a larger

temperature differential between body and environment than smaller ones. Recently, Hobday (1995) studied body size variations of the intertidal gastropod *Lottia digitalis* and their relationship with migratory behavior. According to this author, at the upper limits of the intertidal, small animals with high surface-to-volume ratios are at a disadvantage in comparison to large animals. Consequently, small gastropods may be constrained to lower heights, leading to a size gradient with increasing tidal height. High T_s 's may appear as a limiting factor on the spatial distribution of *N. peruviana* in the field. In fact, in the laboratory, snails significantly avoided high T_s microhabitats. Thus, the use of behavioral thermoregulation, including

preferences for particular substratum temperatures or changes in patterns of spatial distribution and/or aggregation, may allow avoidance of thermal stress (Gendron 1977, Chapman & Underwood 1994, Chapman & Underwood 1996). Also, substratum temperature may influence patterns of spatial distribution of snails over a longer temporal scale. Indeed, Santelices et al. (1986) described a seasonal variation in the vertical distribution of *N. peruviana*, characterized by a downward migration during late spring and summer. Based on our results, we postulate that seasonal migration could be associated to thermal ecology and behavioral thermoregulation.

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