FISIOLOGÍA ECOLÓGICA DE *Microlophus atacamensis* (SQUAMATA:TROPIDURIDAE): RESPUESTAS METABÓLICA Y DIGESTIVA A VARIACIONES DE TEMPERATURA Y PRODUCTIVIDAD

Tesis

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Se informa a la Escuela de Postgrado de la Facultad de Ciencias que la Tesis de Doctorado presentada por el candidato.

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A mi familia, a mis amigos,

y en especial a mi niñito Joaquín

RESUMEN BIOGRAFICO

Nací el 21 de enero de 1974 en la ciudad de Viña del Mar, pero a los pocos meses de vida mi familia y yo nos trasladamos a la ciudad de San Felipe, en donde viví toda mi infancia y gran parte de la adolescencia y de la cual guardo muy lindos recuerdos.

En 1992, y luego de salir del colegio ingresé a la carrera de Biología Marina de la Universidad de Valparaíso. Fue en esta etapa cuando me di cuenta que lo que me interesaba y apasionaba en la vida era la investigación científica. De este modo, en 3er año de mi carrera de pre-grado comencé a realizar estudios en mamíferos marinos, primero chungungos y luego quienes han sido los animales más queridos, los lobos marinos.

Luego de titularme como bióloga marina, pasé algunos años trabajando en diversos proyectos bajo el amparo de la Facultad de Ciencias de la Universidad de Valparaíso, lugar en donde me desempeño a la fecha. En el año 2003 ingresé al programa de Ecología y Biología Evolutiva de la Universidad de Chile, para iniciar de este modo mis estudios de doctorado. Aunque por problemas logísticos no pude realizar mi tesis en lobos marinos, sí pude desarrollar el área que me interesaba en otro sujeto de estudio, como es la protagonista de esta tesis. Aunque esta lagartija no se parece mucho a un lobo marino, ha enriquecido fuertemente mis conocimientos de historia natural, y sin lugar a dudas ha ampliado enormemente mi visión de la ecología.

En todos estos años, y ya desde antes de ingresar al doctorado, he participado activamente en diversos proyectos de investigación. Asimismo, y desde el año 2003, soy docente de la Facultad de Ciencias del Mar de la Universidad de Valparaíso, donde dicto el curso electivo de Mamíferos Marinos para alumnos de Biología Marina. He participado en diversos cursos y congresos, tanto nacionales como internacionales, y soy además miembro de la Sociedad Latinoamericana de Mamíferos Acuáticos (SOLAMAC). Al finalizar esta nueva etapa de mi vida, me arraigo en la ciudad de Viña del Mar, para trabajar en un ambicioso proyecto de investigación y para concretar mis estudios de post-doctorado el año 2008.

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Por último, quiero agradecer todo el apoyo y el amor incondicional de mi familia. En especial a mi mamá por toda su incondicionalidad, cariño, tiempo y paciencia en el cuidado de mi hijo en estos años, y a mi papá por ser desde siempre el pilar en todo lo que he querido hacer. Y a ti Joaquin, porque eres la luz de mi vida y quien me da la fuerza para luchar día a día. Gracias por existir.

INDICE DE MATERIAS

RESUMEN

La ingestión y asignación de los nutrientes y energía necesarios para los distintos procesos biológicos de un organismo son influenciadas por diversos factores ambientales. En vertebrados ectotermos, se ha descrito que el ambiente térmico y la disponibilidad de alimento afectan el presupuesto energético de un individuo a través de limitaciones en las tasas de cosecha (actividad de forrajeo), asimilación (digestión) y utilización (metabolismo) de los recursos. De este modo, diferencias ambientales en temperatura y disponibilidad de alimento pueden determinar las respuestas conductuales y fisiológicas de un organismo, con consecuencias en el presupuesto energético de un animal. Estas diferencias pueden verse reflejadas en variaciones geográficas en el estado fisiológico y/o en rasgos de historia de vida de individuos de una misma especie que habiten en localidades con las diferencias ambientales ya mencionadas.

En este estudio se investigó la variabilidad fenotípica a nivel poblacional de los patrones de abundancia y actividad, la biología térmica, la tasa metabólica estándar y las respuestas digestivas a variaciones ambientales de temperatura y disponibilidad de alimento en la lagartija *Microlophus atacamensis*. Considerando que dentro de su rango de distribución geográfica (Antofagasta a La Serena), y en sentido norte-sur, la temperatura ambiental disminuye mientras que la productividad terrestre aumenta, *M. atacamensis* constituye un buen modelo de estudio para examinar las respuestas fisiológicas y conductuales a estos gradientes ambientales y analizar cómo las consecuencias energéticas de dichas respuestas pueden verse reflejadas en el presupuesto energético y en el desempeño biológico (*"performance"*) de los individuos en distintas poblaciones.

Para regular y optimizar su temperatura corporal, las lagartijas exhiben diversos mecanismos fisiológicos y/o conductuales. Los patrones de actividad diaria y estacional son uno de los principales mecanismos conductuales de termorregulación que las lagartijas usan para lidiar con variaciones espacio-temporales en la disponibilidad de recursos térmicos. Tanto la abundancia como la actividad variaron a lo largo del año en respuesta a cambios en la temperatura ambiente, indicando que el ambiente térmico es un factor clave en la regulación de la actividad diaria y estacional de *M. atacamensis*. La ausencia de diferencias en la biología térmica y en la duración de los tiempos de actividad de la especie a escala geográfica, sugiere que las lagartijas son capaces de compensar las variaciones en el ambiente térmico a través de mecanismos conductuales, más que mediante mecanismos fisiológicos. A diferencia de los presupuestos de actividad y de la biología térmica, la tasa metabólica estándar y la fisiología digestiva a lo largo del rango de distribución de *M. atacamesis* sí varían de acuerdo a los cambios observados tanto en la temperatura ambiente como en la productividad primaria.

A partir de esta tesis se demuestra que los gradientes ambientales en temperatura y disponibilidad de alimento determinan el desarrollo de diferentes respuestas conductuales y fisiológicas de *M. atacamensis*. Las estrategias y adaptaciones empleadas por las distintas poblaciones de *M. atacamensis* permiten que las lagartijas exploten al máximo su ambiente térmico y el alimento disponible, y sean de este modo capaces de satisfacer sus requerimientos energéticos a lo largo de todo su rango de distribución geográfica.

ABSTRACT

The ingestion of nutrients and the proper allocation of that energy are paramount to the diverse biological processes of an organism, and could be influenced by a diverse range of environmental factors. In ectotherms, both the thermal environment and the quantity and quality of food affect the energy budget on an individual, through limitations in nutrient acquisition (foraging activity), assimilation (digestion), and in the utilization (metabolism) of that nutrients. Thus, variation in environmental temperature and food productivity may determinate physiological or behavioral responses of an individual, and consequently its energy budget. These differences could be reflected in geographical variation in the body condition and/or in life history traits for individuals of the same species living along a geographical range with differences in the environmental factors mentioned.

In this study, it was investigated the activity patterns, the thermal biology, the standard metabolic rate, and the digestive responses to variations of environmental temperature and primary productivity in the lizard *Microlophus atacamensis.* Considering that, from north to south, within its geographical range the environmental temperature decrease whereas the terrestrial productivity increases, *M. atacamensis* constitutes a good model to analyze the physiological and behavioral responses to these environmental gradients, and analyze if the energetic consequences of these responses could be reflected in the energy budget and biological performance of lizards dwelling in different localities.

To regulate and optimize their T_b, lizards exhibit a diverse array of behavioral and physiological mechanisms. One of the most important thermoregulatory behaviors to cope with spatial and/or temporal variation in the availability of thermal resources is a change in daily or seasonal activity. Abundance and daily activity patterns varied greatly over the year for the three populations in response to changes in seasonal temperatures, indicating that thermal environment is a key factor that restricts daily and seasonal activity of *M. atacamensis*. Lack of geographical differences in thermal biology of this species, and in daily or seasonal activity times suggest that lizards may compensate adequately the variations in thermal environment through behavioral mechanisms, instead of physiological adjustments. Contrary to activity times and thermal biology, the standard metabolic rate and digestive physiology varies along its geographical range in agreement with the observed changes both in environmental temperature and in primary productivity.

This thesis demonstrates that *M. atacamensis* evolved different behavioral and physiological strategies in response to environmental gradients in both temperature and food quantity and quality. The adaptations and strategies developed by different populations of *M. atacamensis* may allow them to exploit their thermal environment and food availability, and consequently be able to satisfy their energetic requirements along the entire geographical range of this species.

I. INTRODUCCION

Uno de los principales desafíos que deben enfrentar los individuos es la obtención de alimento que les provea de los nutrientes y energía necesarios para la sobrevivencia, el crecimiento y la reproducción (Nagy et al. 1984, Secor 2001). La ingestión de esos nutrientes y la asignación diferencial de la energía a las distintas funciones biológicas son afectadas por diversos factores ambientales (Ballinger 1979). En ectotermos, la temperatura y la disponibilidad de alimento controlan prácticamente todos los procesos fisiológicos y bioquímicos (Huey & Berrigan 2001), afectando de este modo los rasgos de historia de vida y fitness de los organismos (Sinervo & Adolph 1989, Sartorius et al. 2002). En particular, la temperatura afecta directamente el presupuesto energético de los individuos, limitando el crecimiento y las actividades de forrajeo y reproducción (Grant & Dunham 1990, Atkinson 1996, Angilletta et al. 2002). Sin embargo, esta relación está sujeta a una disponibilidad adecuada de alimento (Atkinson 1996), ya que un balance entre producción (crecimiento y reproducción) y mantención, es obtenida a través de la selección de una temperatura que es dictada por la calidad y cantidad de alimento (McNab 2002).

La regulación de la temperatura corporal por parte de un ectotermo, y su variación debido al ambiente, es una de las temáticas centrales en ecología térmica (e.g. Huey 1982, Sinervo & Adolph 1994, Carothers et al. 1998, Bauwens et al. 1999, Ibargüengoytía 2005). Cuando factores bióticos o abióticos restringen la capacidad de termorregulación, las lagartijas pueden seleccionar, o estar restringidas a operar a distintas temperaturas corporales. En consecuencia, para una misma especie, la temperatura corporal puede ser variable en distintas poblacionales, o dentro de una misma población en distintas estaciones del año (Grant & Dunham 1990, Andrews 1998, Catenazzi et al. 2005). Para regular y optimizar su temperatura corporal, las lagartijas exhiben diversos mecanismos fisiológicos y conductuales (Huey 1982, Stevenson 1985). Los mecanismos fisiológicos van dirigidos a modificaciones en la conductancia térmica en respuesta a cambios en la temperatura ambiente (Grigg et al. 1979, Dzialowski & O'Connor 2001). Por ejemplo, se ha reportado que lagartijas que habitan en climas de bajas temperaturas muestran mayores tasas de calentamiento y menores tasas de enfriamiento que lagartijas de ambientes más cálidos (e.g. Grigg et al. 1979, O'Connor 1999). Por su parte, se han documentado diversas estrategias conductuales empleadas por lagartijas para enfrentar variaciones espaciales y/o temporales en la temperatura ambiente (e.g. Hertz & Huey 1981, Van Damme et al. 1989, Bauwens et al. 1996, Gvoždík 2002), destacándose la variación en el tiempo de actividad como una de las principales estrategias (Stevenson 1985, Grant and Dunham 1988, Adolph 1990, Bauwens et al. 1996). Desde la perspectiva del principio de asignación de energía, y asumiendo que las lagartijas se alimentan mientras están activas, la tasa de captura de presas debería aumentar en tiempos de mayor actividad (Avery et al. 1982, Karasov & Anderson 1984, Grant & Dunham 1990, Adolph & Porter 1993).

Lo anterior resalta la importancia del ambiente térmico en la ingesta de nutrientes por parte de un individuo. Sin embargo, la selección de la dieta y la tasa de ingesta del alimento están a su vez condicionadas por la tasa en que el alimento es procesado y asimilado (Kersten & Visser 1996). De este modo, el tracto digestivo representa un puente funcional entre la ingesta de energía (forrajeo) y el manejo y organización de dicha energía dentro del tracto digestivo (Sabat et al. 1998, Naya et al. 2005). De acuerdo a Naya et al. (2005), la anatomía (e.g. tamaño del intestino) y función del tracto digestivo (e.g. niveles de actividad de las enzimas digestivas) de muchas especies es flexible, modificándose en respuesta a variaciones en las condiciones ambientales. Se ha demostrado, por ejemplo, cambios en la eficiencia digestiva y/o en el tiempo del paso del alimento en respuesta a variaciones en cantidad y calidad del alimento (Johnson & Lillywhite 1979), o en respuesta a variaciones en la temperatura ambiente (Du et al. 2000, McConnachie & Alexander 2004). Por lo tanto, diferencias en presupuestos energéticos entre poblaciones expuestas a regímenes térmicos y disponibilidad de alimento contrastantes podrían ser explicados, al menos en parte, por patrones de digestión y asimilación del alimento.

Uno de los principales componentes del presupuesto energético es el metabolismo de mantención, ya que en ectotermos el gasto de energía por este factor puede superar el 80% del gasto energético total (Congdon et al. 1982, Angilletta 2001). Esto hace que el costo energético de mantención sea uno de los principales determinantes de la cantidad de energía disponible para actividad y producción (Angilletta 2001). La capacidad de reducir el componente de mantención del presupuesto energético depende además de los microclimas disponibles, ya que la tasa metabólica de un ectotermo es afectada directamente por la temperatura (Angilletta 2001). La hipótesis de adaptación metabólica al frío (MCA) predice que, a una misma temperatura ambiente, la tasa metabólica de mantención en ectotermos de climas fríos es mayor que las de su co-específicos de climas de mayor temperatura (Lardies et al.

2004). En consecuencia, variaciones geográficas en rasgos de historia de vida pueden ser causadas, al menos en parte, por diferencias en el metabolismo de mantención entre individuos de poblaciones diferentes.

En base a lo expuesto, diferencias ambientales de temperatura y disponibilidad de alimento pueden afectar el presupuesto energético de un individuo a través de limitaciones en las tasas de cosecha (actividad de forrajeo), de asimilación (digestión) y/o de utilización (metabolismo) de los recursos. Dichas restricciones pueden determinar que animales ectotermos desarrollen diversas estrategias fisiológicas y/o conductuales que les permitan adaptarse y optimizar su desempeño bajo diferentes condiciones ambientales (Figura 1). En particular, si una especie se enfrenta a un descenso latitudinal en la temperatura compensado por un aumento en la disponibilidad de recursos, es esperable que modifique su tasa metabólica y procesos digestivos para optimizar la adquisición de energía en un menor tiempo de actividad.

En esta tesis se utilizó como modelo biológico a la lagartija *Microlophus atacamensis*, una especie que habita la zona costera del desierto de Atacama, entre el sur de Antofagasta (23°03'S) y La Serena (29°05'S). Dentro de su rango de distribución, y en sentido norte – sur, la temperatura ambiental decrece mientras que la productividad terrestre aumenta (Fariña et al. ANEXO 3). Estudios previos realizados en esta especie muestran que la importancia relativa de los items alimentarios provenientes de cadenas tróficas marinas o terrestres en su dieta se relaciona con variaciones temporales y espaciales en los niveles de productividad (terrestre y marino), y que a la vez las condiciones térmicas de las zonas costeras pueden determinar sus patrones de actividad, reproducción y alimentación (Hews 1993, Vidal et al. 2002, Fariña et al. en prensa, ANEXO 3). Por lo tanto, y debido a las diferencias en productividad y ambiente térmico a lo largo del rango de distribución de *M. atacamensis*, el objetivo de esta tesis fue analizar las respuestas fisiológicas y conductuales de la especie frente a diferencias en los niveles de productividad terrestre y temperatura a una escala geográfica, y analizar su efecto sobre el presupuesto energético de los individuos.

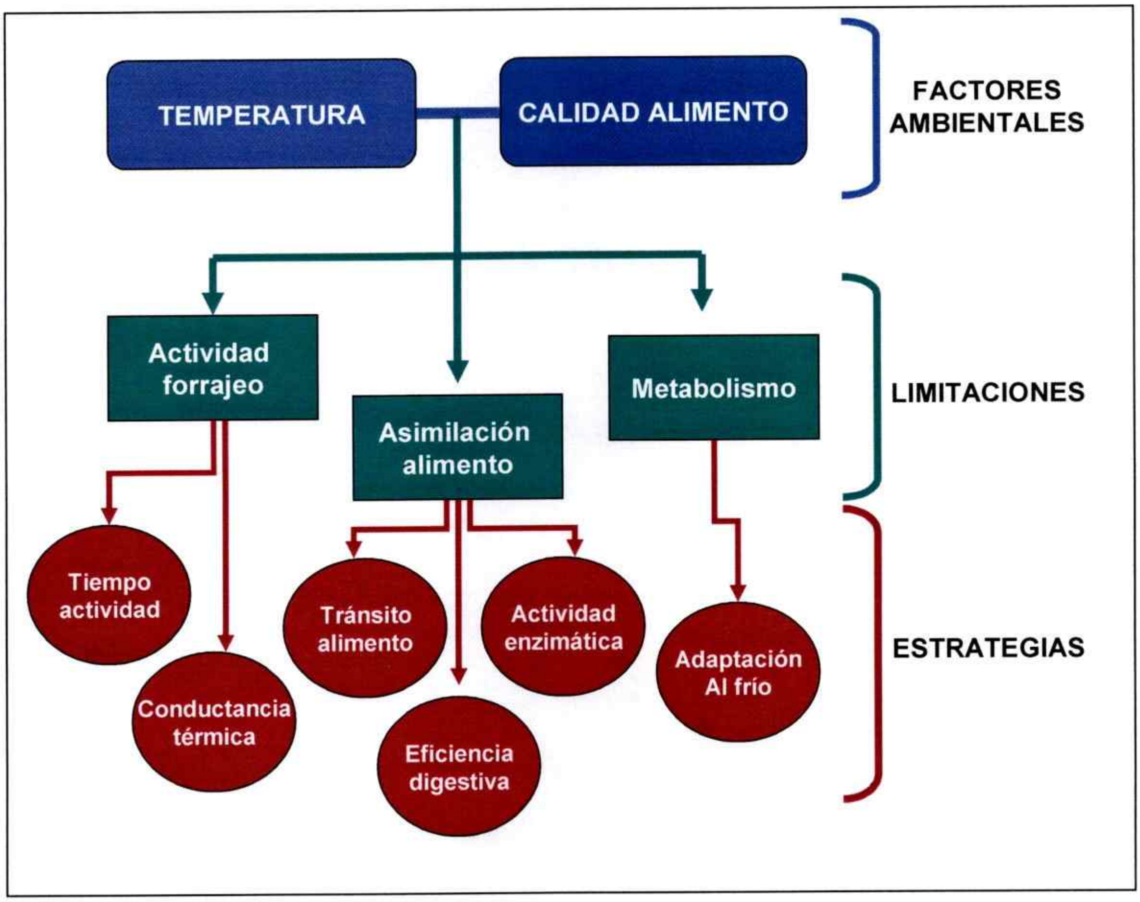

Figura 1. Esquema que muestra la incidencia de la temperatura y la disponibilidad de alimento sobre las tasas de cosecha, de asimilación y de utilización de recursos, y las estrategias fisiológicas y/o conductuales empleadas por organismos ectotermos para enfrentar dichas limitaciones.

A partir de este objetivo, la hipótesis central de esta tesis fue que las respuestas fisiológicas y conductuales, y en definitiva el presupuesto energético de *M. atacamensis*, están determinadas por los niveles de productividad terrestre y por el ambiente térmico. En un contexto energético es esperable que, ante los efectos opuestos de la temperatura ambiente y la disponibilidad de alimento terrestre, lagartijas del extremo sur del rango de distribución de esta especie deban modificar sus procesos metabólicos y digestivos en respuesta a un menor tiempo de actividad. En contraste, aunque lagartijas del extremo norte dispongan de un recurso térmico adecuado, deberán modificar su conducta y actividad de forrajeo en respuesta a la baja disponibilidad de alimento de origen terrestre.

De esta hipótesis se formularon diversas predicciones, las que fueron abordadas en cada uno de los cuatro capítulos que a continuación se anexan.

1. La termorregulación conductual y la conductividad térmica que presentan los reptiles, a un nivel intraespecífico, han sufrido ajustes en una escala microevolutiva, de modo que las temperaturas corporales, preferenciales y las tasas de transferencia de calor varían en forma clinal con el ambiente térmico. Debido a la disminución de la temperatura en sentido N – S, se predice que la temperatura corporal y preferencial son menores en poblaciones australes. Asimismo, se espera que estas poblaciones muestren tasas de calentamiento más rápidas y tasas de enfriamiento más lentas que poblaciones del norte. CAPITULO 1.

2. Debido a su dependencia directa de la temperatura ambiente, el ambiente térmico presenta restricciones a la conducta y patrones de actividad. Asociado a una disminución de temperatura en sentido N – S se predice que, a una escala diaria y estacional, los tiempos de actividad son menores en poblaciones que habitan el extremo austral de distribución de la especie. CAPITULO 2.

3. Los organismos ectotermos presentan ajustes en sus capacidades metabólicas a las condiciones térmicas del ambiente de modo de minimizar o compensar el efecto directo de la temperatura sobre las tasas de reacción (e.g., Q_{10}). A una temperatura ambiente similar, se predice que poblaciones australes de *M. atacamensis* presentarán una tasa metabólica estándar mayor que las del norte. CAPITULO 3.

4. Las tasas de hidrólisis de los nutrientes en ectotermos dependen de la interacción entre la calidad del recurso, la temperatura ambiente y las características (morfología y fisiología digestiva) particulares de los individuos. Así, se predice una mayor eficiencia digestiva en poblaciones del extremo norte de distribución de *M. atacamensis*. De igual modo, se predice que individuos de las poblaciones del extremo norte presentarán tiempos de tránsito del alimento menores que aquellos de la población austral. CAPITULO 4.

II. RESULTADOS

CAPITULO 1.

Seasonal and geographic variation in thermal biology of the lizard *Microlophus atacamensis* (Squamata:Tropiduridae)

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MANUSCRITO EN PRENSA EN LA REVISTA *"JOURNAL OF THERMAL BIOLOGY"*

Abstract

1. We studied physiological thermal adaptation in the lizard *Microlophus atacamensis* along a latitudinal range.
2. Field body temperatures were independent from thermal environmental conditions, and show seasonal, but not geographical differences. Selected body temperature did not differ among localities and seasons, and differs from body temperature in fall, but not in spring. We found no difference among sites for heating and cooling rates.
3. Our results suggest that *M. atacamensis* compensates thermal environmental variation mainly by behavioral means.

Keywords: Heating rate; cooling rate; thermoregulation; body temperature; selected temperature

1. Introduction

Since temperature strongly influences life history traits and fitness of lizards (Grant and Dunham, 1990; Adolph and Porter, 1993), the analysis of how these organisms regulate their body temperature, and how the physical environment influences their thermal biology is a central framework in thermal ecology (e.g. Huey, 1982; Sinervo and Adolph, 1994). When biotic and abiotic factors can prevent thermoregulation, lizards may select, or may be constrained to operate at different body temperatures. As a consequence, for one species body temperatures may be variable in different populations, or within a population during different seasons (Grant and Dunham, 1990; Andrews 1998; Catenazzi et al., 2005). Because of these constraints, field observations of body temperatures alone do not reveal the thermal preferences of lizards. In this sense, the voluntary body temperature that a lizard voluntary selects in the absence of confounding variables (Licht et al., 1966), called selected body temperature (T_{sel}, Pough and Gans, 1982), provides a reasonable estimate of a lizard's preference of environmental constraints for thermoregulation (Hertz et al., 1993; Ibargüengoytía, 2005).

To regulate and optimize their body temperature, lizards exhibit a diverse array of behavioral and physiological thermoregulatory mechanisms (Huey, 1982; Stevenson, 1985). Physiological control permits varying the rate at which these animals warm up or cool down their bodies in response to changes in environmental temperatures (Dzialowski and O'Connor, 2001). Some studies have reported that lizards living at lower temperatures show faster heating rates and slower cooling rates than populations dwelling in warmer climates (e.g. Grigg et al., 1979; O'Connor, 1999), indicating physiological control over their thermal conductance (Grigg et al., 1979). Also, intraspecific variation in heating and cooling rates has been considered as an adaptive physiological mechanism to cope with restrictions imposed on behavioral thermoregulation (Labra et al., 2001).

The genus *Microlophus* is composed of 20 lizard species distributed from Equador to north-central Chile, including the Galapagos archipelago. It has been divided into two monophyletic groups: *occipitalis,* composed of 10 species than inhabit from Equador to Northern Perú and the Galapagos, and *peruvianus,* also composed of 10 species ranging from northern Perú to North-central Chile (Dixon and Wright, 1975; Frost 1992). Within the *peruvianus* group two different lineages may be recognized: one lineage evolved adapted to an arid environment of inland desert and valleys; the other evolved associated with the Pacific coast (Frost, 1992). The latter lineage is composed of 2 species: *Microlophus quadrivittatus* and *M. atacamensis* (Ortiz, 1980). The geographical range of *M. quadrivitattus* (from Caleta Meca, Perú 17°54' S to Antofagasta, Chile 23°3'S) lies within an area where the extreme desert reaches the coast and there is practically no precipitation during the whole year (maximum recorded= 2mm/year, Di Castri and Hajek, 1976). In contrast, *M. atacamensis* is the southernmost species of the genus. Its range extends over 500 km into the so-called Desert Coastal area, which has a gradient of precipitation from 2mm/year in the north (at Antofagasta) to almost 80 mm/year in the south (La Serena, 29°5'S) (Ortiz, 1980; Sepúlveda et al., 2006, ANEXO 2). The diet of *M. atacamensis* is composed of algae, crustaceans, mollusks and insects in the intertidal zone (Fariña et al., 2003), with an increasing proportion of terrestrial items in a north to south gradient (Fariña et al. en prensa, ANEXO 3). The latitudinal gradient in the use of resources may in turn determine differences in the use of the thermal substrate.

The intertidal zone is an unfavorable thermal environment because lizards lose heat quickly by conduction, convection or evaporation when feeding on a wet rock substrate (Catenazzi et al., 2005). For this reason, lizards may face a trade-off between feeding and thermoregulation. Because *M. atacamensis* populations are under different thermal constraints at latitudinal, seasonal, and microhabitat scales, a temporal and geographical variability in their thermal biology is expected.

In this study we explored the physiological adjustment to environmental temperature in *M. atacamensis* by analyzing three populations along the entire geographical range of this species, from 23° S to 29° S. Considering that environmental temperature decreases as latitude increases we specifically attempted to test the hypotheses that (1) field body temperature (T_b) and selected body temperature (T_{sel}) differ among populations and seasons being lower in southern populations of *M. atacamensis* and, (2) that in southern populations of *M. atacamensis* heating rates should be faster and cooling rates slower than in northern populations.

2. Material and Methods

2.1. Study area

The study was performed in spring 2005 (September, October), summer 2006 (January), and fall 2006 (April) (Southern Hemisphere), in three sites on the northern

Chilean coast: Medano (24°37'S; 70°33' W), Zenteno (26°51' S; 70°49' W), and Arrayán (29°41'S; 71°19' W) (Fig. 1). Medano and Zenteno are under a coastal desert climatic regime, characterized by less than 2 mm of rain per year (Di Castri and Hajek, 1976). Mean air temperature in Medano ranges from 16.8 °C in winter to 21.2 °C in summer. In Zenteno air temperature varies between 15.4 °C in winter and 20.7 °C in summer. The southernmost locality, Arrayán, falls into the semi-arid Mediterranean zone (Di Castri and Hajek, 1976). Rainfall in this site averages 60 mm/year, and mean temperatures are around 13.5 °C in winter and 18.2 °C in summer (data for the three sites were obtained from the Servicio Hidrológico y Oceanográfico of the Armada de Chile).

Lizards were captured along the intertidal zone in a stretch of approximately 150-200 m. At these sites beaches consist of flat areas of a mixture of rocks (with heights from 0.2 to 3 m), pebbles, cobblestones, and sand (Vidal et al., 2002).

2.2. Field data recorded

In each season and locality we captured both active and inactive lizards. A lizard was considered as inactive when it was found under pebbles or rocks (generally early in the morning or in cool days) and exhibiting slow movements. Immediately after capture, body temperature (T_b) of lizards was recorded with a Digi-Sense thermocouple thermometer (accuracy 0.1 °C). We only considered the T_b of lizards that were handled less than 30 s after the capture. We manipulated them by holding their legs in order to reduce heat transfer between lizards and the observers. Date of capture, snout-vent length (SVL, ± 0.5 cm), and body mass (± 0.5 g) were registered for each individual. Additionally, substratum temperature (T_s; in rocks or soils) and air temperature (T_a; 10

cm above the ground) were also recorded at the capture sites. Lizards were separated by sex and age class following Ortiz (1980). The non-parametric Kruskal-Wallis test was used to evaluate the effects of seasonality and locality on T_b of lizards because the data were not normally distributed. Active and inactive lizards were analyzed separately. Finally, body temperature of active and inactive lizards was compared using a Kolmogorov–Smirnov Two Sample Test (Sokal and Rohlf, 1995).

To establish an approximation to the thermal conditions of the habitat occupied by lizards, we placed 12 Tidbit^{TM} temperature data loggers at randomly selected microsites for each season and locality. According to Vitt and Sartorius (1999), thermal profiles collected from the electronic devices do not differ substantially from copper lizard models exposed to the same conditions, suggesting that Tidbits may be used directly to monitor operative temperatures (T_e). To test if this assumption was true for our model species, in the laboratory we calibrated the Tidbits measurements with those of dead lizards placed in a thermal gradient. The results showed that recorded from electronic devices are fully correlated with temperatures from dead *M. atacamensis* lizards exposed to identical thermal conditions ($r = 0.99$).

2.3. Selected temperature (T_{sel})

Experimental conditions were set to obtain selected body temperature (T_{sel}) in lizards in spring and fall. For two consecutive days, two lizards were kept in a terrarium (73 x 31 x 28 cm) with sand-floor as substrate. Below the sand floor a thermoconductive cord was used to produce a thermal gradient from approximately 14° to 40 °C. At 8:00 each day, lizards were placed in the cool side of the terrarium to allow habituation to the experimental conditions and left undisturbed for seven hours. Body temperature (cloacal T_b) of each lizard was obtained hourly (at 15:00, 16:00 and 17:00) using a Cu-constant thermocouple and a thermometer. Individuals were captured, and their temperatures were recorded less than 30 s after capture. We considered the central 50% of the consecutive readings of T_b as the lizard's T_{sel} (Hertz et al., 1993). One-way ANOVA was used to compare the effects of seasonality (spring and fall) and locality on T_{sel}.

2.4. Thermoregulatory ability of M. atacamensis

Lizards' thermoregulatory ability was estimated from the indices of thermoregulation proposed by Hertz et al., (1993): d_b, d_e, and E. Indices d_b and *de* are calculated as the mean of the absolute value of the deviations of field active T_b and T_e from T_{sel}, respectively (Hertz et al., 1993; Christian and Weavers, 1996). Mean d_b represents the average to which lizards experience a T_b outside the selected temperature; d_e indicates the thermal quality of the habitat from the lizard's point of view. The index E represents the effectiveness of temperature regulation; it is defined as $E = 1 - (d_b/d_e)$. Usually, this index varies from 0 (when animals do not thermoregulate) to positive values (animals thermoregulating carefully).

For d_e estimation, we used the T_e inferred from the tidbits measurements. At all sites, T_e from the data loggers were registered every 30 min from 0900 to 1800 hours, but because lizards in some of the sites and seasons were active over shorter time periods (Sepúlveda et al., CAPITULO 2), we restrict our estimation of T_e to when lizards were active at a given site and season. Consequently, d_e and E provide information only on thermoregulatory periods of activity (Hertz et al., 1993). d_e data were calculated as the grand mean from daily measurements for each tidbit during the activity period of lizards (i.e., we assume that the multiple measurements on each model were statistically independent, Hertz et al., 1993). We determined the standard deviation of *E* by bootstrap resampling of mean d_b and d_e 1000 times, using the PopTools software. Because our small sample size data preclude effectively testing for differences among populations and seasons without violating statistical assumptions, we did not perform statistical analyses for the *E* index.

2.5. Heating and cooling rates

For heating and cooling rate experiments, a Cu-constant thermocouple was inserted into 1 cm into the cloaca of each experimental lizard, and was taped at its tail base to prevent it from being dislodged. Additionally, individuals were fixed with tape to a pasteboard by their extremities, to prevent movements. The thermocouple was connected to a readout which displayed the lizard's T_b to the nearest 0.1 °C.

To obtain heating rates, lizards were cooled in a refrigerator to a T_b of 14 °C. Thereafter, animals were placed in a metabolic chamber with still air at 38 ± 0.5°C. Body temperatures were recorded every 30 s, beginning when T_b reached 15 °C and ended when they reached 35°C. To obtain cooling rates, lizards were heated in a metabolic chamber to a T_b of 36 °C. They were placed in a refrigerator with still air at 8 ± 0.5°C. T_b were recorded every 30 s, beginning when body temperature reached 35 °C and ending when T_b reached 15°C. Heating and cooling rates were transformed into thermal time constants (tau = τ). The natural logarithm of the difference between T_b and

T_a was plotted against time from the initiation of the temperature step. The thermal time constant was then calculated from the slope of a straight line fitted to the data; b= -0.4343/ τ (Cossins and Bowler, 1987). Because body mass affected heating and cooling rates in a linear fashion, the effects of sex, population, and the interaction between factors upon heating and cooling rates were analyzed with a two-way ANCOVA using body mass as the covariate. All the analyses were performed in Statistica Version 6.0 (StatSoft Inc., Tulsa, OK).

3. Results

Active body temperature did not show geographical differences within a season (Spring: $H_{(2,26)} = 2.55$, $P = 0.28$; Summer: $H_{(2,26)} = 1.42$, $P = 0.49$; Fall: $H_{(1,13)} = 2.54$, $P = 0.11$), but showed seasonal differences within sites. In the extreme localities (Medano and Arrayán), summer mean T_b was significantly higher than in spring and fall (Medano: $H_{(2,30)} = 6.84$, $P = 0.03$; Arrayán: $H_{(2,19)} = 8.03$, $P = 0.02$; Table 1). However, in Zenteno T_b was not significantly different between spring and summer ($H_{(1,16)} = 2.69$, $P = 0.10$). Because field T_b did not differ among sexes (Medano: $H_{(1,30)} = 0.03$, $P = 0.86$; Zenteno: $H_{(1,16)} = 0.03$, $P = 0.86$; Arrayán: $H_{(1,19)} = 0.17$, $P = 0.68$), we pooled the data to compare T_b among populations.

Regarding inactive body temperature, lizards did not differ geographically in spring or fall (Spring: $H_{(2,16)} = 1.78$, $P = 0.41$; Fall: $H_{(2,24)} = 5.1$, $P = 0.08$, Table 1). Similarly, T_b of inactive lizards did not show seasonal differences within sites (Medano: $H_{(1,14)} =$

0.75, $P = 0.39$; Zenteno: $H_{(1,17)} = 0.2$, $P = 0.66$; Arrayán: $H_{(1,9)} = 0.0$, $P = 1$).

Body temperature of active lizards was significantly higher than that of inactive lizards (Mean $T_b = 30.89$ °C and mean $T_b = 20.46$ °C, respectively, localities and seasons combined) (Kolmogorov-Smirnov Two Sample Test, $P < 0.001$, Table 1). In summer, lizards from the three sites were all active, when T_s was above 30 °C (Fig. 2). In spring, the proportion of active individuals in Zenteno and Arrayán were higher than in Medano, although both T_a and T_s were lower. The proportion of inactive lizards was higher in fall (excepting Medano). In Zenteno, no individuals were observed in activity in fall.

Selected temperature did not show significant differences among localities for each season (Spring: $F_{(2,5)} = 0.221$, $P = 0.809$; Fall: $F_{(1,18)} = 0.021$, $P = 0.886$), nor between seasons for Medano and Zenteno (Medano: $F_{(1,13)} = 3.056$, $P = 0.104$; Zenteno: $F_{(1,8)} = 0.245$, $P = 0.634$) (Table 1). Because T_{sel} did not differ between males and females for any season (Spring: $F_{(1,6)} = 0.408$, $P = 0.546$; Fall: $F_{(1,18)} = 0.018$, $P = 0.894$) analyses considered pooled data of both sexes.

Figure 3 shows the indices *db*, *de*, and *E* for the three populations in summer and spring (fall was not compared, because we did not find active individuals in Zenteno in this season, and because in Arrayán only one individual was active). In summer, the *db* index was lower for the three populations, indicating less variation in T_b outside the T_{sel} in this season. d_e index was also lower in summer, representing a better thermal quality of the habitat, from the lizard's perspective. Thermoregulatory efficiency (*E*) seems to be different between seasons and sites. In Medano, and because d_b was nearly identical to d_e in both seasons, the *E* index was near zero, indicating that lizards from this locality are thermoconformers. In Zenteno, d_b was slightly lower than d_e, resulting in a low thermoregulatory efficiency. In Arrayán, d_b was smaller than d_e in summer. Therefore, lizards from this locality are thermoregulating in this period. However, because our data do not permit the use of statistical inference to test differences in the E index, its variation must be considered preliminary and is more a hypothesis than a well established pattern.

There was a positive and significant correlation between the thermal time constant and body mass, both for heating rates ($r = 0.44$, $P < 0.01$) and cooling rates ($r = 0.89$, $P < 0.0001$) (Fig. 4). *M. atacamensis* showed no geographic or sexual variation in thermal rates. Regarding heating rates, thermal time constants did not differ among populations ($F_{(2,41)} = 1.535$, $P = 0.226$), between sexes ($F_{(1,41)} = 0.342$, $P = 0.561$), nor was the interaction between factors ($F_{(2,41)} = 0.050$, $P = 0.951$). Similarly, in cooling rates, there were no differences in thermal time constants among populations ($F_{(2,41)} = 1.711$, $P = 0.198$), between sexes ($F_{(1,41)} = 1.129$, $P = 0.334$), nor interactions ($F_{(2,41)} = 0.671$, $P = 0.517$).

4. Discussion

Our first general hypothesis was that body temperature and selected body temperature differed among populations and seasons. In T_b, we found no geographical differences among populations of *M. atacamensis*. Several studies reported very little variation in field T_b among conspecific or congeneric species (e.g. Huey, 1982; Andrews, 1998; Carothers et al., 1998). Also, similar T_b has been measured in closely related taxa with different physical characteristics (e.g., body size or coloration), using different microhabitats or having different thermoregulatory strategies (Adolph, 1990; Carothers et al., 1998). For example, Adolph (1990) showed that T_b in two species of *Sceloporus* from southern California varied little with elevation, despite a sharp decrease in air temperatures. Nevertheless, other studies demonstrated geographic variation in T_b for different populations (e.g. Grant and Dunham, 1990; Andrews 1998), including Catenazzi et al. (2005), who found latitudinal differences in T_b between two populations of *M. peruvianus*, a species that belongs to the *M. peruvianus* group, as does *M. atacamensis*. Why might these species differ? A possible explanation might be that the maximum distance separating the Chilean populations is 500 km, whereas populations studied in Perú are separated for about 1,000 km, with a consequently greater latitudinal gradient in T_a. However, due to the small sample size we have for each season, our results should be taken with caution. Differences in T_b among the studied populations should be corroborated by further observations.

Although we did not find geographical variation in T_b, seasonal differences within sites were encountered. Summer T_b was significantly higher than spring and fall T_b. A similar result was found by Catenazzi et al. (2005), who encountered that winter T_b were from 2-8 °C lower than summer T_b. This result suggests that both *M. peruvianus* and *M. atacamensis* lizards are under environmental constraints for thermoregulation, at least for some seasons (Vidal et al., 2002).

Microlophus atacamensis showed a lower T_b than populations of *M. peruvianus* (Huey, 1974; Catenazzi et al., 2005) and *M. quadrivittatus* (Báez and Cortés, 1990), but is higher than those reported by Vidal et al. (2002) for *M. atacamensis,* who found a T_b

of around 24 °C (although, these authors captured lizards mostly in winter months). For *M. peruvianus*, Catenazzi et al. (2005) reported a mean T_b of about 36 °C in summer and 33 °C in winter. For the same species, but a northern population, Huey (1974) reported a mean winter T_b of 35 °C. For *M. quadrivittatus,* summer and winter T_b were in the range of 36 and 34 °C, respectively (Báez and Cortés, 1990). A similar latitudinal decrease was found in T_{sel}, in which *M. atacamensis* had mean T_{sel} values of about 34 °C. However, northern species of the genus showed a mean T_{sel} of about 35.6 – 36 °C (Huey, 1974; Báez and Cortés, 1990; Catenazzi et al., 2005). These results confirm that T_b and T_{sel} decrease along a north to south gradient, due to a decrease in air temperatures (Catenazzi et al., 2005).

Although all the three populations were active during summer months, lizards from Medano had the lowest *E* index, indicating less effective temperature regulation by this population during this season. This is accordance with the idea that northern localities offer better quality thermal conditions (Catennazi et al., 2005), and lizards will not need to thermoregulate carefully. However, low *E* values, resulting from a thermal environment of high quality, may incorrectly indicate that a population (or species) is an ineffective thermoregulator (see Christian and Weavers, 1996).

For Arrayán, *E* value was high in summer, indicating the presence of thermoregulation. This fact implies that lizards are able to exploit the available thermal environment to the maximum extent possible, and thus maintaining a field T_b that approximates to T_{sel} (Sinervo and Adolph, 1994). However, in spring the effectiveness of thermoregulation was low and *M. atacamensis* from this locality must be active at suboptimal body temperatures (Huey, 1982). Thermoregulatory indices of Zenteno were also positive (both in spring and summer), but significantly lower than from Arrayán in summer.

The indices of thermoregulation estimated suggest that *M. atacamensis*, across its geographical range, and even locally, varies from being a thermoconformer to being a thermoregulator (Huey, 1974; Hertz et al., 1993), similar to what was reported previously by Vidal et al. (2002). This thermal condition allows for this species to forage actively in the intertidal zone or close to it.

Our second hypothesis was that in southern populations of *M. atacamensis*, heating rates should be faster and cooling rates slower. Our results indicate that, similar to body temperatures, heating and cooling rates did not vary between populations. Similar results were reached by Van Damme et al. (1990) and by Gvoždík and Castilla (2001), suggesting again that differences in thermal environment across 500 km were too small to induce physiological adjustments in this species. This result probably implies that the thermoregulation function in *M. atacamensis* is mainly behavioral (Ibargüengoytía, 2005; Rice et al., 2006). Lizards can increase physiological heating rates not only by selecting microhabitats for basking, but also by changing body shape or orientating the body plane perpendicular to the sun (Gvoždík, 2002). Most behavioral adjustments serve to increase heating rates, and hence reduce basking time, not heat loss.

Although heating and cooling rates were similar among *M. atacamensis* populations, there was a correlation between thermal time constants and body size. The effect of body size on heating and cooling rates has been demonstrated in various species of lizards (Rice et al., 2006). Smaller lizards heat up more quickly and larger lizards cool down more slowly (Porter et al., 1973). This may be related to daily activity cycles in

M. atacamensis. In fact, in all three populations, the first age class that emerges from the burrows in the morning is the juveniles. In afternoon in contrast, the last individuals to disappear are the adults (Sepúlveda et al., CAPITULO 2).

Differences in environmental temperatures could exert significant effects on a lizard's physiology. In fact, considering a Q_{10} of near 2 to 2.5 for *M. atacamensis* (Sepúlveda et al., CAPITULO 3), aerobic metabolism may increase from 26 and 40 % when animals experience a rise of only 3 °C in environment temperature (the difference in mean maximum temperatures between the northern and southern sites). Hence, few degrees of differences may exert a significant effect on, for example, the energy budget of a lizard species. However, lack of intraspecific variation in thermal biology in *M. atacamensis* among our populations suggests that lizards may compensate adequately the variations in their thermal environment through a behavioral mechanism instead of physiological adjustment.

According to Stevenson (1985) behavioral mechanisms contribute to changes in T_b that may be four to five times greater than those provided by physiological mechanisms. This is because behavior is seemingly more plastic than physiology; conventional evolutionary wisdom asserts that an animal's first responses to a selective pressure are behavioral (Feder et al., 1987). The response of *M. atacamensis* to varying temperatures in a latitudinal gradient seems to support this idea.

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Tables

Table 1

Field body temperature (T_b) and selected temperature (T_{sel}) of active and inactive *M. atacamensis* in Medano, Zenteno, and Arrayán in spring, summer, and fall. Values are expressed as mean ± SD. Number of individuals in indicated in parentheses.

eason	Sex	Medano			Zenteno			Arrayán		
		Active	Inactive	T_{sel}	Active	Inactive	T_{sel}	Active	Inactive	T_{sel}
ring	Male	30.3 ± 4.0 (4)	20.6 ± 2.2 (4)	34.6 (1)	29.1 ± 1.9 (5)	23.5 (1)	33.9 (1)	27.6 ± 4.2 (7)	24.1 (1)	-
	Female	28.3 ± 1.5 (3)	21.6 ± 1.8 (5)	33.2 ± 2.7 (3)	28 ± 1.5 (2)	18.2 ± 0.8 (2)	-	26 ± 4.9 (5)	20 ± 1.2 (3)	33.9 ± 2.9
	Both	29.4 ± 3.2 (7)	21.2 ± 1.9 (9)	33.6 ± 2.4 (4)	28.8 ± 1.7 (7)	20 ± 3.1 (3)	33.9 (1)	27 ± 4.4 (12)	18.8 ± 3.7 (4)	33.9 ± 2.9
mmer	Male	34.1 ± 2.4 (4)	-	-	30.5 ± 4.4 (6)	-	-	33.8 ± 0.6 (2)	-	-
	Female	32.4 ± 3.3 (7)	-	-	30.9 ± 5.9 (3)	-	-	32.9 ± 3 (4)	-	-
	Both	33.0 ± 3.0 (11)	-	-	30.6 ± 4.6 (9)	-	-	33.3 ± 2.4 (6)	-	-
ll	Male	30.3 ± 2.6 (8)	24.4 ± 0.5 (3)	34.4 ± 2.2 (8)	-	19.1 ± 1.2 (6)	35.6 ± 1.6 (6)	-	19.5 ± 2.7 (2)	-
	Female	29.1 ± 3.9 (4)	19.6 ± 1.5 (2)	36.6 ± 1.8 (3)	-	20.5 ± 1.9 (8)	33.9 ± 2.6 (3)	21.8 (1)	17.6 ± 2.4 (3)	-
	Both	30.4 ± 2.5 (12)	22.5 ± 2.7 (5)	34.6 ± 2.3 (11)	-	19.9 ± 1.7 (14)	35.2 ± 2.1 (9)	21.8 (1)	18.4 ± 2.4 (5)	-

Figure Captions

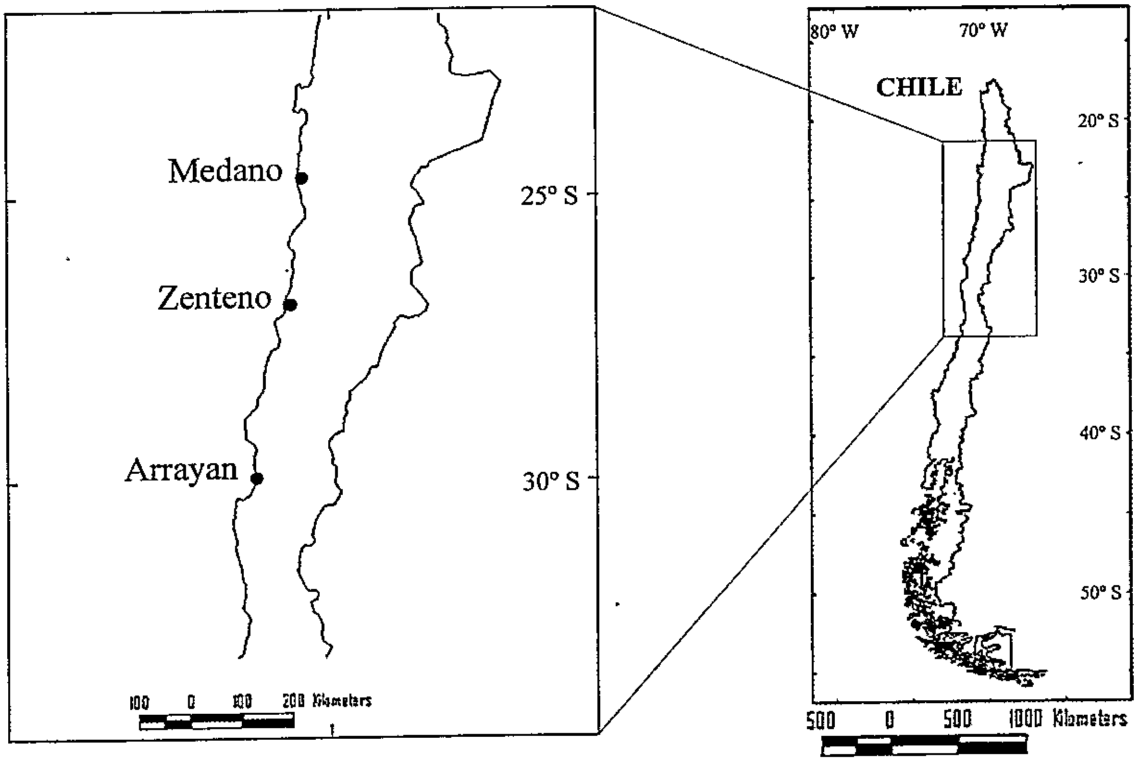
Fig. 1. Study map showing the geographic location of the collecting sites of *Microlophus atacamensis*.

Fig. 2. Proportion of active (gray portion of the bar) and inactive (white portion) *M. atacamensis* lizards in spring, summer, and fall for Medano, Zenteno, and Arrayán sites. Above the figure it is indicated both T_a (black circles) and T_s (white triangles) for each season and site.

Fig. 3. Mean and standard error of d_b, d_e and E indices.

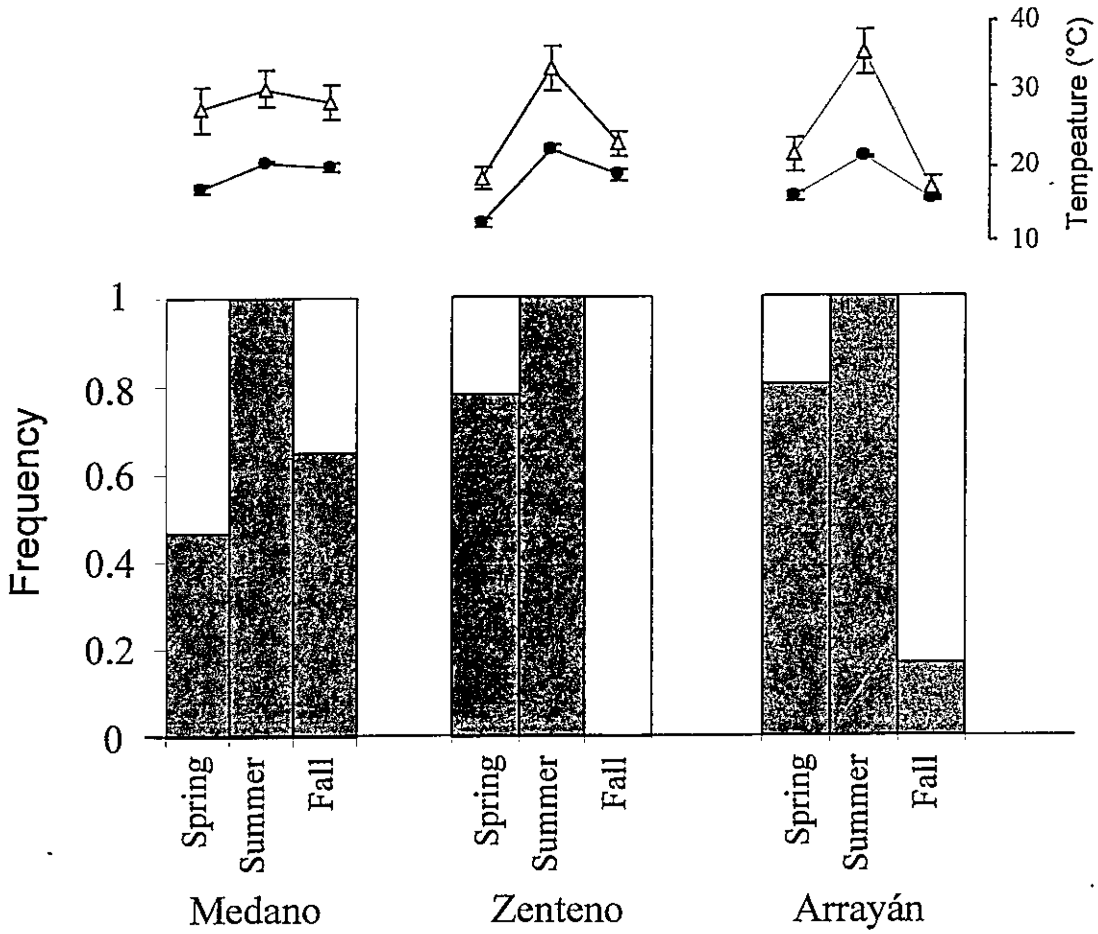
Fig. 4. Relationships between the thermal time constant (τ) and body mass of *M. atacamensis* heating and cooling rates.

*Figure 1



Medano
Zenteno
Arrayan
25° S
30° S
100 0 100 200 Kilometers
80° W
70° W
CHILE
20° S
30° S
40° S
50° S
500 0 500 1000 Kilometers

*Figure 2



40
30
20
10
Tempeature (°C)
Frequency
1
0.8
0.6
0.4
0.2
0
Spring
Summer
Fall
Spring
Summer
Fall
Spring
Summer
Fall
Medano
Zenteno
Arrayán

*Figure 3

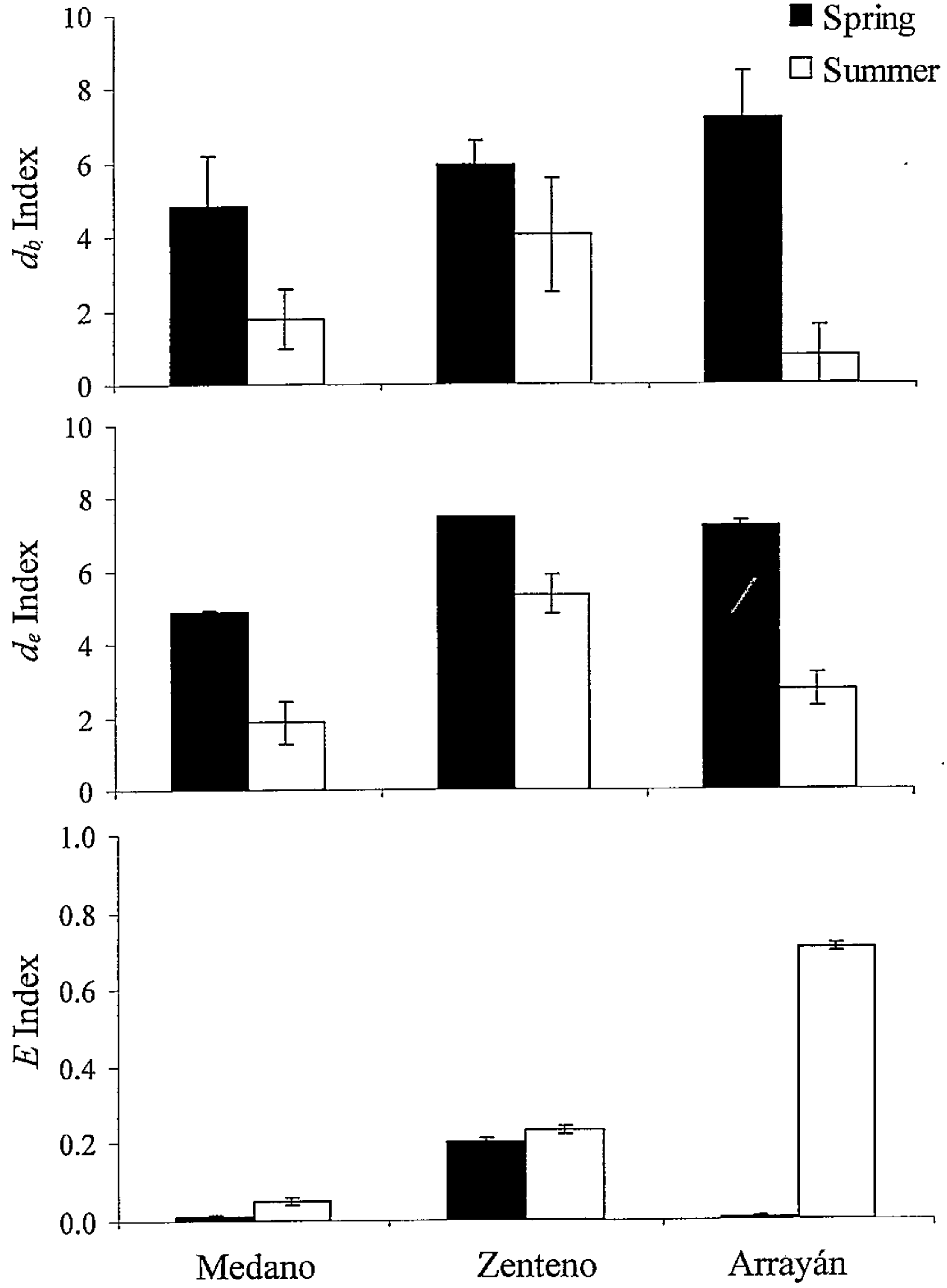
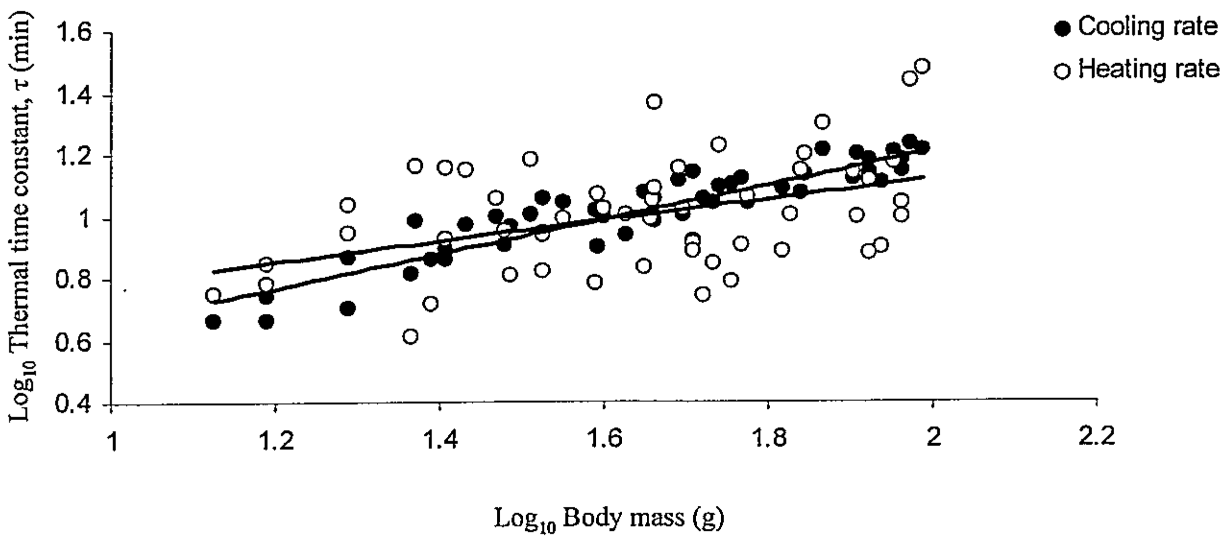

■ Spring
☐ Summer
d_b Index
10
8
6
4
2
0
d_e Index
10
8
6
4
2
0
E Index
1.0
0.8
0.6
0.4
0.2
0.0
Medano
Zenteno
Arrayán

*Figure 4



Cooling rate
Heating rate
Log_{10} Thermal time constant, τ (min)
1.6
1.4
1.2
1
0.8
0.6
0.4
1
1.2
1.4
1.6
1.8
2
2.2
Log_{10} Body mass (g)

CAPITULO 2.

Abundance and activity patterns of the lizard *Microlophus atacamensis*: thermal environmental effect

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MANUSCRITO CON FORMATO PARA REVISTA "*OECOLOGIA*"

Abstract

Lizards exhibit a diverse array of behavioral mechanisms to cope with spatial and/or temporal variations in thermal resources. One of the most important of these mechanisms is the activity times, which has been proposed to explain variations in energy acquisition and ultimately on life history traits. A longer time a lizard can maintain activity, more time to forage and an expected larger and heavier adult body size. In this study we explored the behavioral adjustments to environmental temperature on daily and seasonal scales in three natural populations of the lizard *Microlophus atacamensis* along a latitudinal gradient. Abundance and daily activity patterns varied greatly over the year for the three populations in response to changes in seasonal temperatures. In summer and spring, the daily activity times was higher, and reduced on fall and winter seasons. In summer, when stressful heat load should prohibit activity over a midday gap, lizards did not show bimodal patterns of activity. Instead, they move to the intertidal habitat, thus extending their activity period a longer time. Abundance and thermal quality in the southernmost site was lower, but lizards did not show shorter daily or seasonal activity times. Contrary to expected, lizards from this locality showed heaviest body sizes. Our results indicate that thermal environment is a key factor that restricts daily and seasonal activity of *M. atacamensis* lizards, and importantly influence their abundance and body size.

Key words: *Microlophus*, latitudinal gradient, body size, daily activity

Introduction

One of the principal challenges for animals is to obtain food to provide nutrients and energy needed for survival, growth, and reproduction (Nagy et al. 1984; Secor 2001). Energy intake and its assignation to different biological functions is affected by diverse environmental factors (Ballinger 1979). In lizards, temperature controls practically all of the physiological and biochemical processes (Huey and Berrigan 2001) and thus it affects the life history traits and the fitness of these organisms (Sinervo and Adolph 1989; Grant and Dunham 1990; Adolph and Porter 1993; Sartorius et al. 2002). The analysis of how lizards regulate their body temperature (T_b), and how the physical environment influences their thermal biology is a central framework in thermal ecology (e.g. Huey 1982; Sinervo and Adolph 1994; Carothers et al. 1998; Bauwens et al. 1999; Ibargüengoytía 2005). To regulate and optimize their T_b, lizards exhibit a diverse array of behavioral and physiological mechanisms (Grigg et al. 1979; Huey 1982; Stevenson 1985; Rice et al. 2006). Behavioral thermoregulation may reduce environmental temperature variations, for example, varying basking frequency and microhabitat use (Hertz and Huey 1981; Christian et al. 1983; Adolph 1990; Bauwens et al. 1996), changing body shape and/or body orientation to the sun (Bauwens et al. 1996; Gvoždík 2002), and changes in activity time (Stevenson 1985; Van Damme et al. 1989).

One of the most important thermoregulatory behaviors to cope with spatial and/or temporal variation in the availability of thermal resources is a change in daily or seasonal activity (Stevenson 1985; Grant and Dunham 1988; Adolph 1990). Assuming that lizards are foraging while active, longer activity times should increase the daily prey capture rate (Avery et al. 1982; Karasov and Anderson 1984; Grant and Dunham 1990; Adolph and Porter 1993), thus increasing the energy acquisition and ultimately the reproductive success of lizards.

Daily and seasonal activity may also lead to specific geographic patterns in growth and body size. Lizards with longer activity seasons spend more time at high T_b and therefore are expected to grow faster (Adolph and Porter 1993). For example, in sagebrush lizards, Sears (2005) found that longer seasonal activity was associated with an increase in individual growth and larger adult body size. Therefore, variation in thermal environment, through its effect on thermoregulatory behavior and activity time, may have a profound and direct impact on time budgets of the lizards, and cause some of the observed variation in life histories among widespread populations (Dunham et al. 1989; Grant and Dunham 1990; Adolph and Porter 1993; 1996).

The family *Tropiduridae* is mostly composed by terrestrial feeders, but some species that dwell in desert coastal areas (with low levels of terrestrial productivity), feeds almost exclusively on intertidal or subtidal zones (Donoso-Barros 1966; Wikelski and Wrege 2000). In Chile, two species from the genus *Microlophus* use this feeding strategy: *Microlophus quadrivittatus* and *M. atacamensis* (Ortiz 1980). For *M. atacamensis*, Fariña et al. (2003) reported that the diet of this species is composed both of intertidal (algae and crustacea) and terrestrial (isopoda, coleoptera) prey. The importance of each of these dietary items is associated with spatial and temporal variation in the productivity levels of both habitats, with an increasing proportion of terrestrial items in a north to south gradient (Fariña et al. en prensa, ANEXO 3).

The intertidal zone is an unfavorable thermal environment because lizards lose heat quickly by conduction, convection and evaporation when feeding on a wet rock substrate (Catenazzi et al. 2005). For that reason, lizards may face a trade-off between feeding and thermoregulation. Because *M. atacamensis* populations are under different thermal constraints at latitudinal, seasonal and microhabitat scales, a temporal and geographical variability in their thermal biology is expected. Lack of physiological intraspecific variation in thermal biology in *M. atacamensis* (Sepúlveda et al. 2007, CAPITULO 1) suggests that lizards may compensate adequately the variations in their thermal environment through a behavioral mechanism instead of physiological adjustment.

In this study we explored the behavioral adjustments to environmental temperature on daily and seasonal scales in *M. atacamensis*. We selected three populations along the entire geographical range of this species, from 23° S to 29° S. Considering that environmental temperature decreases as latitude increases, we specifically asked whether the duration of daily and seasonal activity times decrease with increasing latitude. Associated with this hypothesis, it is expected that body size should decrease in populations that showed shorter activity times.

Materials and methods

Organism and study sites

From July 2005 to April 2006 we studied the abundance and activity patterns in three sites on the northern Chilean coast: Medano (24°37'S; 70°33' W), Zenteno (26°51' S; 70°49' W), and Arrayán (29°41'S; 71°19' W) (Fig. 1). These sites cover the entire range of geographical distribution of *M. atacamensis* (~ 500 km). Medano and Zenteno are under a coastal desert climatic regime, characterized by less than 2 mm of rain per year (Di Castri and Hajek 1976). Mean air temperature in Medano ranges from 16.8 °C in winter to 21.2 °C in summer. In Zenteno air temperature varies between 15.4 °C in winter and 20.7 °C in summer. The southernmost locality, Arrayán, in contrast, falls into the per-arid Mediterranean zone. Rainfall in this site averages 60 mm/year, and mean temperatures are around 13.5 °C in winter and 18.2 °C in summer (data for the three sites were obtained from the Servicio Hidrológico y Oceanográfico of the Armada de Chile). Terrestrial productivity also shows a gradient, with a significant increment of plant cover, from 0% in Medano to 23% in Arrayán (Fariña et al. en prensa, ANEXO 3). Lizards live along the intertidal zone in a stretch of approximately 150-200 m dominated by flat areas of a mixture of rocks (with heights from 0.2 to 3 m), pebbles, cobblestones, and sand (Vidal et al. 2002).

Abundance

For each site, and every four months, we counted the number of active *M. atacamensis* lizards by visual searching. In each occasion, and for two consecutive days, censuses data were collected by walking parallel to the shoreline, covering both intertidal and the adjacent terrestrial (supralitoral) substrates. Censuses were made at 0900, 1100, 1300, 1500, and 1700 h, walking in each occasion for one hour and covering approximately 1 km of coast. The maximum number of lizards sighted during a census period was used as a relative index of abundance. This index does not provide a measure of the actual density of lizards, but allows the between-habitats and between-seasons comparison of abundance at a geographical scale (Díaz and Carrascal 1991). Lizards were differentiated by age class (juveniles or adults), recording their position on intertidal or terrestrial habitats. Air and substrate temperatures (T_{air} and T_{soil}) were measured immediately prior and after each census.

Daily activity patterns

Parallel to the abundance analysis, one observer counted lizards from 0900 to 1800 h in a 1500 m^2 area, recording the number of lizards sighted every 30 min. As before, lizards were differentiated according to age classes (juveniles or adults) and substrate (intertidal or terrestrial habitat). To establish an approximation of thermal conditions of the habitat occupied by lizards, we placed six Tidbit^{TM} temperature data loggers with an internal temperature sensor (three in the intertidal zone and three in terrestrial zones) at randomly selected microsites for each season and locality. Temperatures in the data loggers were registered every 30 min. According to Vitt and Sartorius (1999), thermal profiles collected from the electronic devices do not differ substantially from copper lizards models exposed to the same conditions, suggesting that Tidbit^{TM} could be used directly to monitor operative temperatures (T_e). To test if this assumption was true for our model species, in the laboratory we calibrated the tidbits measurements with those of dead lizards placed in a thermal gradient. The results showed that recorded from electronic devices are fully correlated with temperatures from dead *M. atacamensis* lizards exposed to identical thermal conditions ($r = 0.99$). Besides, we calculated the d_e index, which represents the thermal quality of the habitat, from the lizard perspective (Hertz et al. 1993). This index is calculated as the mean of the absolute value of the deviations of T_e from selected temperature (T_{sel}) of the corresponding site and season. Selected temperature was considered as 34.34 °C, independent of the season and locality (Sepúlveda et al. 2007, CAPITULO 1).

Body size

Individuals from the three populations were captured during the study period (N = 55 for Medano, N = 50 for Zenteno, and N = 27 for Arrayán). Two measures of body size were registered at each capture: (1) snout-vent length (SVL), which was measured to the nearest millimeter using a caliper, and (2) mass which was measured to the nearest 0.1 g using a Pesola. The analyses were restricted to adults and, because this species exhibits a clear sexual dimorphism in body size (Ortiz 1980; Vidal et al. 2002), sexes were analyzed separately.

Statistical analyses

The abundance of *M. atacamensis* was analyzed with a two-way ANOVA test (Zar, 1996), using sites and seasons as factors, with 3 and 4 levels, respectively. Kendall-rank correlations were used to determine whether the mean number of lizards was correlated with T_{air} or T_{soil}. We used means of T_{air} and T_{soil} to compute this statistic. Thermal conditions during the daily activity patterns (using the d_e index) were compared among sites and seasons using a two-way ANOVA test. Body size data (SVL and mass) was analyzed with a two-way ANOVA, using sites and sex as factors. Normality of the data was checked by Shapiro-Wilk's test of normality and, when appropriate, the data were log-transformed. Post-hoc comparisons were performed using a Tukey's honest significance difference test. All comparisons were performed using Statistica 6.0 for Windows (StatSoft Inc. 2001).

Results

Abundance

The abundance of *M. atacamensis* was significantly different among sites ($F_{2,12} = 14.40$, $P < 0.001$), seasons ($F_{3,12} = 9.73$, $P = 0.002$), and for the interactions between these factors ($F_{6,12} = 4.44$, $P = 0.014$). Highest mean values occurred in Medano and Zenteno (at the north and mid geographical range, respectively) compared to the southern most site (Arrayán) (Fig. 2). In terms of seasonality, fewer individuals were found in winter, compared to the summer. Both T_{air} and T_{soil} were higher in summer, related to the other seasons (Table 1). T_{air} and T_{soil} were significantly correlated with the number of lizards observed during the censuses, for the three sites studied ($\tau = 0.49$ and $\tau = 0.35$ in Medano; $\tau = 0.35$ and $\tau = 0.40$ in Zenteno; $\tau = 0.18$ and $\tau = 0.14$ in Arrayán, for T_{air} and T_{soil}, respectively) (all Kendall rank correlation coefficients significant at $P < 0.001$).

Activity patterns

Daily activity patterns varied greatly among seasons for the three populations. During summer, lizards emerged from their burrows as early as 0900 h, when T_e was above 20 °C. Lizards remain active during all day, and did not show a clear abundance pattern (Fig. 3). When we finished our observation period (1800 h), we could still observe some individuals above the rocks. Both juveniles and adult emerged at 0900 h, and remain active until 1800 h.

The activity pattern was shorter in fall and winter, especially for Medano and Arrayán sites. Lizard's appearance coincided with an increase in T_e, showing a unimodal activity behavior. In general, juveniles emerged earlier than adults in the three sites and disappear before them in late afternoon. In spring, daily activity pattern was similar to fall and winter, showing a unimodal activity pattern, with maximal abundances near midday for both juveniles and adults. The activity period was similar to summer, but lizards emerged around 1000 h for the three sites. Again, juveniles emerged earlier than adults, but disappear before them in the afternoon.

Operative temperature was strongly correlated with the number of observed active lizards, for the three sites studied ($\tau = 0.62$ in Medano; $\tau = 0.34$ in Zenteno; $\tau = 0.57$ in Arrayán) (all Kendall rank correlation coefficients significant at $P < 0.001$). The deviation of T_e from T_{sel} (d_e) varied significantly among sites ($F_{2,216} = 9.19$, $P < 0.001$), seasons ($F_{3,216} = 35.52$, $P < 0.001$), and for the interaction of these two factors ($F_{6,216} = 8.80$, $P < 0.001$). Thus in Medano, average d_e was smallest (i.e. a highest thermal quality) than in the other sites. Seasonally, d_e index was lowest in summer and highest in winter. No differences were found between spring and fall (Fig. 4). As shown in Figure 3, T_e varied considerably with time of day for each season and site. In summer, and for all sites, thermal suitability for lizards was high during all the day, with T_e surpassing 30°C. In contrast, in the other seasons thermal suitability was low, especially in early morning and late afternoon, and higher at midday hours, when lizards were active.

Microlophus atacamensis also shows geographical and seasonal differences in the use of intertidal and terrestrial habitats. In Medano, lizards show a clear pattern of use of both habitats. Individuals move to the intertidal zone when T_e in this habitat surpasses 25 °C. In winter, when T_e never exceeds this temperature, lizards remain in the terrestrial areas (Fig. 5). In summer and spring, lizards from Zenteno and Arrayán were found both in the intertidal and terrestrial habitats during all day. In fall, only few individuals were found in the intertidal zone during a short period of time. In winter, no individual were found in the intertidal zone for any site.

Body size

Body size (SVL and mass) differed significantly among sites and sexes (Table 2). For SVL comparisons, females were significantly smaller than males in all the sites studied. However, for each sex, lizards from Medano, Zenteno, and Arrayán were similar in size. With regard to body mass, males were heavier than females. In females, body mass of Arrayán lizards was greater than both Medano and Zenteno lizards. Medano and Zenteno lizards were similar in weight. In the case of males, body mass from Medano lizards was lesser than from Zenteno and Arrayán lizards. Body mass was similar between the two last sites.

Discussion

Our results indicate that thermal environment is a key factor in regulating the activity patterns on *Microlophus atacamensis* lizards. Our hypothesis was that lizards from northern sites should have longer daily and seasonal activity times because they experience a warmer environment. According to this hypothesis, we found a small d_e in Medano, implying that this northern locality offers better quality thermal conditions for the activity of lizards (Catenazzi et al. 2005). Although in the southernmost site (Arrayán) thermal quality of the environment is lower, we did not find that daily or seasonal activity times were lower. It is possible that lizards from Arrayán confront thermal restrictions by increasing their activity time during the day (Huey et al. 2003), compensating the high time cost of thermoregulation by allocating more time to basking than to other activities. According to Dunham et al. (1989) and Adolph and Porter (1993; 1996) an increase in basking time activities can affect the energy budget, and ultimately the reproductive success of lizards in high-latitude populations. Number of lizards in Arrayán is significantly lower than in Medano and Zenteno, suggesting that in this southern locality the animals are under a higher cost of thermoregulation than the other populations. Lizards from Arrayán should allocate more energy to thermoregulation, with a consequent less proportion of the energy budget allocated to growth and reproduction.

We found that lizards shift their daily activity pattern over the year in response to changes in seasonal temperatures. In summer and spring, the daily activity time was higher, and reduced on fall and winter seasons. Similarly, d_e index was highest in these seasons, indicating a low thermal quality for the activity of lizards. Lower body temperature in winter, compared to the summer T_b (Sepúlveda et al. 2007, CAPITULO 1), suggest that in winter lizards are under environmental constraints for thermoregulation and should operate as low-energy systems (Catenazzi et al. 2005).

Patterns of daily activity varied seasonally for *M. atacamensis*. During fall, winter, and spring seasons, lizards showed a unimodal activity pattern, being active around midday, when solar radiation and T_e was high. This pattern is typical of several species of lizards (e.g. Labra et al. 2001; Niewiarowski 2001). Particularly, *M. peruvianus* (a species that belongs to the *M. peruvianus* group, as does *M. atacamensis*) also shows a unimodal pattern of activity in this period of time (Catenazzi et al. 2005).

A shift of activity from unimodal to bimodal had been found in several species of diurnal desert lizards (e.g. Porter et al. 1973; Díaz and Cabezas-Díaz 2004), associated with an increase in environmental temperatures in summer. Around midday lizard avoid the high temperatures not leaving their burrows, but becomes active again during the afternoon. Similar to other lizard's species, during summer *M. atacamensis* face a stressful heat load in midday hours, which should prohibit activity over a midday gap. However, they did not show a bimodal pattern of activity. Apparently, lizards use the behavioral strategy of moving to the intertidal habitat, in which temperature is lower. This probably strategy allow lizards to present a continuous daily activity patterns associated with the use of different substrates, extending their activity period a longer time, close to the source of food, without overheating. Outside summer, lizards could be restricted to visit to the intertidal habitat, because the low T_e increases the heat lose by conduction or evaporation (Catenazzi et al. 2005). This could affect differentially the energy acquisition for populations of *M. atacamensis*. Fariña et al. (en prensa, ANEXO 3), found latitudinal variations in the diet composition of *M. atacamensis*. The diet of lizards from Medano is composed almost exclusively of intertidal invertebrates and algae. In contrast, they found an increase in the proportion of terrestrial items in a north to south gradient. In this sense, lizards from Medano may be under a trade-off between feeding and thermoregulation, which may in turn determine differences in the use of the thermal substrate. Due to the lower T_e outside warmer months, lizards from Medano are restricted to visit intertidal habitats and thus probably affect the ingestion of intertidal preys. This energy restriction can explain the lower body mass found in Medano lizards. Although longer seasonal activity is usually associated with a larger and heavier body size (Sears 2005), we found that lizards (both males and females) from Arrayán, and not from Medano, were heavier.

The activity pattern of *M. atacamensis* seems to be different between juvenile and adults. In fact, we found that juveniles emerge before adults and become inactive before them in the afternoon. At least two not mutually exclusive explanations can be hypothesized. First, and because smaller lizards heat up quickly and larger lizards cool down slowly (Porter et al. 1973; Sepúlveda et al. 2007, CAPITULO 1), it has been suggested that body size should play an important role in setting activity patterns of large versus small lizards (Carothers et al. 1998). Such effect has been argued to explain why during the day juveniles are active earlier and adult later (Cowles and Bogert 1944). Second, social interactions within this species could explain a temporal segregation between age classes. Vidal et al. (2002) found a highly territorial behavior of adults and aggressive behavior towards juveniles. For this reason, it could be possible that juveniles emerge before in order to prevent interactions with adults.

In conclusion, we found that thermal environment is a key factor that restricts daily and seasonal activity of *M. atacamensis* lizards, and importantly influence their abundance and body size. Lack of some physiological adjustments among populations of this species (Sepúlveda et al. 2007, CAPITULO 1) indicates that *M. atacamensis* mostly employ behavioral strategies to cope with spatial and temporal variation in the thermal environment.

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Tables

Table 1. Air, soil, and operative temperature in Medano (M), Zenteno (Z), and Arrayán (A) sites during the four seasons of the year. Data are based on two sampling days of each season.

Season	Air temperature (°C)			Soil temperature (°C)			Operative temperature (°C)		
	M	Z	A	M	Z	A	M	Z	A
Summer	20.4 ± 0.5	24.4 ± 0.6	22.3 ± 0.1	31.2 ± 1.5	36.8 ± 1.5	33.4 ± 2.2	33.3 ± 1.0	37.6 ± 1.1	37.5 ± 1.2
Fall	20.0 ± 0.5	20.4 ± 1.9	18.4 ± 1.0	30.9 ± 2.5	26.5 ± 0.2	23.6 ± 3.4	30.0 ± 1.2	25.4 ± 1.1	20.6 ± 0.9
Winter	18.3 ± 0.2	15.6 ± 0.7	18.2 ± 1.4	24.8 ± 1.3	18.2 ± 1.2	20.1 ± 2.8	20.9 ± 0.8	23.1 ± 0.9	21.9 ± 1.0
Spring	18.0 ± 0.0	13.7 ± 0.5	18.7 ± 1.3	33.8 ± 0.4	23.5 ± 1.7	26.3 ± 1.0	28.9 ± 1.3	22.5 ± 0.7	27.8 ± 1.3

Table 2. ANOVA results for body size comparisons among sites, and sexes. SVL: Snout-vent length, W_b: body mass.

Dependent variable	Effect	Df	MS	F	P-level
SVL	Site	2	0.00	0.9	0.34
	Sex	1	0.21	100.9	**< 0.001**
	Site × Sex	2	0.00	1.2	0.31
	Error	118	0.00		
W_b	Site	2	0.14	6.93	**< 0.001**
	Sex	1	2.57	128.75	**< 0.001**
	Site × Sex	2	0.03	1.66	0.19
	Error	126	0.02		

FIGURE CAPTIONS

Figure 1. Study map showing the geographic location of the collecting sites of *Microlophus atacamensis*.

Figure 2. Seasonal and geographical comparisons of mean lizard abundance.

Figure 3. Daily activity pattern of *M. atacamensis* in summer, fall, winter, and spring for Medano (a-d), Zenteño (e-h), and Arrayán (i-l) populations. White bars represent the number of juveniles; the black ones represent the adult abundance. Circles represent Te (measured with Tidbits^{TM} data loggers) in the intertidal habitat; triangles represent Te in supralitoral habitat.

Figure 4. Mean and standard error of d_e' index.

Figure 5. Diel variation of the percentage of active lizards in supralitoral and intertidal habitats in summer, fall, winter, and spring for Medano (a-d), Zenteno (e-h), and Arrayán (i-l) populations. White bars represent the proportion of individuals in the supralitoral zone; the gray ones represent the proportion in the intertidal zone. Maximal abundance in the day was considered as 100%. Circles represent T_e (measured with Tidbits^{TM} data loggers) in the intertidal habitat; triangles represent T_e in supralitoral habitat.

*Figure 1

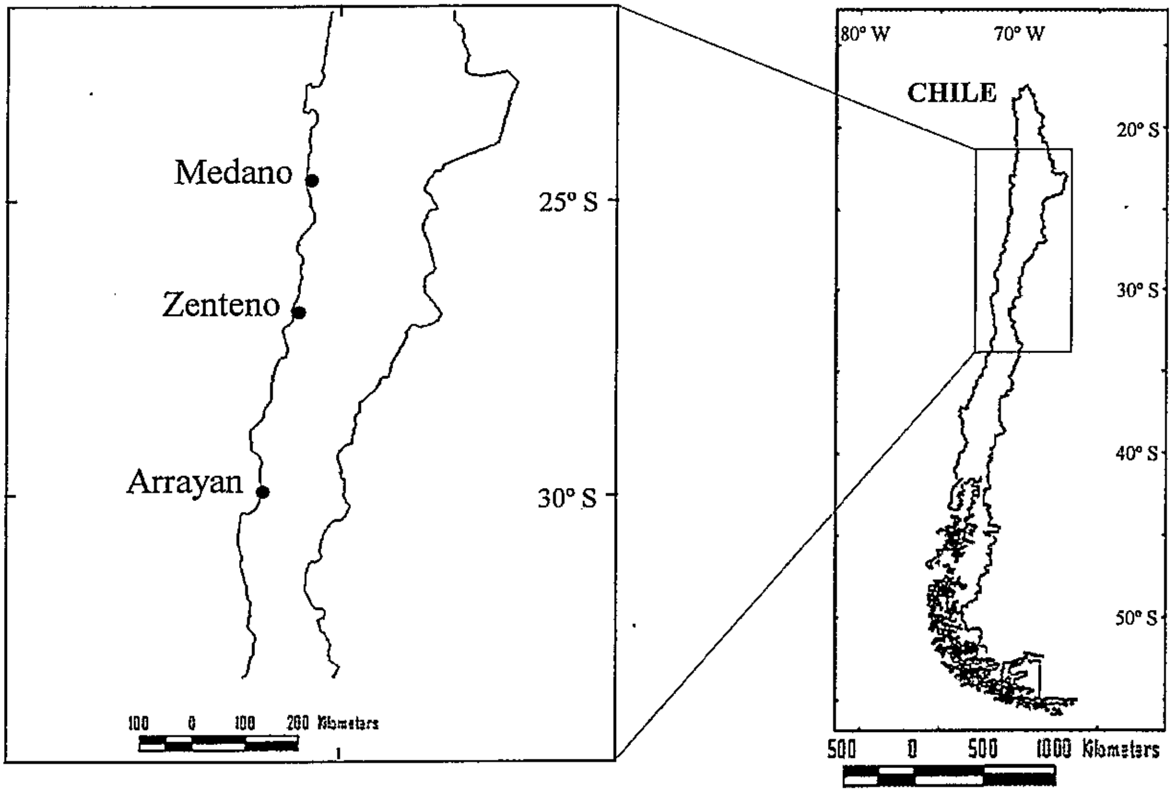
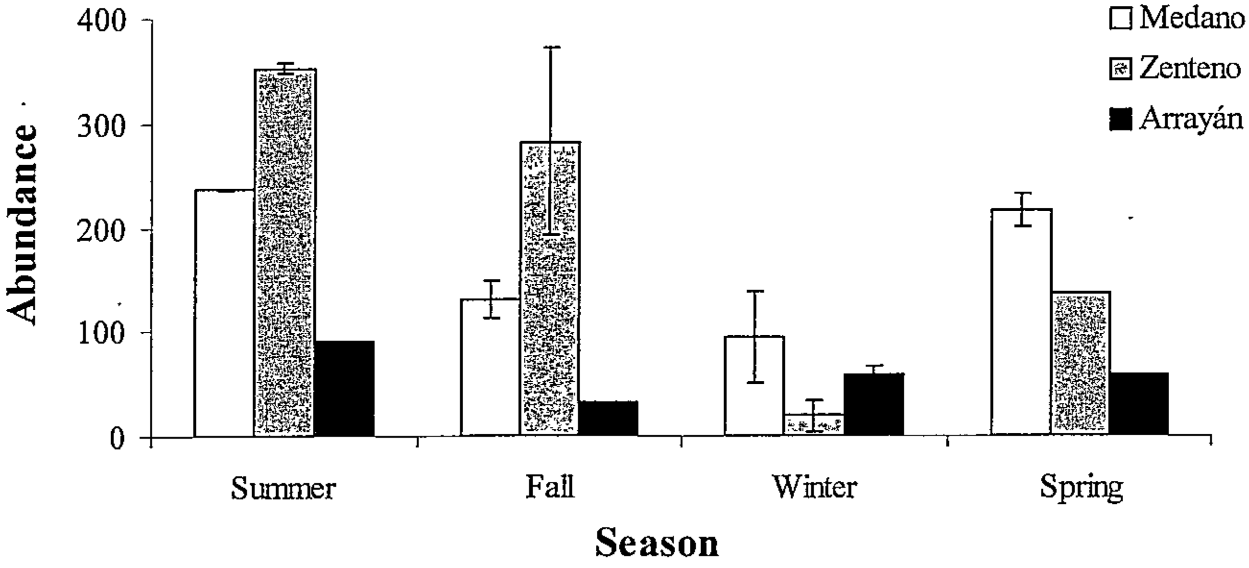

Medano
Zenteno
Arrayan
25° S
30° S
100 0 100 200 Kilometers
80° W
70° W
CHILE
20° S
30° S
40° S
50° S
500 0 500 1000 Kilometers

*Figure 2



□ Medano
▨ Zenteno
■ Arrayán
Abundance
400
300
200
100
0
Summer
Fall
Winter
Spring
Season

*Figure 3

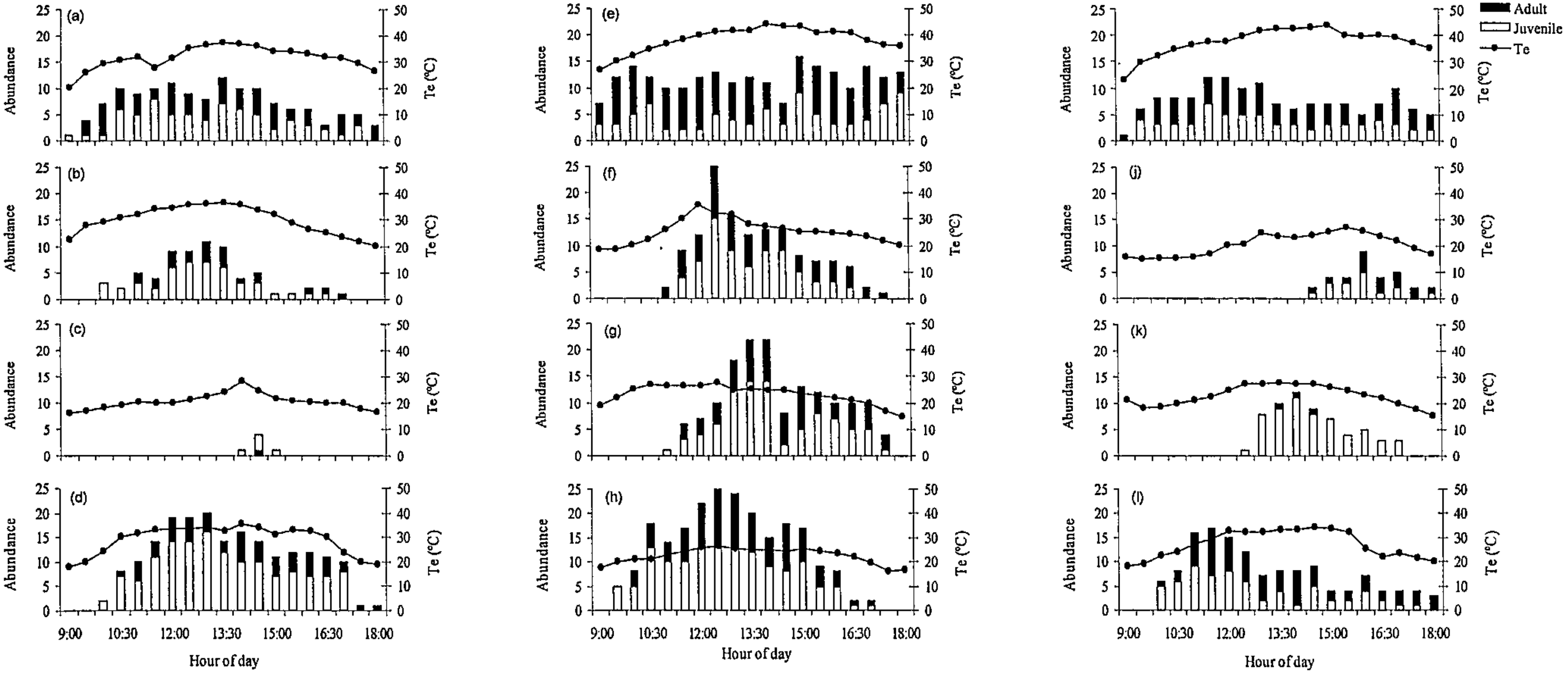
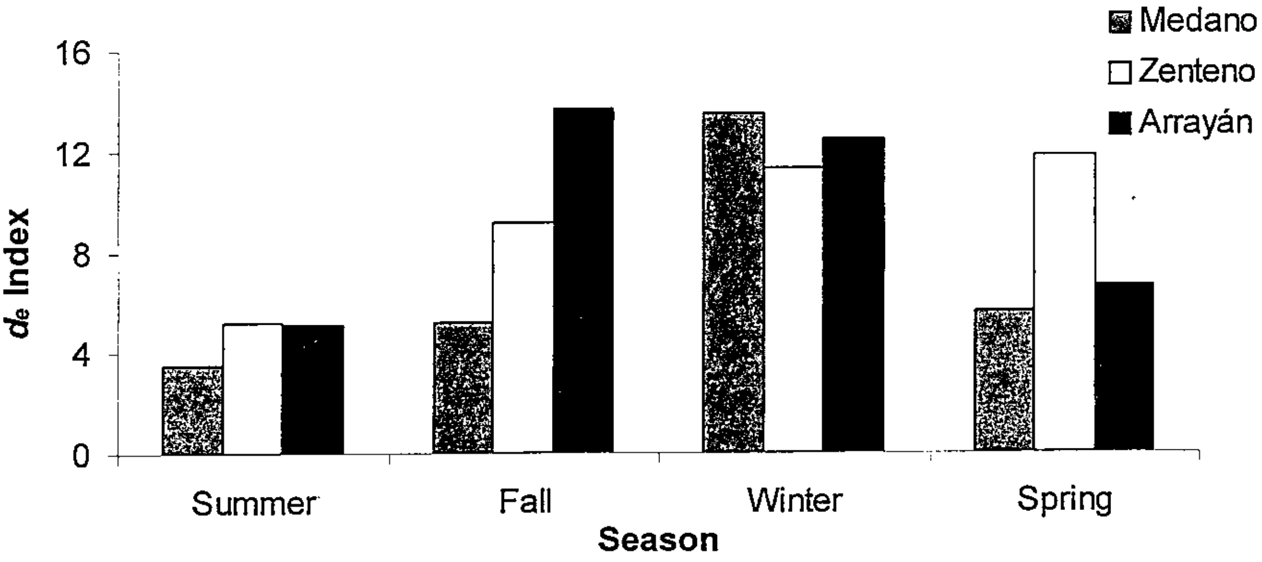
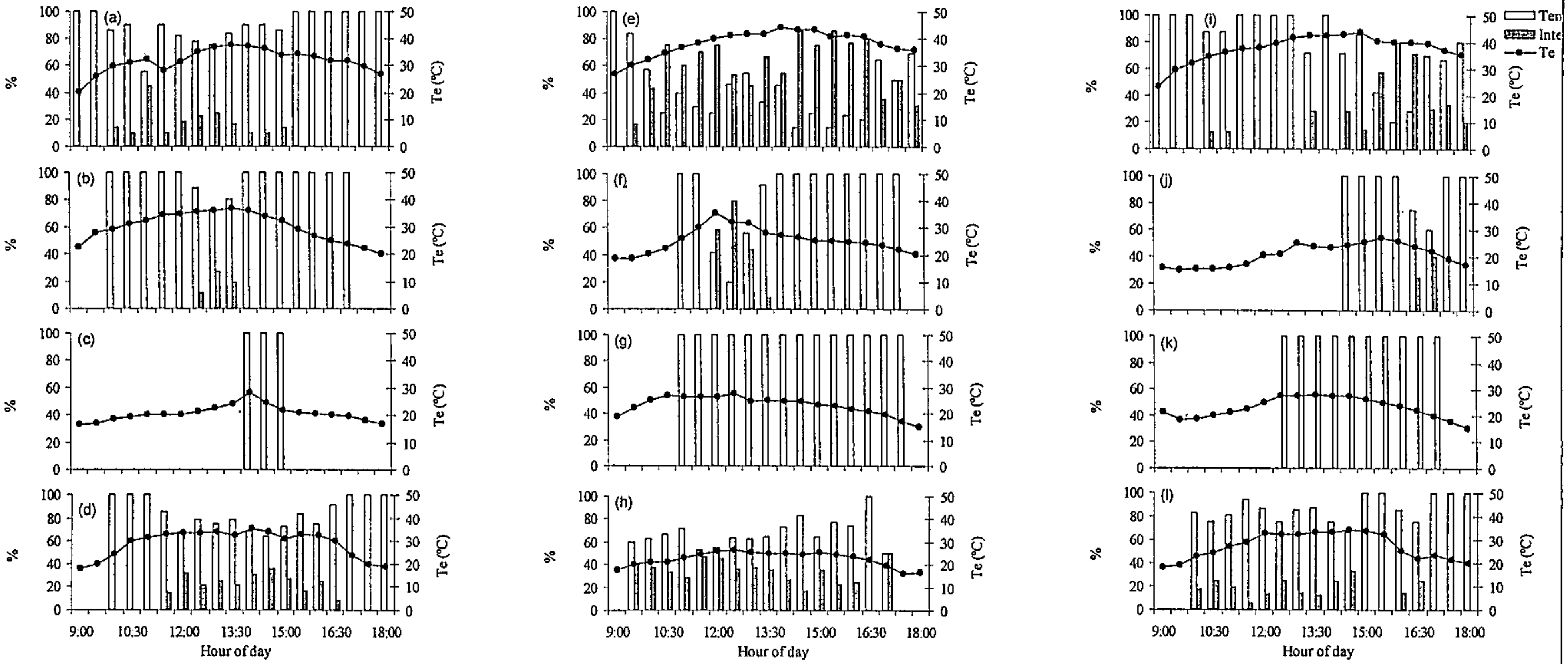

Adult
Juvenile
Te
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
Abundance
Te (°C)
0
5
10
15
20
25
0
10
20
30
40
50
9:00
10:30
12:00
13:30
15:00
16:30
18:00
Hour of day

*Figure 4



Medano
Zenteno
Arrayán
16
12
8
4
0
d_e Index
Summer
Fall
Winter
Spring
Season

*Figure 5


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
%
Te (°C)
0
20
40
60
80
100
0
10
20
30
40
50
9:00
10:30
12:00
13:30
15:00
16:30
18:00
Hour of day
Ten
Inte
Te

CAPITULO 3.

Geographical and seasonal variation in standard metabolic rate: an intraspecific comparison in the lizard *Microlophus atacamensis* (Squamata:Tropiduridae)

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MANUSCRITO CON FORMATO PARA REVISTA "*JOURNAL OF THERMAL BIOLOGY*"

Abstract

1. The metabolic cold adaptation (MCA) hypothesis predicts that ectotherms from colder environments might have higher metabolic rates than animals from warmer habitats.
2. We quantified the effects of environmental temperature on standard metabolic rate (SMR) in the lizard *Microlophus atacamensis* in two populations along a latitudinal range, and tested the MCA hypothesis.
3. SMR showed geographical differences. Contrary to the MCA hypothesis, lizards from the northern site showed higher SMR. This difference is maintained after a month of acclimation.
4. Then, our results do not support the MCA hypothesis and suggest that multiple factors affect the energy expenditure of this lizard species.

Keywords: *Microlophus atacamensis*; metabolism; metabolic cold adaptation; latitudinal gradient; temperature

1. Introduction

Because temperature controls nearly all physiological and biochemical processes of ectotherms, it is one of the most important environmental factors affecting their energy budget (Huey and Berrigan, 2001). Energy use by an individual is usually reflected in measurements of energy expenditure, being the rate of metabolism the most common and studied component (Nespolo et al., 2003). The quantification of metabolic demands is central to studies of ecological energetics, because the requirements of maintenance must be met before any other allocation (e.g., growth, storage and reproduction) can be made (Congdon et al., 1982; Zaidan, 2003).

In reptiles, energy lost due metabolism may compose over 80% of total energy expenditure (Congdon et al., 1982; Angilletta, 2001). Opportunities of reducing the maintenance component of field metabolic rate depend on available microclimates, because metabolic rate of an ectotherm is affected greatly by temperature (Angilletta, 2001). In this sense, intraspecific variation in physiological and life history traits of individuals dwelling in geographical ranges with conspicuous thermal climatic differences can be explained, at least in part, by differences on their maintenance metabolism (Beaupre, 1996; Angilletta 2001). Such variations could be induced throughout non genetic mechanisms of acclimatization (phenotypic flexibility, sensu Piersma and Drent, 2003), or they can reflect adaptations to local environmental conditions (Stearns, 1989). Because individuals are able to change or transform their phenotype in response to spatial or temporal variations in local conditions,. they could maintain, or even increase, their biological performance (e.g. Sabat et al., 1995).

One of the most common adaptive hypotheses proposed to explain general patterns of metabolic rates is the metabolic cold adaptation (MCA) hypothesis (Clarke, 1993). This hypothesis predict that, when exposed to the same environmental temperature, ectotherms from populations of higher latitudes (i.e., colder) will exhibit a higher metabolic rate than those from lower (i.e., warmer) latitudes (Scholander et al., 1953). Higher metabolic rates have been interpreted as advantageous in ectotherms because it enables them to metabolize food stuffs more rapidly, and for to meet the elevated energy cost of growth and development necessary for completion of life cycles in a relatively reduced period of favorable environmental conditions (Clark, 1993; Chown and Gaston, 1999).

Studies testing the MCA hypothesis have emphasized the analysis of species as a unit (e.g. Addo-Bediako et al., 2002). However, and depicting its importance, few studies have tested the MCA hypothesis between populations of the same species inhabiting different habitats within a region (but see Lardies et al., 2004). Nevertheless, such studies are crucial for understanding how differences in physiological variables evolve and can be affected by ecological and geographical factors. Consequently, studying populations from the same region, but from different habitats, should provide the most effective tool for understanding physiological tolerances, and their consequences for the MCA hypothesis (Hodkinson, 2003; Lardies et al. 2004). In this study we quantified the effects of environmental temperature on standard metabolic rates (SMR) on the lizard *Microlophus atacamensis* along a latitudinal gradient in Northern Chile, and tested de MCA hypothesis.

2. Materials and methods

2.1. Animal's collection and study site

Microlophus atacamensis lizards were collected during austral fall (April), winter (July/August), and spring (September/October) 2006. This species is widely distributed along the desert area in northern central coast of Chile, from Antofagasta (23°3'S) to La Serena (29°5'S) (Ortiz, 1980; Sepúlveda et al., 2006, ANEXO 2). Individuals were obtained from two populations: Medano (24°37'S; 70°33' W) and Zenteno (26°51' S; 70°49' W). The climate in these study areas is under a coastal desert climate regime, characterized by less than 2 mm of rain per year (Di Castri and Hajek, 1976). Mean air temperature in Medano ranges from 16.8 °C in winter to 21.2 °C in summer. In Zenteno mean air temperature varies between 15.4 °C in winter and 20.7 °C in summer (data obtained from the Servicio Hidrológico y Oceanográfico de la Armada de Chile).

2.2. Metabolic rate measurements: Acclimatization

A total of 33 lizards were captured in Medano (16 in fall; 3 in winter; and 14 in spring season) and 30 in Zenteno (16 in fall; 5 in winter; and 9 in spring season). Lizards were collected by hand, and transferred to the laboratory. In the laboratory, individuals were housed at 20 ± 2 °C under a natural photoperiod in plastic-mesh cages with mealworms (*Tenebrio mollitor*) and water ad libitum.

Standard metabolic rate (SMR) (measured as the rate of oxygen consumption, VO_2) of each individual was determined at two temperatures (20° and 30°C). Measures were made at one temperature per day and during the night, which corresponds to the rest phase in this species. VO_2 was determined using'closed system' metabolic chambers, in which lizards were maintained for 2 – 2.5 hours in a controlled temperature cabinet at a constant temperature before measurements. At the end of this period, O_2 concentration was determined by connecting the metabolic chamber to a computerized respirometry system (Sable Systems, Henderson, Nev.). For each lizard and temperature, rate of oxygen consumption (in mL O_2h^{-1}) was calculated as the integral of O_2 consumption by hour, which is proportional to volume of oxygen depletion by the lizard, divided by trial time. This system was not intended to measure the instantaneous rate of metabolism, since each measurement is an average of oxygen consumption over several hours (Nespolo et al., 2003). Values of Q_{10} were computed for each individual as SMR(T_2)/SMR(T_1) for acclimatization experiments, where T_2 and T_1 were either 30° and 20°C, respectively.

One-way analysis of covariance (ANCOVA) was used to test differences between populations for 20° and 30° metabolic measurements, using mean body mass (M_b) as the covariate, and ANCOVA with repeated measures was used to examine the within-subjects effects of T_a over SMR. The data were log-transformed to fit normality assumptions. Additionally, we performed common linear regressions of M_b and SMR for each temperature, and compared M_b between populations using a one-way ANOVA.

2.3. Metabolic rate measurements: Acclimation

In order to test if the putative differences in metabolic rates between populations are due to acclimatization to local environmental conditions, we performed thermal acclimation experiments. After SMR measurements, lizards captured in fall (13 from

Medano and 13 from Zenteno sites) were housed individually in plastic-mesh cages, under a 12h: 12h dark: light cycle, with mealworms and water ad libitum. A preliminary experiment revealed that *M. atacamensis* do not respond well when were acclimated to temperatures below 30 °C (animals loss weight and do not ingest food nor drink). Hence, individuals of both populations were assigned to one of two treatments: one group was housed in a constant temperature room at 30 ± 2°C (warm acclimated group, n = 14) and the other at 35 ± 2°C (hot acclimated group, n = 12). Lizards were maintained on the acclimation period for 30 d. After this period, we measured SMR at 30°C, using the same protocol described above. A two-way ANCOVA was used to analyze the effect of population and treatment on SMR, using mean body mass (M_b) as the covariate. Post-hoc comparisons were performed using a Tukey's honest significance difference test. Besides, we performed common linear regressions of M_b and SMR for each treatment, and compared M_b between populations and between treatments using a one-way ANOVA. All comparisons were performed using Statistica 6.0 for Windows (StatSoft Inc., 2001).

3. Results

3.1. Standard metabolic rate at the field

Body mass of *M. atacamensis* was similar between Medano and Zenteno populations ($F_{(1,59)} = 1.400$, $P = 0.241$), but was significantly lower in winter season ($F_{(2,59)} = 3.306$, $P = 0.043$). SMR was significantly and positively correlated with body mass at both temperatures for Medano and Zenteno populations (Table 1). The slope of

SMR and M_b increased with T_a (Fig. 1). Standard metabolic rate did not differ between males and females for any population at 20°C (Medano: $F_{(1,28)} = 1.321$, $P = 0.265$; Zenteno: $F_{(1,26)} = 3.975$, $P = 0.063$), or at 30°C (Medano: $F_{(1,26)} = 0.055$, $P = 0.817$; Zenteno: $F_{(1,26)} = 0.434$, $P = 0.517$). Similarly, SMR did not show seasonal differences within sites at 20°C (Medano: $F_{(2,28)} = 0.376$, $P = 0.690$; Zenteno: $F_{(2,25)} = 1.919$, $P = 0.168$), or at 30°C (Medano: $F_{(2,28)} = 0.260$, $P = 0.773$; Zenteno: $F_{(2,25)} = 3.386$, $P = 0.057$). For these reason, analyses considered pooled data for sex and seasons. After controlling for M_b effects, SMR increased significantly between 20° to 30°C both for Medano (repeated measures ANCOVA $F_{(1,30)} = 10.486$, $P = 0.003$), and Zenteno populations ($F_{(1,26)} = 21.013$, $P < 0.001$). Both at 20°C and 30°C, SMR of the northern site (Medano) was significantly higher than the southern site (Zenteno) (20°C: $F_{(1,59)} = 9.366$, $P = 0.003$; 30°C: $F_{(1,59)} = 4.231$, $P = 0.044$, Fig. 2).

3.2. Standard metabolic rate in the laboratory

At the end of the acclimation period, body mass was similar between warm and hot treatments ($F_{(1,20)} = 0.034$, $P = 0.856$) and between Medano and Zenteno populations ($F_{(1,20)} = 1.116$, $P = 0.303$). Contrary to the acclimatization experiments, SMR was not correlated with body mass for any treatment. Only in the hot treatment in Zenteno population, SMR was positively correlated with body mass ($r^2 = 0.595$, $P = 0.002$). Medano showed a higher SMR than Zenteno, due to a significant higher SMR in Medano lizards under the warm treatment (Table 2, Fig. 3).

3.3. Q_{10} measurements

In acclimatization experiments, individual Q_{10} were not correlated with M_b neither for Medano (r^2 = 0.008, P = 0.968) or Zenteno (r^2 = 0.024, P = 0.434) populations (Medano: Mean ± SD Q_{10} = 2.49 ± 0.80; Zenteno: Mean Q_{10} = 2.46 ± 0.89, P = 0.501).

4. Discussion

This study confirms the common pattern found for ectothermic organisms, i.e., metabolic rate increases as temperature rises. Nevertheless, our data do not support the metabolic cold adaptation hypothesis. Indeed, we detected an increment in SMR in the population from low latitude, instead of the population from high latitude (Fig. 2). Lack of metabolic cold adaptation in *M. atacamensis* lizards is also supported by the absence of geographical variation in thermal sensitivity (Q_{10}) values between the studied populations. Traditionally, it is supposed that a better cold adapted is a species, a lower activation energy and more probably that higher Q_{10} values will be observed (Davies and Bennett, 1981; Nielsen et al., 1999). However, our mean Q_{10} values of metabolic rates were similar between lizards from Medano and Zenteno populations, and is very close to the reported mean of Q_{10} (2.4) for the order Squamata (Andrews and Pough, 1985). In this sense our results indicate the absence of metabolic cold adaptation in *M. atacamensis* lizards in the studied populations.

The MCA hypothesis is one of the most polemical in comparative physiological ecology (Chown and Gaston, 1999). Although several studies have reported latitudinal increment of SMR for a suite of both terrestrial and marine species (e.g., Torres and

Somero, 1988; Addo-Bediako et al., 2002; Zaidan, 2003; Pulgar et al., 2006), many others have found little support for this phenomenon at both inter and intraspecific level. (Nylund, 1991; Clarke and Johnston, 1999; Angilletta, 2001; Drud Jordan et al., 2001; Steffensen, 2002; Lardies et al., 2004). Following Clarke (1993), the MCA hypothesis cannot be upheld for different empirical and theoretical reasons. First, MCA may represent a fitness cost to ectotherms, because burn up reserves and waste energy as heat (Clarke, 1993), and hence is unlike to evolve. Second, the use of annual mean temperatures to characterize the lizard's effective environmental temperature could be inappropriate because the microhabitat temperatures to which lizards are effectively exposed can differ significantly from the annual mean temperatures (Sepúlveda et al., 2007, CAPITULO 1). So far, empirical support to MCA hypothesis comes principally from meta-analyses of data sets on insects (Addo-Bediako et al., 2002). However, and following Hodkinson (2003), although this meta-analysis is a valuable tool for large-scale comparisons, it should not be used to extrapolate beyond the measured data range. Possible confounding factors, such as activity, life stage, feeding, and experimental acclimation are not considered in meta-analyses approaches (Hodkinson, 2003).

In endotherms, it has been suggested that environmental productivity (as an index of food availability) is positively correlated with basal metabolic rate (Mueller and Diamond 2001). In our study sites, Fariña et al. (en prensa, ANEXO 3), found that primary productivity at intertidal zones seems to be similar between Medano and Zenteno sites, but terrestrial plants representation increase significantly from north to south (from 0 g/m2 in Medano to 115 g/m2 in Zenteno). Associated with this north to south increment in terrestrial productivity, insects (principally diptera, isopoda, and coleoptera), and potential preys of *M. atacamensis* lizards, showed high abundances in the southern sites. An increase in environmental productivity in Zenteno site, and based on the Mueller and Diamond (2001) results, we should expect that metabolic rate of lizards from this southern site will be higher, supporting the MCA hypothesis. But contrary to predicted, we found a higher metabolic rate in the northern and lesser productive site. Other factors however should be taken in account. The diet composition of *M. atacamensis* lizards seems to be different at a latitudinal gradient, composed mostly of marine-vegetal (algae) preys in Medano population, to a more omnivorous diet (both terrestrial and marine preys) in Zenteno population (Fariña et. al. en prensa, ANEXO 3). Shifts in the dietary habits, together with other local factors, such as the solar radiation and primary productivity may be affecting the level of energy expenditure of animals, making difficult to separate the causal effects of environment temperature alone (Clarke, 1993; Mueller and Diamond, 2001).

On the other hand, after the acclimation period, in spite of the common experimental temperatures experienced by lizards, SMR remains different between both populations. Lizards from Medano population showed a higher metabolic rate than lizards from Zenteno. These finding suggest a possible adaptation to local environmental conditions in *M. atacamensis* lizards, and a genetic-heritable basis for this trait (Stearns, 1989; Leroi et al., 1994; Bennett and Lenski, 1997; Kingsolver and Huey, 1998). We cannot discount the possibility that maternal and acclimation effects are operating, or that variation in metabolic rate results from processes during early development (or developmental plasticity, sensu Piersma and Drent, 2003), but we are not able to control the entire possible environmental signals that could affect the variability in metabolic rate between populations (Lardies et al., 2004).

Our measured values of SMR in acclimatization experiments were in average 44 and 25% higher than predicted by the allometric equations of McNab (2002) ($SMR = 0.096*W_b^{0.8}$ for 20°C, and $SMR = 0.24*W_b^{0.83}$ for 30°C), for 20° and 30°C, respectively. However, values are well within the ranges predicted both for 20°C ($\chi^2 = 65.92$, $P > 0.05$) and 30°C ($\chi^2 = 102.16$, $P > 0.05$), and showed the typical pattern found for all ectothermic species, in the sense that the metabolic rate increase with increasing temperature (Bennett and Dawson, 1976; Clarke and Johnston, 1999).

Several studies have reported marked seasonal differences in metabolic rates for a given temperature (Tsuji, 1988; Beyer and Spotila, 1994; Angilletta, 2001; Hodkinson, 2003). Nevertheless, we did not find seasonal differences in SMR for any population. Three possible non exclusive explanations could be hypothesized to explain this phenomenon. First, it is possible that thermal variation between both localities might be no strong enough to explain the patterns of energy expenditure in this species. However, and considering a Q_{10} value near 2 to 2.5, aerobic metabolism should increase from 15 to 20% when animals experience a rise of only 2 °C in environment temperature (the difference in mean maximum temperatures between the two populations). Hence, few degrees of differences may exert a significant effect on, for example, the energy budget of a lizard species. Second, lack of seasonal differences can be explained because seasonal acclimatization is a complex phenomenon driven by a multitude of metabolic processes (Clarke, 1993), such as tissue synthesis (Wieser, 1994), food intake (Secor and Diamond, 1997), and physiological state (Angilletta and Sears, 2000). In addition, lizards can exhibit behavioral responses which may compensate adequately the variations in their thermal environment, thus reducing costs associated with maintenance metabolism. In fact, we recently reported that *M. atacamensis* mostly employ behavioral strategies, and not physiological adjustments to cope with temporal variation in the thermal environment (Sepúlveda et al. 2007, CAPITULO 1). Finally, as mentioned above, multiple factors can affect patterns of energy expenditure between populations of *M. atacamensis*. Further efforts are necessary to carry out an integrative approach to test and elucidate the relative contribution of behavioral and physiological mechanisms to explain the ability of lizards to cope with changes in environmental temperature, both at temporal and geographic scale.

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Tables

Table 1

Mean ± SE and regressions statistics between SMR and M_b. Results from acclimatization experiments.

T_a (°C)	SMR (mL O_2 h^{-1})	Slope	Intercept	R^2	N
Medano					
20	3.236 ± 0.245	0.007 ± 0.001***	0.125 ± 0.051**	0.646***	33
30	7.237 ± 0.617	0.008 ± 0.001***	0.483 ± 0.052***	0.633***	33
Zenteno					
20	3.022 ± 0.273	0.007 ± 0.001***	0.071 ± 0.046	0.734***	30
30	7.305 ± 0.690	0.008 ± 0.001***	0.373 ± 0.065***	0.662***	30

T_a = ambient temperature; SMR = standard metabolic rate; R^2 = coefficient of determination; N = number of individuals. ***P*<0.01 ****P*<0.001

Table 2

ANCOVA of the effects of treatment and population on standard metabolic rates (mL $O_2 h^{-1}$) of *Microlophus atacamensis*. Results from acclimation experiments.

Effect	df	MS	*F*	*P*
Treatment	1,20	0.059	1,784	0.197
Population	1,20	0.168	5.057	**0.036**
Treatment x Pop.	1,20	0.150	4.532	**0.045**

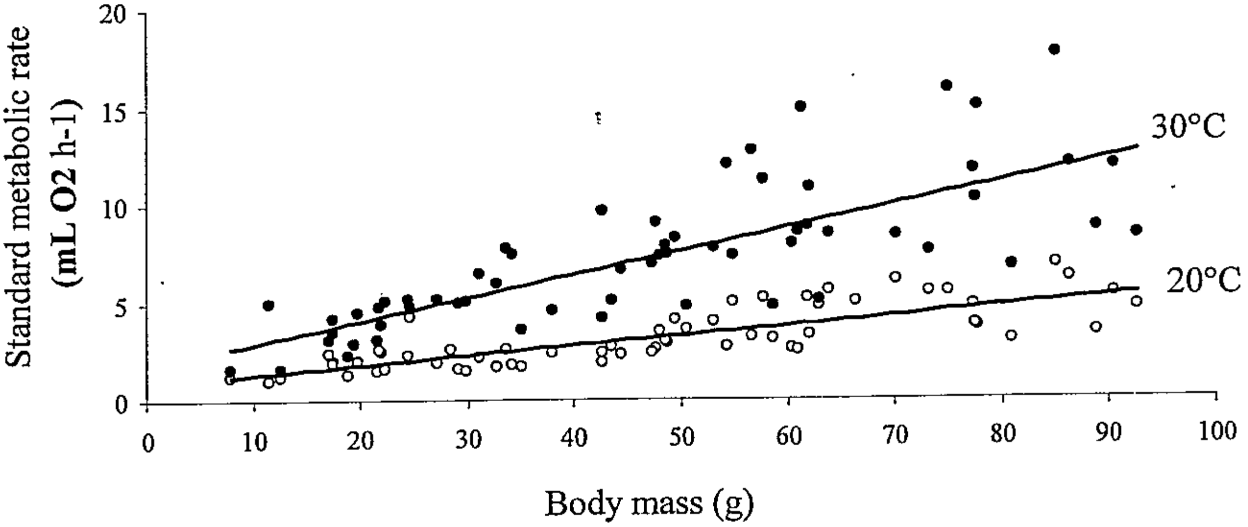
Figure Captions

Fig. 1. Standard metabolic rate and body mass for lizards measured at 20° and 30°C metabolic acclimatization measurements. See Table 1 for means and regression statistics.

Fig. 2. Standard metabolic rate for lizards from Medano and Zenteno populations of *Microlophus atacamensis* measured at 20° and 30°C metabolic acclimatization temperatures. Data are reported as mean ± S.E.

Fig. 3. Standard metabolic rate for lizards from Medano and Zenteno populations of *Microlophus atacamensis*. Results are showed separately for warm treatment (a), and hot treatment (b) acclimation temperatures. Letters denote temperatures at which metabolic rate did not differ significantly (Tukey'test, $P > 0.05$).

*Figure 1



Standard metabolic rate (mL O2 h-1)
20
15
10
5
0
0
10
20
30
40
50
60
70
80
90
100
Body mass (g)
30°C
20°C

*Figure 2

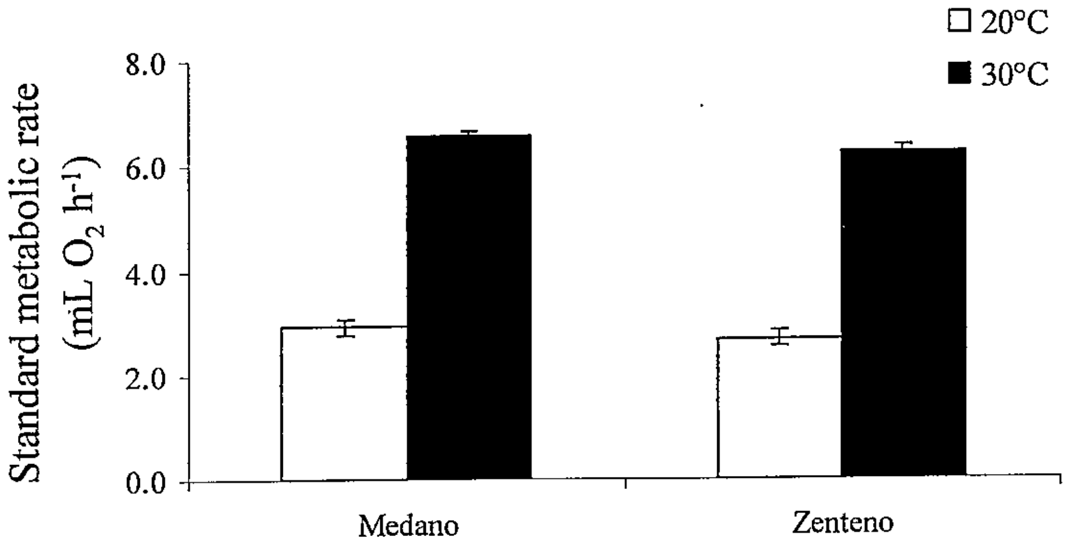
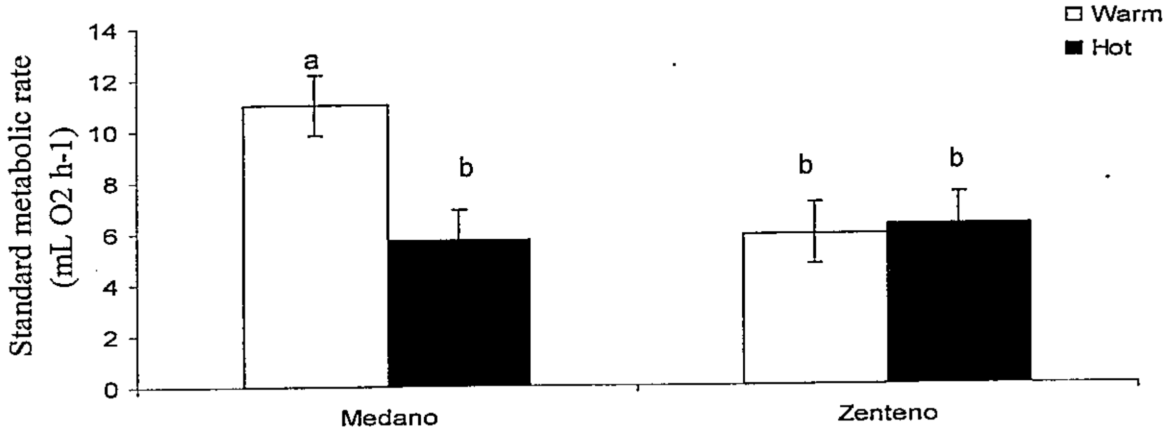

□ 20°C
■ 30°C
Standard metabolic rate
(mL O_2 h^{-1})
8.0
6.0
4.0
2.0
0.0
Medano
Zenteno

*Figure 3


☐ Warm
■ Hot
Standard metabolic rate (mL O2 h-1)
14
12
10
8
6
4
2
0
a
b
b
b
Medano
Zenteno

CAPITULO 4.

Digestive efficiency in the lizard *Microlophus atacamensis*: geographical response to the effects of temperature and diet composition

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Running title: Digestive efficiency in *Microlophus atacamensis*

MANUSCRITO CON FORMATO PARA REVISTA "*COMPARATIVE BIOCHEMISTRY AND PHYSIOLOGY, PART A*"

Abstract

Microlophus atacamensis is a lizard living on the coastal range of the Atacama Desert where, depending on food availability it consumes terrestrial or marine (intertidal) food. From north to south, within its geographical range the environmental temperature decrease whereas the terrestrial productivity increases. Using stable isotope and digestive enzymes analysis, we investigated whether the reliance on marine versus terrestrial food resources varied from north to south. Besides, and since digestive processes may influence many aspects of an animal's life history, we analyze its digestive responses (assimilation efficiency, gut passage time, and appetite) to temperature and diet composition. Stable isotopes indicate that diet composition of northern populations is composed mostly on marine items, with a gradual increase in the proportion of terrestrial preys from north to south. As expected, we found a decrease in gut passage time and an increase in the appetite at high temperatures. The assimilation efficiency, although independent of the temperature, showed higher values in diets composed by terrestrial items, than marine items. We highlight the importance of food and temperature on the digestive physiology of *M. atacamensis*, and explore the ecological link between digestive processes and foraging ecology.

Key words: *Microlophus atacamensis*, latitudinal gradient, stable isotopes, digestive efficiency, digestive enzymes.

1. Introduction

Diet selection, the rate of food acquisition, and the successful allocation of the obtained energy, are essentials tasks to the organism's survival, growth, and reproduction (Nagy et al., 1984; Secor, 2001). However, the time and type of food consumed by an individual is determined by the rate in which the food is processed and assimilated (Kersten and Visser, 1996). In this sense, digestive processes represent a functional link between the physiological processes inside the digestive tract (management and allocation) and the foraging ecology (Sabat et al., 1998; Naya et al., 2005).

It has been demonstrated that many animals are able to shift their diet as their food sources change in space and/or time (e.g. Malo et al., 2004; Galarowicz et al., 2006), and that individuals showed a phenotypic flexibility (sensu Piersma and Drent, 2003), i.e. they can modulate morphological or physiological traits in response to the changing conditions. Field and laboratory studies had demonstrated that the anatomy and function of the digestive tract change in response to variations in food quality and quantity (Naya et al., 2005). For example, in lizards, the time of food processing is highly dependent on diet composition. Johnson and Lillywhite (1979) found that lizards maintained with a diet composed of mealworms showed a faster gut passage time (GP) than when maintained on fruits. Similarly, changes in diet composition can modify the digestive enzyme levels, because the activity of these enzymes is correlated with the chemical composition of dietary substrates (Hernández and Martínez del Río, 1992). Temporal or seasonal diet composition may also influence the digestive efficiency of the individuals

(Slade et al., 1994). In lizards, the digestive efficiency generally approach the 90% (McConnachie and Alexander, 2004), but may vary according the type of food consumed. Johnson and Lillywhite (1979) found that the assimilation efficiency in the lizard *Klauberina riversiana* is about 5% greater when feed on mealworms, that when feed on apple, thus suggesting a higher efficiency in carnivorous reptiles, than in herbivores. Thus, a feeding behavior and, consequently, a pattern of energy use and expenditure could be greatly influenced by physiological and biochemical constraints on the digestive system (Sabat et al., 1995).

As mentioned, digestive processes may influence many aspects of an animal's life history. However, for ectotherms, temperature controls nearly all physiological and biochemical processes (Huey and Berrigan, 2001), playing a strong role in the digestive performance of these species. Two related components of digestion are particularly influenced by changes in thermal conditions, GP and the efficiency of energy acquisition (McConnachie and Alexander, 2004). For several lizard species it has been demonstrated a decrease in the GP with an increase in environmental temperature (Ji et al., 1996; Du et al., 2000; McConnachie and Alexander, 2004). In the same vein, the efficiency of energy intake (commonly expressed as digestive and assimilation efficiencies) increases with higher temperatures (Du et al., 2000; but see McConnachie and Alexander, 2004).

The family *Tropiduridae* is composed by terrestrial feeders, but some species that dwell in desert coastal areas (with low levels of terrestrial productivity), feeds almost exclusively on intertidal or subtidal zones (Donoso-Barros, 1966; Wikelski and Wrege, 2000). In Chile, two species from the genus *Microlophus* use this feeding strategy:

Microlophus quadrivittatus and *M. atacamensis* (Ortiz, 1980). For *M. atacamensis*, Fariña et al. (2003) reported that the diet of this species is composed both of intertidal (algae and crustacea) and terrestrial (isopoda, coleoptera) prey. The importance of each of these dietary items is associated with spatial and temporal variation in the primary productivity of both habitats, with an increasing proportion of terrestrial items in a north to south gradient (Fariña et al. en prensa, ANEXO 3). But considering that environmental temperature decreases as latitude increases, the latitudinal gradient in the use of resources may be influenced by the thermal environment.

By analyzing different populations of *M. atacamensis* along the entire geographical range of this species, we explored the digestive adjustments to changes in diet composition and in environmental temperature. Specifically, we attempted to test if: (1) latitudinal change in diet composition is traduced in differences in isotope stable signatures; (2) the digestive enzyme activity differs among populations in response to latitudinal changes in diet composition; and (3) if the appetite, gut passage time and assimilation efficiency differs in lizards under different regimes of temperature and diet composition.

2. Material and methods

2.1. Study area

Lizards were collected from July 2005 to September 2006 at five sites along the geographical range of *M. atacamensis* on the Atacama Desert coast (Fig. 1): Santa

María (23°29'S), Medano (24°37'S), Zenteno (26°51' S), Huasco (28°07'S), and Arrayán (29°41'S). Santa María and Medano are under a hyperarid desert climate regime, characterized by less than 2 mm of rain per year (Di Castri and Hajek, 1976). Mean air temperature in these sites ranges from 16.8 °C in winter to 21.2 °C in summer. Zenteno and Huasco receive ~25 mm of rain per year, with air temperature of 15.4 °C and 20.7 °C in winter and summer, respectively. Finally, Arrayán falls into the semi-arid Mediterranean zone (Di Castri and Hajek, 1976). Rainfall in this site averages 60 mm/year, and mean temperatures are around 13.5 °C in winter and 18.2 °C in summer (data for the sites were obtained from the Servicio Hidrológico y Oceanográfico of the Armada de Chile).

Sites were selected because they are similar in exposition to waves, and similar in terrestrial (supralitoral) and intertidal physical characteristics. At these sites beaches consist of flat areas of a mixture of rocks (with heights from 0.2 to 3 m), pebbles, cobblestones, and sand (Vidal et al., 2002). Lizards were captured along the intertidal zone in a stretch of approximately 150-200 m.

2.2. Stable isotopic analysis

To analyze the relative contribution of marine and terrestrial preys to the diet of *M. atacamensis*, we estimated the $\delta^{13}C$ and $\delta^{15}N$ stable isotopes ratios of lizard tissues from the five sites. Values of $\delta^{13}C$ and $\delta^{15}N$ are higher for marine organisms and/or for terrestrial plants and consumers of localities with high marine inputs of marine-derived energy and nutrients, than for terrestrial producers and consumers without marine input (Mizutani and Wada, 1988; Catenazzi and Donnelly, 2006).

In each site, we captured lizards by hand, and released after a small sample of snails or muscle (from the tail) was extracted. We also included muscle samples from lizards collected for digestive enzymes analysis (see below). Stable isotopes analyses were determined following standard procedures (e.g. Sabat el al., 2006; Catenazzi and Donelly, 2006). Briefly, samples were placed in heat-sealed Ankom filter bags, refluxed with petroleum ether to remove hydrocarbons and lipids, and then dried and ground into a powder. Stable carbon and nitrogen ratios were measured on a continuous flow isotope ratio mass spectrometer (VG Isotech, Optima) at the University of Wyoming stable isotope facility. The precision of the analyses was ± 0.3 (‰) (SD). Stable isotope ratios were expressed using standard delta notations (δ) in parts per thousand (‰) as:

$$\delta(^{13}\text{C or }^{15}\text{N}) = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1{,}000$$

where R_{sample} and R_{standard} are the molar ratios of the sample ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) and the reference, respectively. Samples were referenced against international standards, Vienna Pee DeeBelemnite (VDPD) for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$.

2.3. Digestive enzyme activity

Lizards from Medano and Zenteno populations were collected using air-compressed guns (hunting permit # 98 from the Chilean Agricultural and Livestock Service, SAG). Immediately after capture, individuals were weighed (± 0.5 g), stored in liquid nitrogen and transferred to the laboratory. In the laboratory, lizards were measured (snout-vent length, SVL, ± 0.5 cm), sexed, and their digestive tracts extracted. Intestines were measured and washed with a 0.9% NaCl solution. Tissues were thawed and homogenized (in an Ultra Turrax T25 homogenizer at maximum setting) in 20 volumes of 0.9 % NaCl solution. Disaccharidases (maltose and trehalose) and aminopeptidase-N activity were determined according to the protocol described by Martínez del Río et al. (1995) and Meynard et al. (1999), respectively. Briefly, for disaccharidases, 100 mL of tissue homogenates were incubated at 25°C with 100 mL of 56 mmol L^{-1} sugar solutions (maltose, trehalose) in 0.1 M Maleate/NaOH buffer, pH 6.5. After 10 min incubation, reactions were stopped by adding 3 mL of a stop/develop Glucose-Trinder (Glucose Trinder 500 reagent, Sigma Diagnostics, Saint Louis, Missouri) in 250 mL 0.1 mol L^{-1} TRIS/HCl, pH 7 plus 250 mL of 0.5 NaH_2PO_4, pH 7). Absorbance was measured at 505 nm with an Espectronic 21 spectrophotometer after 18 min. For aminopeptidase-N, analyses were done using L-alanine-p-nitroanilide as a substrate. 100 mL of homogenate were diluted with 0.9% NaCl solution and mixed with 1 mL of assay mix (2.04 µmol L21 L-alanine-p-nitroanilide in 0.2 mol L^{-1} NaH_2PO_4/Na_2HPO_4, pH 7). The reaction was incubated at 25°C for 10 min and stopped with 3 mL of ice-cold acetic acid 2 N. Absorbance was measured at 384 nm. On the basis of absorbance, standardized intestinal enzymatic activities were calculated. The selected pHs for measuring the activities were determined as the optimum for each enzyme. The enzyme activity was measured in the whole intestine to avoid an underestimation of activity. The activity is presented as standardized hydrolytic activity, (total UI, where UI = μmol hydrolyzed/min).

2.4. Assimilation efficiency, appetite and gut passage in the field

We analyzed assimilation efficiency, appetite, and gut passage time to the effects of temperature and diet composition in lizards from three populations, Medano, Zenteno, and Huasco. Individuals from the three populations were randomly assigned to one of two thermal experimental treatments: one group was housed in a constant temperature room at 30 ± 2°C (warm group, N = 11) and the other at 35 ± 2°C (hot group, N = 12). Lizards were housed individually in plastic-mesh cages, under a 12h:12h dark:light cycle, with water ad libitum. Lizards from the two groups were maintained under two dietary treatments. First, they were feed with a diet composed of mealworms *Tenebrio mollitor* (hereafter the terrestrial diet) for seven days. After finishing with the experiment, lizards were left at room temperature at 20 ± 2 °C under a natural photoperiod for a week, with unlimited amount of food and water. After this period, lizards were again separated in the two thermal treatments and maintained with a diet composed of green algae *Ulva* sp. (hereafter the marine diet) for seven days. We assumed that the inter-trial period removed the effects of the previous feeding trial (McConnachie and Alexander, 2004). In the experiments with terrestrial diet, lizards were offered a known quantity of mealworms per day. Uneaten mealworms and faeces (plus excreta) were collected every day, dried, and weighed. In marine experiments, and due to lizards do not feed algae spontaneously, we must every day forced-feeding a known quantity of algae to each individual and left undisturbed in the respective thermal treatment. Faeces were collected every day.

Assimilation efficiency method was similar to used by Johnson and Lillywhite (1979) and McConnachie and Alexander (2004). Briefly, collected faeces were dried up at 60 °C during 3 days, and then grounded to a powder. The energetic content was measured by subjecting a known quantity of faeces to a bomb calorimetry (Parr 1261, Isoperibol calorimeter). Energy content of mealworms and algae was measured in the same way. Apparent assimilation efficiency (AAE, see McKinon and Alexander, 1999) was calculated using the next equation (Johnson and Lillywhite, 1979):

$$AAE(\%) = [(C - (F + U)) / C] \times 100$$

where DE represents the calories absorbed through gut, C is the energy consumed, and F and U are the energy of faecal and urinary waste, respectively. Faeces and urinary waste were measured together.

Gut passage time was measured by force-feeding lizards three small plastic beads on day 1, both for marine (blue beads) and terrestrial trials (red beads), and recording the number of days taken for the beads to appear in the lizards' faeces. We considered the GP as the number of days between consumption and the first day appearance of beads in faeces (one or more beads). Finally, and because only in terrestrial trials lizards feed voluntary, we measured the appetite as the total mass of mealworms consumed in the 7-day trials, determined by subtracting the mass of the uneaten mealworms from the total mass of mealworms offered to each lizard (all days together). Mass of uneaten mealworms was corrected to compensate for weight loss that mealworms experience due to dehydration during trials according to the protocol described by McConnachie and Alexander (2004). Briefly, we kept a sample of weighed mealworms at the same thermal conditions than GP trials; but without lizards. After 24 h, we reweighed the mealworms and estimate the mean rate of weight loss.

2.5. Statistical analyses

All data was examined for assumptions of normality and homogeneity of variance, using Kolmogorov–Smirnov and Levene tests, respectively. If necessary it was transformed to achieve the normality assumptions, or analyzed through non-parametric statistics. The effect of latitude on each isotopic composition was evaluated using a linear model. The latitude was considered as a surrogate variable of rainfall and temperature, since latitude is measured without error, whereas rainfall and temperature are measured as averages with associated variances (Sabat et al. 2006). For enzyme activity, one-way analysis of covariance (ANCOVA) was performed to test the effect of population on enzymes activity, using body mass (M_b) as the covariate. Additionally, we performed common linear regressions between M_b and stomach and intestinal lengths, and compared M_b between populations using a one-way ANOVA. A correlation matrix was performed to examine relationships among the digestive enzymes.

The appetite of lizards was compared among populations and thermal treatments with a two-way ANCOVA, using body mass as covariate. The effects of food type, thermal treatments, and populations on GP were compared using a Kolmogorov–

Smirnov Two Sample Test (Sokal and Rohlf, 1995). Since appetite and GP were not significantly different between males and females, data were pooled. Effect of M_b on appetite and GP was investigated using regression analysis. All the analyses were performed in Statistica Version 6.0 (StatSoft Inc., 2001).

3. Results

3.1. Stable isotopic analysis

Variation in reliance on marine against terrestrial sources along the latitudinal gradient was apparent in *M. atacamensis*. $\delta^{15}N$ signatures decreased significantly with latitude ($F_{1,36}$(latitude) = 38.02, $P < 0.0001$, Fig. 2). The tissues of Santa María population were enriched in $\delta^{15}N$ over those of Arrayán by approximately 3.2‰ (Table 1). In contrast, there were practically no geographical differences in the $\delta^{13}C$ signatures ($F_{1,36} = 1.007$, $P = 0.322$, Fig. 2).

3.2 Digestive enzyme activity

Body mass was similar between Medano and Zenteno populations (Medano: 53.3 ± 35.6 g, N = 8; Zenteno: 35.9 ± 23.9 g, N = 7; $F_{1,13} = 1.202$, $P = 0.293$). When data from both populations were pooled, a positive correlation between body mass and stomach length ($r^2 = 0.646$; $P < 0.001$), and intestinal length ($r^2 = 0.952$; $P < 0.0001$, Fig. 3) were found. Also, a positive correlation was found between the maltose and trehalose enzymes ($r = 0.97$, $P < 0.05$). Similarly, aminopeptidase-N was positively correlated both with maltose ($r = 0.97$, $P < 0.05$) and with trehalose ($r = 0.94$, $P < 0.05$). After controlling for M_b, Medano showed a marginal increment in aminopeptidase-N and maltose activity (ANCOVA $F_{1,12} = 3.840$, $P = 0.073$; $F_{1,12} = 4.454$, $P = 0.056$, respectively), but not in trehalose activity ($F_{1,12} = 3.029$, $P = 0.107$, Fig. 4).

3.3. Appetite and gut passage time (GP)

Lizards showed an average of 39% higher appetite, judging by food consumption, with increasing temperature (ANCOVA $F_{1,16} = 5.830$, $P = 0.028$), but there were no differences among populations ($F_{2,16} = 2.299$, $P = 0.132$), or for the interaction between these two factors ($F_{2,16} = 0.122$, $P = 0.886$). An expected effect of body mass was found. Larger lizards ate proportionally more mealworms than smaller ones ($r^2 = 0.43$, $P < 0.001$, Fig. 5).

Gut passage time (in days) decreases significantly with increasing temperature in marine trial ($H_{1,17} = 5.566$, $P = 0.018$), but not in terrestrial trial ($H_{1,16} = 0.292$, $P = 0.589$, Fig. 6, populations combined). If we compare the GP between our experimental diets, we found that GP do not differ between marine and terrestrial diet at 30°C ($H_{1,12} = 0.248$, $P = 0.619$). At 35°C however, GP of marine diet is significantly lower than terrestrial diet ($H_{1,21} = 4.278$, $P = 0.039$, Fig. 6). We did not find a geographical effect on the GP at 30°C for marine or terrestrial trial ($H_{2,7} = 4.630$, $P = 0.099$; $H_{1,5} = 1.667$, $P = 0.197$, respectively), but at 35°C Zenteno population had a marginal higher GP than

Huasco population ($H_{2,10} = 6.000$, $P = 0.050$) when fed on marine food. When fed on terrestrial food, lizards from Medano had a higher GP than Huasco animals ($H_{1,8} = 4.573$, $P = 0.032$). Interestingly, there was not effect of body mass on the GP, for any thermal (30°C: $r = 0.115$, $P = 0.722$; $r = 0.313$, $P = 0.180$) or food treatment (marine trial: $r = 0.422$, $P = 0.091$; $r = 0.088$, $P = 0.755$).

3.4. Apparent assimilation efficiency (AAE)

In marine trials, the mean (±SD) energy contents, per gram dry mass, for algae and faeces (plus excreta) were 10.80 ± 0.47 kJ/g and 9.95 ± 1.85 kJ/g, respectively. AAE averaged 15.7%. For these lizards consuming terrestrial food item, the energy contents for mealworms and faeces (plus excreta) were 27.68 ± 0.12 kJ/g and 11.03 ± 1.28 kJ/g, respectively, with and AAE of 60.15%. An ANCOVA using populations, thermal treatments and diet as factors, and body mass as covariate, revealed that lizards feeding on algae showed a significantly lower AAE than lizards eating mealworms ($F_{1,28} = 43.27$, $P < 0.0001$).

4. Discussion

Habitat use and trophic patterns of *Microlophus atacamensis* along its geographical range varies in agreement with the observed changes both in environmental temperature and in primary productivity. Associated with contrasting gradients in these factors (i.e., a decrease in environmental temperature in a north to south direction, but an increase in terrestrial productivity), lizards modify their reliance on marine and terrestrial food sources, and showed different kinds of responses in some parameters of their digestive physiology. We will first discuss the latitudinal change in reliance on different food resources and their relation with the stable isotopes analysis and the digestive enzyme activity. Then, we will discuss the effect of temperature and diet composition on the appetite, gut passage time and assimilation efficiency on this species.

We found a clear geographic trend in the isotopic composition. Significant higher values in $\delta^{15}N$ (i.e., more enriched) were observed in the individuals from Santa María (the northernmost population), and showed a gradual decrease to the southern populations. In the case of $\delta^{13}C$, we did not found a clear latitudinal pattern in the values of this isotope, although Santa Maria showed higher values, suggesting a latitudinal variation in the reliance of terrestrial against marine sources in the diet of *M. atacamensis*. Previous results indicate that a clear geographical trend in the incidence of marine v/s terrestrial preys in the diet of *M. atacamensis* can be found (Fariña et al. en prensa, ANEXO 3). From north to south, the representation of marine items decreases from 90% in northern populations to less than 55% in southern populations. On the contrary, they found an increase in the representation of terrestrial-animal and a reduction in algae items in the diet. Trophic levels calculated by Fariña et al. (en prensa, ANEXO 3) in three of the five populations (Medano, Zenteno, and Huasco), indicated values of 2.0 in Medano, 2.2 in Zenteno, and 2.6 in Huasco, which correspond to a category of herbivory, omnivory, and carnivory-omnivory in the three populations, respectively. Thus, diet composition in lizards from northern populations depends almost exclusively on marine sources, and a latitudinal and gradual increase in terrestrial preys occurs towards the south.

We found that the energy content of algae and the assimilation efficiency (10.80 ± 0.47 kJ/g, 15.7%) were significantly lower compared to mealworms (27.68 ± 0.12 kJ/g, 60.15%). Then, why lizards eat marine food sources?. Polis et al. (1997) postulated that the inclusion of marine items in a terrestrial consumer occurs in response to a low resources availability in terrestrial habitat, or to an improved nutrition of marine preys. This trophic expansion has been found in several species of terrestrial mammals (Navarrete and Castilla, 1993; Rose and Polis, 1998; Sleeman et al., 2001; Stapp, 2002; Delibes et al., 2004), terrestrial reptiles (Quijada-Mascareñas, 1992; Grismer, 1994; Catenazzi and Donnelly, 2006) and terrestrial birds (Sabat et al., 2006). The almost null productivity that characterizes the coast of Atacama Desert obligates to lizard to be subsidized by the marine environment.

Because the expression of digestive enzymes should be modulated in response to the ingestion of their respective substrates (the so-called adaptive modulation hypothesis; Diamond, 1991), we should expect an increase in the enzyme maltose (a disaccharide present mainly on vegetal tissues) in lizards fed on marine diet, and an increase in trehalose (which hydrolyzes the trehalose present in insects) and aminopeptidase-N (associated with the breakdown of proteins) in diets composed by animal items. As expected, Medano population showed (although marginal) an increase in the maltose activity, compared with Zenteno population. However, this last population did not show an increase in trehalose activity. Lack of differences in the activity of this enzyme may be due to the low proportion of animal items in the diet of Zenteno lizards (less than

20%, Fariña et al. en prensa, ANEXO 3). It is possible that an increase in the trehalose activity could be found in individuals from southern populations, in which terrestrial items account for more than 55% of the diet (Fariña et al. en prensa, ANEXO 3).

Our results showed a reduction in the gut passage time (and an increase in the digestive rate) at higher temperatures. This finding follows the typical pattern of several species of lizards (e.g. Van Damme et al., 1991; Beaupre et al., 1993; Du et al., 2000; McConnachie and Alexander, 2004). A reduction in the GP is associated with an increase in the appetite, simply because allows to process more food (McConnachie and Alexander, 2004). But why the appetite increases with temperature?. Sepúlveda et al. (CAPITULO 3) found that the metabolic rate increases as temperature rise, which implies higher rates of energy expenditure (Angilletta, 2001), obligating lizard to eat more food to meet the increase in energy requirements. An interesting finding was that, at the same temperature, lizards from southern populations showed a reduction in the GP. Sepúlveda et al. (CAPITULO 2) registered lower environmental temperatures in southern populations, and consequently poor quality thermal conditions for the activity of lizards. It is possible that lizards from southern populations confront thermal restrictions by reducing the gut passage, and consequently be able to process more food in a shorter time.

The AAE of lizards maintained with a diet composed on mealworms was 60.15%. This value lies in the range previously described in the literature (from 30 to 93%, see Table 1 in Johnson and Lillywhite, 1979). In the case of lizards maintained on algae diet, the AAE was significantly lower (15.7%). Unfortunately, we do not have previous records to compare this value, but a comparison between lizards eating apples and mealworms (Johnson and Lillywhite, 1979), indicate a similar pattern: lizards exhibit a lower assimilation efficiency when feed on vegetables. It is possible that lizard may not be able to assimilate the cellulose present in the algae (Nagy, 1977), and consequently cannot extract the maximum possible energy. Besides, the energy content of mealworms was about three times more energy per unit weight than do algae. This difference indicates that a *M. atacamensis* feeding exclusively on algae would have to ingest a three-fold greater food volume in order to obtain the same energy and nutrients than would a lizard feeding on mealworms. We speculated that the lower energy content on algae could be associated with a lower body weight in lizards from northern populations (Sepúlveda et al. CAPITULO 2).

Although assimilation efficiency differs with type of food, we did not detect a temperature effect on AAE nor differences between populations. This thermal insensitivity is similar to reported by other authors (Ji et al., 1997, McConnacchie and Alexander, 2004, but see Du et al., 2000), and may be associated to the decrease in the gut passage at higher temperatures. At lower temperatures, digestion and absorption occurs at slower rates, and the passage of the meal is at a pace that matches its digestion and absorption. Thus, slower rates of extraction may be compensated for by slower turnover rate, enabling the lizards to fully digest their meals at low temperatures. This temperature independence may represent a practical strategy for lizards to extract the maximum possible energy from the meal, regardless of whether or not the lizard is able to maintain its body temperature in the selected range (McConnacchie and Alexander, 2004).

In summary, our results highlight the importance of temperature and food quality on

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the digestive physiology of *M. atacamensis.* Differences among populations of this species could be interpreted as result of different strategies that lizards use to cope with restrictions imposed for the thermal environment and the food productivity.

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Tables

Table 1. $\delta^{13}C$ and $\delta^{15}N$ stable isotopes values for five populations of *M. atacamensis* lizards along a latitudinal gradient. Values are shown as mean ± SE.

Population	Latitude	$\delta^{13}C$	$\delta^{15}N$	N
Santa María	23°29' S	-13.26 ± 0.50	22.30 ± 0.29	6
Medano	24°37' S	-15.41 ± 0.50	19.98 ± 0.29	6
Zenteno	26°51' S	-14.73 ± 0.43	19.60 ± 0.25	4
Huasco	28°07' S	-14.01 ± 0.61	19.68 ± 0.35	8
Arrayán	29°41' S	-14.77 ± 0.33	19.10 ± 0.19	14

Figure captions

Figure 1. Study map showing the geographic location of the collecting sites of *Microlophus atacamensis.*

Figure 2. Signatures of $\delta^{13}C$ and $\delta^{15}N$ stable isotopes along a north to south latitudinal gradient. Upper panel shows the $\delta^{13}C$ values (open points, $y = -0.09\,x - 12.07$). Lower panel shows the $\delta^{15}N$ values (closed point, $y = -0.38\,x + 30.24$).

Figure 3. Relationships between body mass and length of stomach and length of intestine. Regression equations are: Log stomach length = 0.39 log M_b + 1.75; and Log intestine length = 0.25 log M_b + 1.31.

Figure 4. Hydrolytic activity of the digestive enzymes aminopeptidase-N, maltose, and trehalose in *M. atacamensis* lizards from Medano and Zenteno populations. Data are showed as mean ± SE.

Figure 5. Effect of the body mass on lizard's mealworms consumption. The regression equation is food mass = 0.0195 M_b + 0.0004.

Figure 6. The effects of temperature and food type on gut passage time in *M. atacamensis* lizards. Data are showed as mean ± SE.

*Figure 1

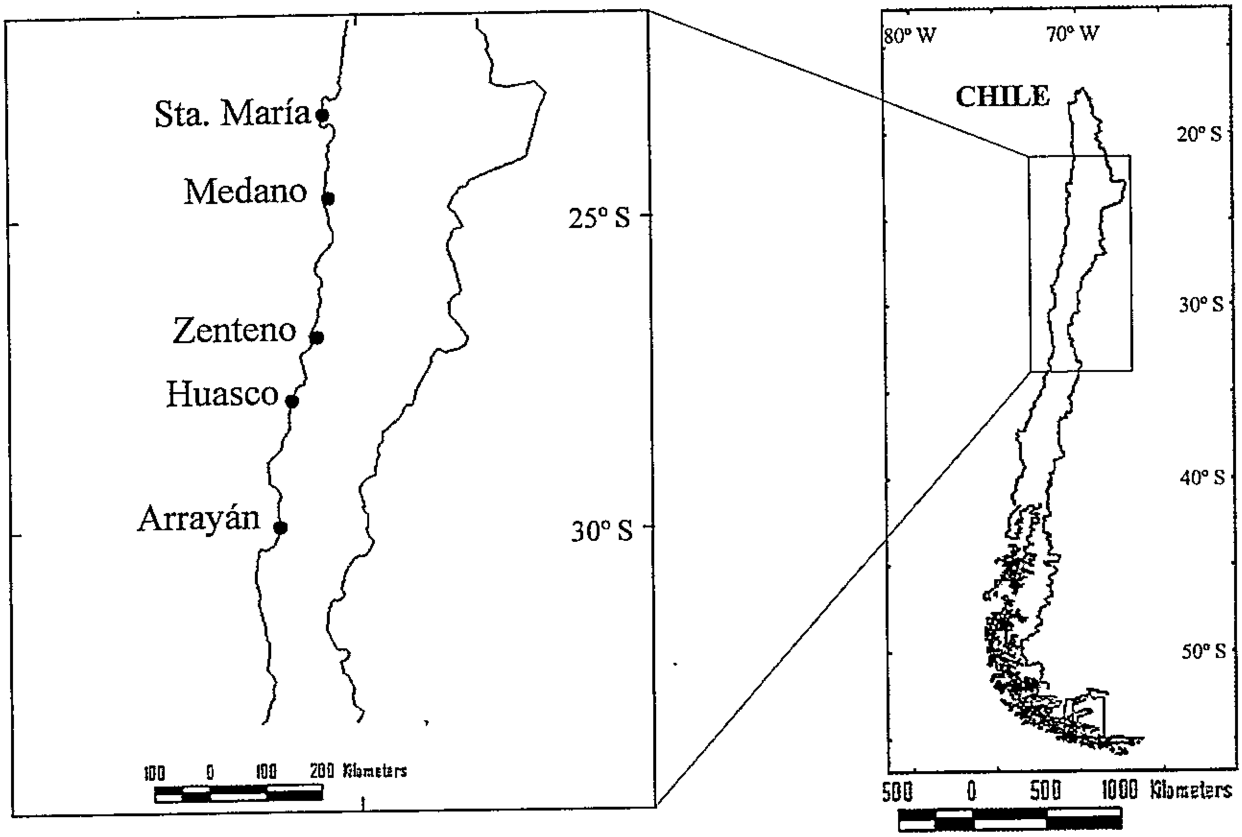
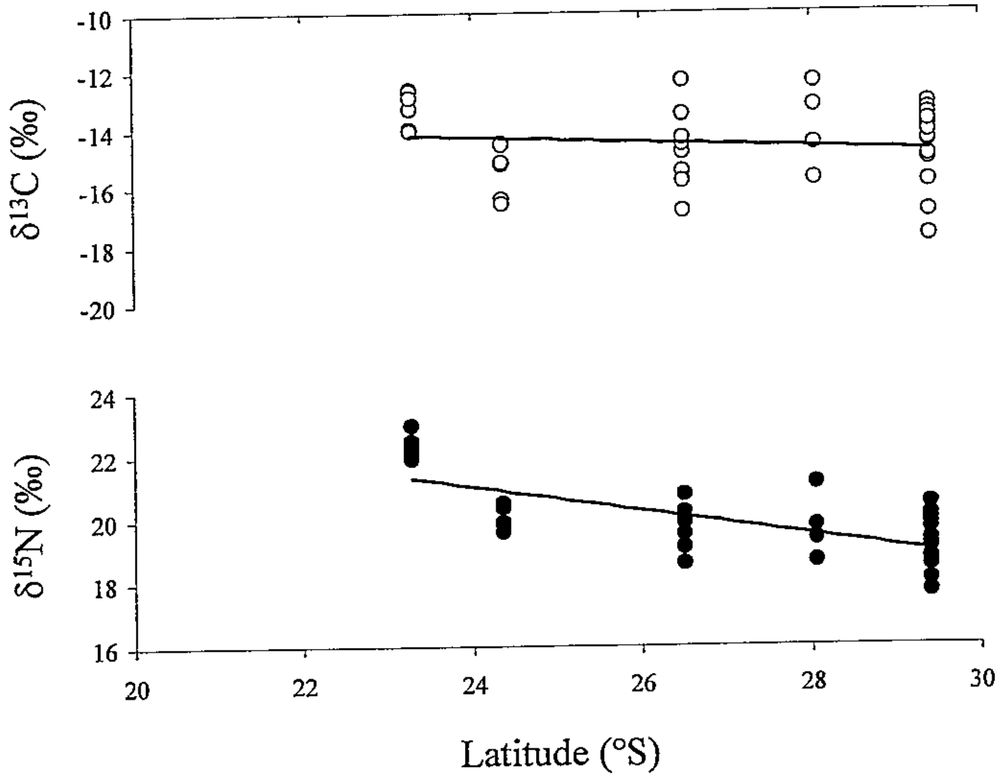

Sta. María
Medano
Zenteno
Huasco
Arrayán
25° S
30° S
100 0 100 200 Kilometers
80° W
70° W
CHILE
20° S
30° S
40° S
50° S
500 0 500 1000 Kilometers

*Figure 2



δ13C (‰)
-10
-12
-14
-16
-18
-20
δ15N (‰)
24
22
20
18
16
20
22
24
26
28
30
Latitude (°S)

*Figure 3

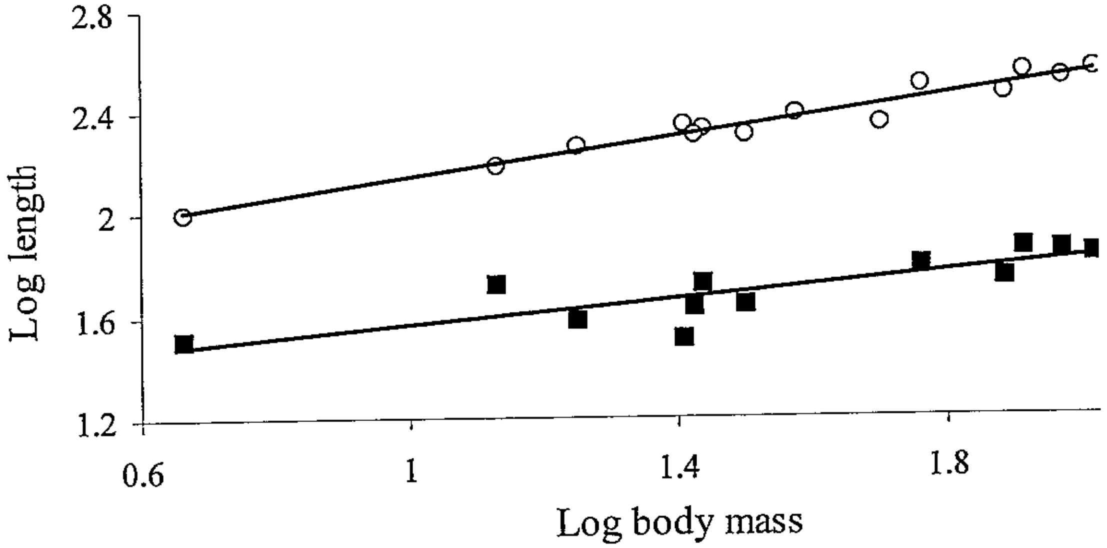


*Figure 4

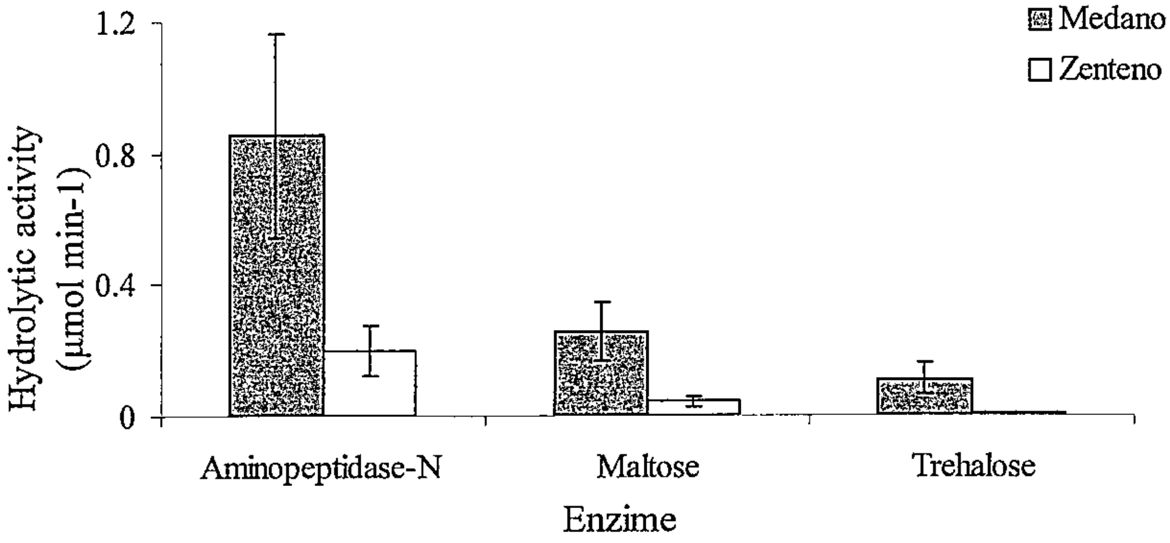

1.2
0.8
0.4
0
Hydrolytic activity
(µmol min-1)
▨ Medano
☐ Zenteno
Aminopeptidase-N
Maltose
Trehalose
Enzime

*Figure 5

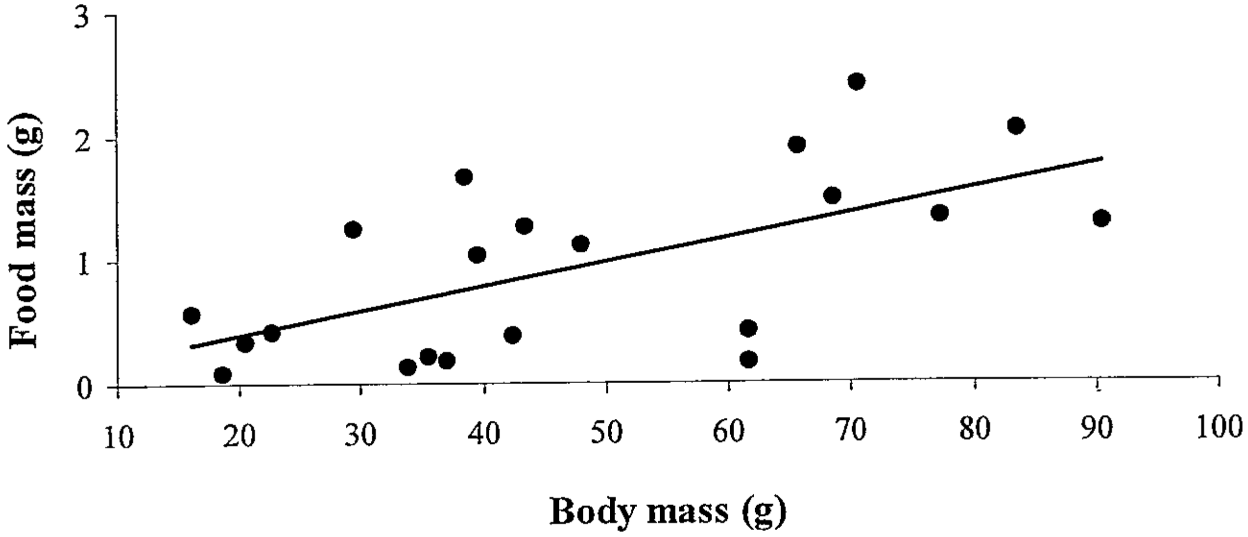
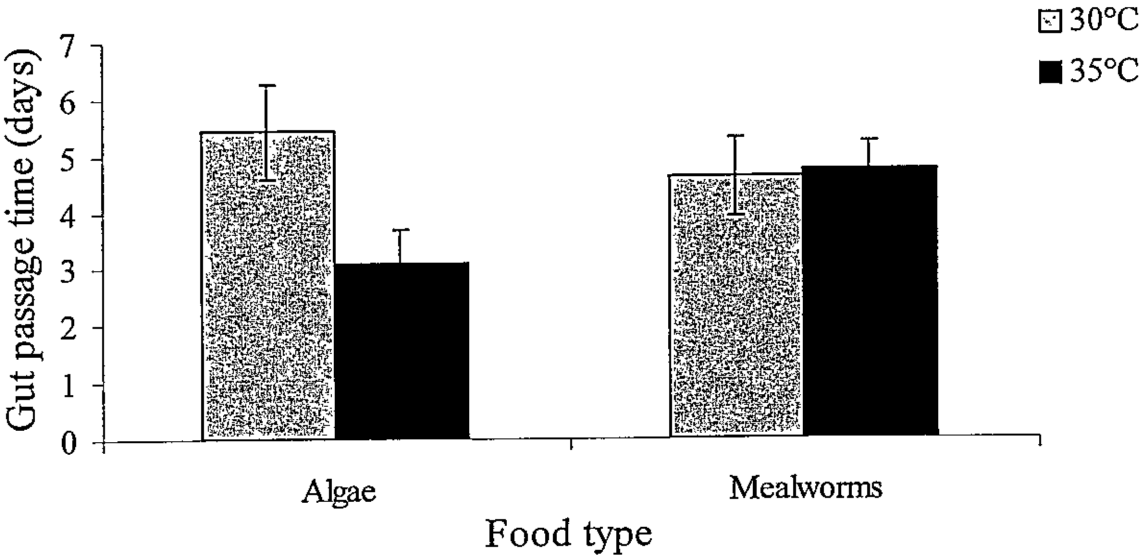


*Figure 6


▨ 30°C
■ 35°C
Gut passage time (days)
7
6
5
4
3
2
1
0
Algae
Mealworms
Food type

III. CONCLUSIONES FINALES

A lo largo de su rango de distribución y también a una escala temporal, *Microlophus atacamensis* debe enfrentarse a restricciones tanto en la disponibilidad de alimento como en la temperatura ambiente. En términos generales, mientras que las poblaciones del norte se benefician de mayores temperaturas ambientales, carecen sin embargo de alimento de origen terrestre. En contraste, poblaciones del sur sí tienen acceso a una mayor productividad terrestre, pero están restringidos a operar bajo temperaturas ambientales menores. Considerando estos compromisos, surgen las preguntas: (1) ¿qué ventajas y desventajas existen para cada una de las poblaciones?, (2) ¿cuáles han sido las estrategias (fisiológicas y/o conductuales) que han desarrollado las distintas poblaciones para enfrentar las restricciones mencionadas?, y (3) ¿cómo afectan estas estrategias el presupuesto energético y desempeño biológico de los individuos?. A partir de los resultados de esta tesis, es posible construir un esquema general sobre las estrategias empleadas a escala local y temporal por distintas poblaciones de *M. atacamensis*.

Las lagartijas de las poblaciones del norte habitan en un ambiente de mejor calidad térmica que las poblaciones de mayores latitudes y se alimentan casi en su totalidad de presas de origen marino. La alta temperatura ambiente permite una prolongada actividad de los individuos, tanto a una escala diaria como estacional. En diversas especies de lagartijas, se ha demostrado que cambios diarios y estacionales en la temperatura ambiente pueden explicar diferencias en rasgos de historia de vida entre poblaciones de una misma especie (ver Grant & Dunham 1990). Por ejemplo, un aumento en el período de actividad permite a las lagartijas asignar más tiempo al consumo de alimento (Grant & Dunham, 1988). En este sentido, un aumento en la disponibilidad de temperatura, y en consecuencia en el tiempo de forrajeo, permite a un individuo asignar más energía a las funciones de mantención, crecimiento, y reproducción (Avery et al. 1982, Adolph & Porter 1993, Grant & Dunham 1988, 1990). Sin embargo, la prácticamente nula disponibilidad de presas terrestres en estos sitios obliga a las lagartijas a la inclusión de presas de origen marino en su dieta, lo que representa fuertes desventajas para los individuos. En primer lugar porque el contenido energético que aportan las algas es tres veces inferior al que se obtiene en presas de origen animal, lo que indica que una lagartija debe ingerir tres veces más alimento en orden a obtener la misma energía y nutrientes que una lagartija alimentándose de dieta animal. En segundo lugar porque las lagartijas muestran una eficiencia de asimilación significativamente menor cuando se alimentan de algas, respecto de cuando se alimentan de larvas de *T. mollitor*. Finalmente, y debido a la menor temperatura operativa en los meses de otoño e invierno, las lagartijas están fuertemente restringidas a visitar la zona intermareal, con un consecuente impacto negativo sobre la ingesta de presas de origen marino. En este sentido, las lagartijas de poblaciones de bajas latitudes están bajo un fuerte compromiso entre alimentarse y termorregular.

En el caso de las poblaciones australes de *M. atacamensis* se encuentra el efecto opuesto. La alta productividad terrestre permite a las lagartijas de estas localidades alimentarse mayoritariamente de presas de origen terrestre-animal, pero deben operar en un ambiente de menor calidad térmica para las lagartijas. Tanto el contenido energético de las presas de origen animal, como la eficiencia de asimilación sobre este tipo de recursos tróficos son altos, lo que permite a los individuos extraer la mayor cantidad de energía posible, e independiente de la temperatura ambiente. De igual modo, los individuos de poblaciones australes de *M. atacamensis* aparentemente son capaces de asimilar el alimento en un menor tiempo que poblaciones de menores latitudes, lo que les permite procesar una mayor cantidad de alimento en un menor tiempo, y con ello confrontar las restricciones térmicas impuestas por el ambiente. Las lagartijas de estas poblaciones parecen afrontar las restricciones térmicas principalmente a través del presupuesto diario de actividad, el que no difiere del encontrado en poblaciones de menores latitudes, pese a la menor calidad térmica. Es posible que, en términos comparativos, las lagartijas de estas localidades deban asignar un mayor tiempo a calentarse que a otras actividades, lo que puede afectar su presupuesto energético y en consecuencia el éxito reproductivo de estas lagartijas (Dunham et al. 1989, Adolph & Porter 1993).

Diferencias en el uso del hábitat y en los patrones tróficos que se registran entre las distintas poblacionales de *M. atacamensis* pueden ser interpretadas como estrategias que las lagartijas utilizan ante las restricciones impuestas por el ambiente térmico y la productividad terrestre. La falta de variaciones intraespecíficas en la biología térmica de esta especie (temperaturas corporal y preferencial, tasas de calentamiento y enfriamiento), sugiere que las lagartijas compensan las diferencias térmicas utilizando estrategias conductuales de termorregulación, más que estrategias fisiológicas. De acuerdo a Stevenson (1985), la plasticidad de la conducta por sobre la fisiología de un organismo, permite que los mecanismos conductuales contribuyan a cambios en la temperatura corporal que pueden ser hasta cinco veces mayores a lo aportado por mecanismos fisiológicos. Ello sugiere que, en términos evolutivos, la respuesta de *M. atacamensis* a las presiones selectivas de los factores ambientales son principalmente conductuales, y no fisiológicas.

Las mayores abundancias de individuos se registraron en las poblaciones del centro y en menor grado en las del norte. Un aumento en el tamaño poblacional suele ser asociado con condiciones ambientales óptimas para un individuo, y que corresponden en forma más cercana a los requerimientos de una especie (Brown 1984). Esto sugiere que la combinación de los niveles de temperatura y de productividad terrestre que se registran en la localidad de Zenteno es la óptima para el desempeño biológico de las lagartijas. Sin embargo, y aunque la localidad de Arrayán registra la menor abundancia poblacional, los individuos de esta localidad presentan el mayor índice de condición corporal. Esto último sugiere que, aunque las lagartijas de las distintas poblaciones están bajo restricciones del ambiente físico, han sido capaces de desarrollar diversas estrategias fisiológicas y/conductuales que les han permitido explotar al máximo su ambiente térmico y de disponibilidad de alimento, siendo de este modo capaces de satisfacer sus requerimientos energéticos a lo largo de todo su rango de distribución geográfica. En la figura que se incluye a continuación se esquematizan las diferentes respuestas, a nivel fisiológico y conductual, que han desarrollado las diversas poblaciones de *M. atacamensis* estudiadas (Fig. 1).

Al finalizar esta tesis, es importante destacar algunos puntos relevantes. En primer lugar, esta tesis incorpora y analiza dos factores ambientales, y su efecto conjunto sobre la ecología y fisiología de una especie modelo de ectotermo. Aunque existen diversos factores que afectan la fisiología de un organismo, gran parte de los estudios ecológicos y fisiológicos se han centrado en tratar de explicar las variaciones a nivel intra o interespecífico en torno a un solo factor ambiental, generalmente la temperatura (e.g. Atkinson 1996, Carothers et al. 1998, Labra et al. 2001). Sin embargo, esto representa una visión limitada de las respuestas de una especie, ya que muchos factores pueden afectar los patrones de gasto energético entre poblaciones de una misma especie. En este contexto, esta tesis demuestra y recalca la importancia de incorporar diversos factores ambientales en el estudio de la fisiología ecológica de las especies.

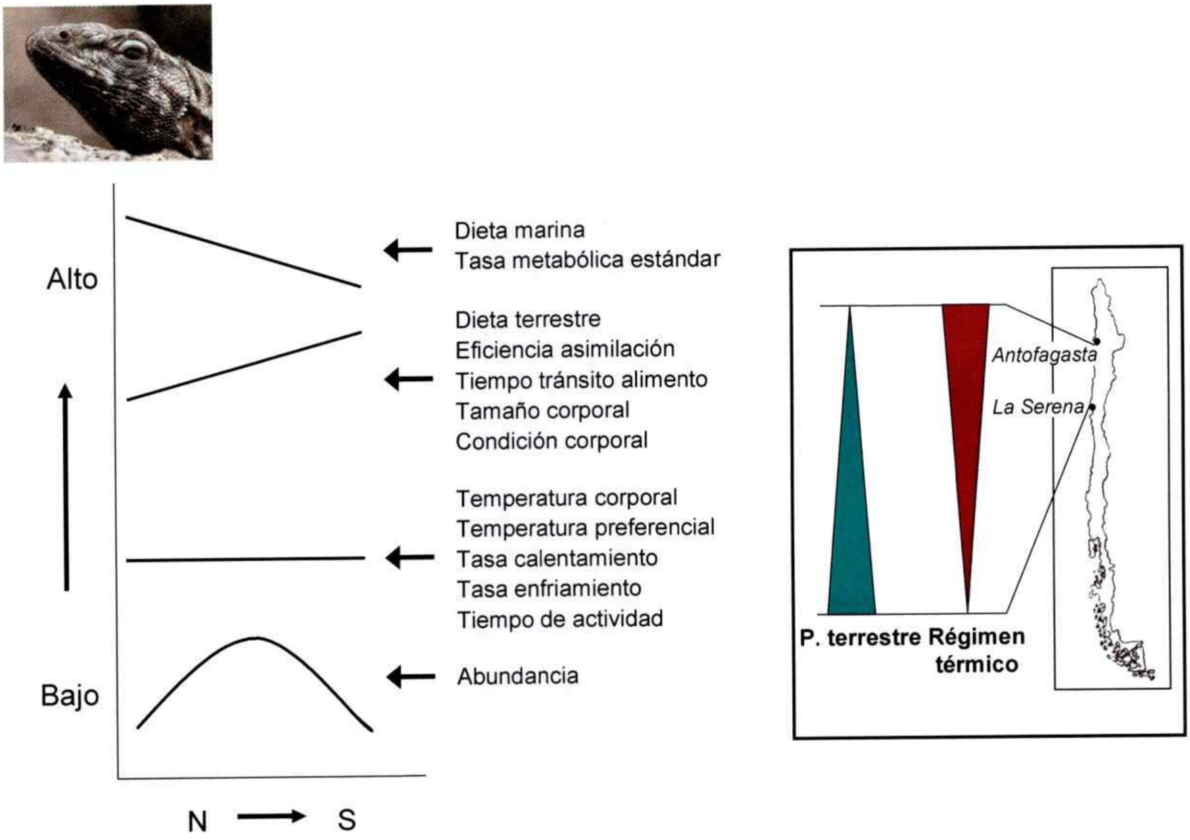


Figura 1. Esquema que resume las respuestas fisiológicas y conductuales de *M. atacamensis* a lo largo de un gradiente latitudinal en temperatura y productividad terrestre.

En segundo lugar, es de esperar que los resultados de esta tesis contribuyan al conocimiento de la ecofisiología de las lagartijas, y en especial que ayude en comprender cómo las diferencias poblacionales en los rasgos de historia de vida de una especie pueden ser explicadas por diferencias a nivel fisiológico en un individuo. Espero asimismo, que esta tesis aporte en el aún escaso conocimiento que tenemos de este grupo taxonómico en Chile.

IV. PROYECCIONES DE LA TESIS

A partir de los resultados de esta tesis, surgen una serie de interrogantes que pueden ser abordadas en futuras investigaciones. En particular, quisiera destacar los siguientes aspectos:

A través de los análisis de dieta y de isótopos estables se encontró que las poblaciones del norte de *M. atacamensis* dependen en forma casi exclusiva de alimento de origen marino. Sin embargo, la ingesta de presas marinas potencialmente conlleva un aumento en la ingesta de electrolitos, lo que podría representar una alta carga osmótica en los consumidores. De este modo, surge la interrogante acerca de los mecanismos osmorregulatorios presentes en esta especie para mantener un balance hídrico adecuado y sus posibles variaciones geográficas.

En general, no se encontraron diferencias latitudinales en las respuestas fisiológicas de *M. atacamensis* para enfrentar las restricciones térmicas. Sin embargo, comparaciones con especies relacionadas filogenéticamente, pero que experimentan diferentes niveles de productividad y régimen térmico (*M. quadrivitattus*, que se distribuye al norte de *M. atacamensis*, y *M. peruvianus* que se encuentra en las costas de Perú), muestran diferencias en temperatura corporal y preferencial. En este sentido, sería interesante analizar las estrategias termorregulatorias de estas especies y determinar sin en ellas operan mecanismos fisiológicos y/o conductuales similares a los encontrados en *M. atacamensis*.

Como se ha visto, la temperatura y la disponibilidad de alimento son factores ambientales críticos para el presupuesto energético de *M. atacamensis*. Un aspecto no abordado hasta ahora consiste en determinar en qué medidas estas diferencias inciden en los rasgos de historia de vida de las distintas poblaciones. ¿Qué explica, por ejemplo, la baja abundancia de la población más austral de la especie (Arrayán)?, ¿un aumento de la mortalidad, una baja tasa de natalidad o una combinación de ambos factores?. De este modo, el estudio de los parámetros poblacionales de *M. atacamensis* a lo largo de su rango de distribución (como por ejemplo, el número de puestas y de huevos en un año, el tamaño de inicio de la madurez sexual, la incidencia de la depredación, entre otros) puede tener implicancias no sólo para la ecología de poblaciones, sino que además podría entregar información acerca de la evolución de los rasgos de historia de vida.

Desde un punto de vista comunitario, un aspecto no considerado es el rol que juega *M. atacamensis* en las tramas tróficas marinas y terrestres de la costa desértica del norte de Chile. La importancia de los depredadores tope como organismos estructuradores de comunidades ha sido ampliamente reconocida en la literatura. Por ello, los cambios de patrones tróficos y uso de hábitats de *M. atacamensis* a lo largo de su rango de distribución (pasando de una dieta marina herbívora en el norte a una terrestre carnívora en el sur), pueden tener una influencia trascendental en la estructuración y funcionamiento de las comunidades biológicas.

Al presente, no sabemos si las diferencias en las variables fisiológicas y conductuales encontradas en las distintas poblaciones de *M. atacamensis* son producto de variaciones genéticas o de una flexibilidad fisiológica que les permite a estas lagartijas habitar bajo diferentes condiciones ambientales. Las diferencias interpoblacionales registradas en la tasa metabólica estándar, aún después de un mes de aclimatación bajo las mismas condiciones de laboratorio, además de un reciente hallazgo de haplotipos diferentes de *M. atacamensis* a lo largo de su rango de distribución (Pérez 2007), sugiere que en esta especie podrían estar operando algunos eventos microevolutivos. Un aspecto interesante sería realizar mayores estudios sobre la base genética de la variación intraespecífica en los rasgos fisiólogicos y conductuales analizados. Para esto, una aproximación sería realizar experimentos de jardin común, ya sea en terreno o en laboratorio. Por ejemplo, trasladando huevos de individuos de una población a otra, y luego analizar los rasgos fisiológicos y conductuales de interés en los individuos adultos; o en laboratorio, manteniendo lagartijas de distintas poblaciones, y desde las primeras etapas de su ciclo de vida, y mantenerlas bajo las mismas condiciones térmicas y de disponibilidad de alimento hasta las mediciones experimentales.

Finalmente, quisiera destacar un aspecto en que confluyen la ecofisiología con la biología de la conservación. Actualmente, tanto en forma legal como ilegal, la extracción descontrolada de macroalgas en el intermareal y submareal del norte de Chile está provocando cambios drásticos en las condiciones ambientales que pueden tener efectos devastadores en la fauna asociada a estos sistemas. Estos cambios pueden afectar tanto en forma directa a *M. atacamensis* (por modificaciones severas en la trama trófica), como indirecta (por ejemplo, los cambios en el sistema del oleaje debido a la ausencia de macroalgas puede repercutir en la termorregulación de esta lagartija en el hábitat intermareal). En este sentido, el reconocimiento de las conexiones entre fisiología y conservación puede ser un importante aporte en la predicción y anticipación de problemas futuros en la conservación de *M. atacamensis* en el norte de Chile.

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VI. ANEXOS

ANEXO 1.

Indice de condición corporal en *Microlophus atacamensis*

La condición corporal de cada animal se calculó como el valor residual de la regresión lineal de la masa corporal sobre la longitud hocico-cloaca, lo que representa un índice de la cantidad relativa de grasa almacenada y con ello de la condición física o el estado nutricional del individuo (López et al. 2005).

Se estimó la condición corporal en lagartijas de las localidades de Medano (N= 55), Zenteno (N= 50) y Arrayán (N= 19). Debido a que los machos mostraron un índice corporal superior al de las hembras ($H_{1,124} = 25.558$, $P < 0.001$), los análisis se realizaron en forma separada para cada sexo. Para el caso de las hembras, lagartijas de Arrayán muestran una condición corporal significativamente superior a las de Medano ($H_{2,63} = 7.558$, $P = 0.023$). Lagartijas de la localidad de Zenteno no difieren significativamente ni con las hembras de Medano ni con las de Arrayán. De modo similar, lagartijas machos de las localidades de Zenteno y Arrayán muestran un índice de condición corporal mayor que las lagartijas de Medano ($H_{2,61} = 14.240$, $P = 0.001$).

ANEXO 2.

Microlophus atacamensis (Atacama Desert Runner). Predation

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Interspecific predation, like that between lizards and snakes in the Chilean Atacama desert (Labra and Niemeyer 2004. Ethology 110:649-662), is well documented in reptiles (e.g. Jackson et al. 2004. Zoology 107:191-200). *Microlophus atacamensis*, a lizard endemic to the coastal zones of northern Chile (Donoso-Barros 1966. Reptiles de Chile. Ediciones de la Universidad de Chile, Santiago, Chile. 458 pp.), feeds on marine (crustaceans and green algae) and terrestrial (isopods, coleopterans, dipterans) prey (Ortiz 1980. Actas I Reunión Iberoamericana Zool. Vert., La Rábida, pp.355-377). No studies have reported predation on *M. atacamensis,* implying that this species is a top predator (Fariña et al. 2003. Ecol. Appl. 13:1533-1552). Nonetheless, here we describe predation by the Long-tailed Snake, *Phylodrias chamissonis* on *M. atacamensis*, a diurnal hunter whose diet consists of anurans, passeriform birds, rodents, lagomorphs, and in particular, lizards of the genus *Liolaemus* (Greene and Jaksic 1992. Rev. Chil. Hist. Nat. 65:485-493).

During diurnal sampling for *M. atacamensis* at 1530 h on 10 July 2005, we encountered a male *Phylodrias chamissonis* (667 mm SVL, 105.6 g, 12.8 mm head width) feeding on an adult male *M. atacamensis* (93.5 mm SVL, 89.5 g, 22.7 mm head width; FIG. 1). The observation was made in a coastal zone at Arrayán, La Serena, Coquimbo's Province, Chile (29°41'S, 71°19'W, datum: WGS84; elev. 8 m). The habitat corresponds to an arid Mediterranean biome with thorny shrubs (di Castri 1968. *In* Delamare and Rapoport (eds.), Biologie de l'Amérique Austral, pp.7-52. Edition du Centre National de la Recherche Scientifique, Paris), including *Nolana lycioides* (Nolanaceae) and *Heliotropium stenophyllum* (Boraginaceae) as dominant species. When first encountered, the lizard was being ingested by the head, with its hind limbs and tail still exposed. Upon capturing the snake, the lizard was released.

This is the first record of predation on *M. atacamensis* and indicates that this species may not always be a top predator in the trophic web of the northern Chilean coast. Additional observations of this interaction will be required to understand its frequency and relevance to *M. atacamensis* population dynamics.

The snake (SSUC7233) and lizard (SSUC7234) were deposited in the collection Prof. Patricio Sánchez Reyes, Pontificia Universidad Católica de Chile. We thank María Victoria Reyna for field assistance and Fondecyt 1040783 for financial support to JMF.

ANEXO 3.

Geographical variation in the use of intertidal rocky shores by the lizard *Microlophus atacamensis* in relation with changes in terrestrial productivity along the Atacama Desert coast.

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Running headline: Lizards at intertidal habitats of the Atacama Desert

MANUSCRITO ACEPTADO EN LA REVISTA "*JOURNAL OF ANIMAL ECOLOGY*"

Summary

1. The movement of materials and organisms between ecosystems is a common process in nature.

2. In the present study we investigate the hypothesis that the movement of consumers between ecosystems depends not only on the differences in productivity between ecosystems and prey availability, but also on these animals' biological characteristics.

3. To address this hypothesis we investigated the changes in abundance, habitat utilization and diet of the lizard *M. atacamensis* along its geographical range on the coast of the Atacama Desert. Within this range, intertidal rocky shore communities do not show important variations in their species composition and abundance, but terrestrial communities show a steep gradient of productivity associated with the increase in rainfall from north to south.

4. Our results showed that the use of intertidal habitats and the consumption of intertidal prey by *M. atacamensis* effectively change within its geographic range: in the north, the species uses intertidal areas and behaves as an herbivore consuming mostly algae, whereas in the south it expends most of the time in terrestrial habitats as a carnivore mainly of arthropods.

5. Our study gives new evidence for cross-ecosystem connections created by consumer movement between habitats of contrasting but variable productivity levels.

Key-words: green algae, linear mixing models, stable isotopes, habitat use, thermoregulation, reptiles, primary productivity.

Introduction

The movement of materials and organisms between ecosystems is a common process in nature (Heatwole 1971, Lord & Burger 1984, Bustamante, Branch & Eekhout 1995, Polis & Hurd 1995, 1996, Anderson & Polis 1998, Nakano & Murakami 2001, Fariña, Castilla & Ojeda 2003, Fariña et al 2003, Ellis, Fariña & Witman 2006). These movements can be categorized into three major groups: a) transport of nutrients, organisms and materials exerted by physical agents such as water or wind, b) transport of nutrients and materials by biotic or biogenic agents, and c) movement of prey and consumers between habitats (Polis, Anderson & Holt 1997). Recently Polis et al. (Polis 1991, Polis & Hurd 1996, Huxel & McCann 1998, Huxel, McCann & Polis 2002) generated the theoretical frameworks and generalizations for these phenomena, although the exchanges have been noted in both terrestrial and aquatic communities since the work of Elton (1927). This group, working in the desert island ecosystems of the Sea of Cortez, described that terrestrial food webs on the islands were subsidized by the input of marine materials and predicted that if two ecosystems differ greatly in their levels of productivity, nutrients would move from the less to the more productive habitat. In spite of this, the logical counterpart: that consumers should move from the less to the more productive habitat, one of the core predictions of the optimal foraging theory (Parker & Stuart 1976), was not explicitly considered in the model.

Several studies show that terrestrial mammals (Navarrete & Castilla 1993, Rose & Polis 1998, Stapp 1999, Sleeman et al. 2001, Delibes et al. 2004), terrestrial reptiles (Quijada-Mascarreñas 1992, Grismer 1994, Catenazzi & Donnelly 2006) and terrestrial birds (Sabat 2000, Sabat et al. 2006) effectively consume marine prey on desert islands.

Indeed, Carlton and Hodder (2003) recognized that the phenomena of terrestrial mammals entering into intertidal areas to consume prey occur on all continents (except in Antarctica). To describe these mammals, they proposed the term "Maritime Mammals" to define the "predators that utilize living intertidal energy resources and transfer these to the land". In most of the above-mentioned studies it has been postulated that the inclusion of marine prey in the consumers' diet, referred as trophic broadening, occurs in response to the low availability of resources in terrestrial habitats (energetic explanation) or to the improved nutrition of marine prey (nutritional explanation, for details see Polis et al. 1997). These two factors (availability and nutritional quality of prey) vary in both time (e.g., seasonally) and space (e.g., geographically) and it is expected that the food preference of consumers will track this variation. For example, deer in Alaska and foxes at the Bering Sea visit intertidal areas only during the winter season (O'Clair & O'Clair 1998, Fay & Stephenson 1989). On the British Columbian Islands, before the arrival of marine birds (or if the density of nesting birds is reduced), rodents usually expand their trophic spectra to include intertidal prey (Drever et al. 2000). In spatial terms, Stap, Polis & Sanchez-Piñero (1999) showed that due to the reduced precipitation on the islands of Baja California, rodents usually consume more intertidal prey on islands where the vegetation cover is almost null or extremely low. During the El Niño Southern Oscillation (ENSO) years on these islands, precipitation increased substantially (almost 200%) and in response to the associated increase in plant vegetation, rodents shifted towards granivory, depending exclusively on terrestrial foods (Anderson & Polis 1998). Thus in coastal areas, the consumption of marine food by terrestrial consumers is a dynamic phenomenon that can be affected by the spatiotemporal variability of productivity. Specifically, it is expected that the inclusion of marine food in the diet of terrestrial consumers occur more frequently in sites or seasons where terrestrial productivity is lower than marine productivity.

The Atacama and Peruvian Deserts form a belt that spans more than 3,500 km from the border of Ecuador and Peru (5°00'S) to La Serena in north-central Chile (29°55'S) and make up two of the driest and least productive terrestrial ecosystems in the world (Rundel et al. 1991). The Peru-Chile current system washes the coast of this desert and is one of the most productive marine ecosystems in the world (Ahumada, Pinto & Camus 2000). On the coast of this region, where the unproductive terrestrial system meets the productive marine ecosystem, it is possible to find many terrestrial vertebrates consuming marine prey (Fariña et al. 2003).

The genus *Microlophus* is composed of 20 lizard species distributed from the Galapagos to north-central Chile. It has been divided into two main groups (Dixon & Wright 1975): *Occipitalis* composed of 10 species living in the Galapagos and northern Peru and *Peruvianus* also composed of 10 species ranging from southern Peru to northern Chile. Within the Peruvian group two different subgroups can be recognized. The inland group, composed of 8 species living in the desert mountains and valleys and the coastal group composed of 2 species: *Microlophus quadrivittatus* and *Microlophus atacamensis*. The geographical range of *M. quadrivitattus* (from Arica 18°00' S to Antofagasta 20°32'S) falls into an area where the extreme desert reaches the coast and there is practically no annual precipitation (maximum recorded= 2mm/year, di Castri & Hajek 1976). Whereas the geographical range of *M. atacamensis,* the subject of this study and southernmost species of the genus, runs 500 km into the so-called Desert

Coastal area which presents a gradient of precipitation from 2mm/year in the north (at Antofagasta) to almost 100 mm/year in the south (La Serena).

Within this gradient and in concordance with the generalizations previously mentioned, we tested the hypothesis that the use of intertidal areas and maritime food should change within the geographical range of this lizard: in the north where terrestrial productivity is almost null, dependence on intertidal food should be high and it should decrease towards the south. The objective of the present study was to evaluate the changes in abundance, habitat utilization and diet of *M. atacamensis* along its geographic range, with special emphasis on the use of intertidal v/s terrestrial areas.

Methods

STUDY AREA

The study was conducted from November 2004 to November 2006 along the entire geographical range (~500 km) of *Microlophus atacamensis* on the Atacama Desert Coast (Victoriano et al, 2003, Fig 1). Within this range, rocky shores and exposed bays with few sand areas characterize the coast. Boulders and small (flat) benches compose most of the intertidal rocky shores, whereas sand patches occurring between high rocks dominate the ~500m of the adjacent terrestrial area (hereafter referred to as "terrestrial" habitat). Three sites similar in their exposure to waves (exposed), intertidal morphology (boulders and flat rocky benches) and terrestrial morphology (sand patches alternating with big rocks) were chosen from the geographical range of *M. atacamensis* (Fig. 1): 1) Taltal (24°37'09.8' S, '70°33'25.1''W) at the northern extreme, 2) Zenteno (26°51'40.8'S, '70°47'39.7''W) at the center, and 3) Huasco (28°07'46.3'S, '70°09'40.4''W) at the southern extreme. DiCastri & Hayek (1976) give a good description of the climate in the study areas: at Taltal the climate corresponds with the hyperarid desert with less than 2 mm of rainfall per year and mean temperatures between 21°C in summer and 14°C in winter. Zenteno receives ~25 mm of rain per year with mean temperatures of 22°C and 17°C in summer and winter, respectively. Huasco is on the border of the area known as coastal desert receiving 128 mm of rain per year with mean temperatures of 21°C in summer and 16°C in winter.

CHARACTERIZATION OF INTERTIDAL AND TERRESTRIAL AREAS

Intertidal rocky shores in our study area have been described as being dominated by ephemeral green and seasonal red algae (mostly, *Ulva* sp and *Porphyra columbina*, Broitman et al 2001) with high levels of productivity (around 300 g/m2/year, Fariña et al. 2003). Because the study area falls into the same marine biogeographic region, no important spatial variations in intertidal species composition, abundance and productivity have been found along it (Santelices 1991, Camus 2001). Fariña & Castilla (2001) confirmed this observation. For terrestrial habitats there are no specific studies but rather general descriptions that characterize the coastal area of Taltal (Hyperarid desert) as vegetation-less (Rauh 1985, Rundel et al. 1991, Marquet et al 1998). The area of Huasco presents several plant species such as *Nolana divaricata*, *Heliotropum* sp, *Oxalis gigantea*, *Tetragonia maritime*, *Trichocereus coquimbanus* and *Eulychnia acida*, whereas at Zenteno the vegetation is restricted to the lower reaches of quebradas and on the coast it is occasionally possible to find some individuals of *Nolana* sp. Despite the lack of descriptions for productivity levels at terrestrial habitats within our study area, following previous works on desert systems (Polis and Hurd 1996, Catenazzi and Donnelly 2006) an estimation using a model of primary productivity as a function of precipitation (Lieth 1978) gives a range from 4.4 to 242.9 g/m2/year, from Taltal to Huasco.

At the intertidal habitat of each site, the diversity, abundance, and composition of the species living on rocky substrates were assessed. Every four months, a series of 20 plots of 0.25 x 0.25 m were randomly placed parallel to the shoreline at both high and mid intertidal levels. Each plot was divided into a grid of 100 equally spaced intersection points. Intertidal levels were determined a priori using the high and low water marks predicted by tide tables, during days of similar tidal and sea conditions. Sessile algae or invertebrate species occurring underneath each point were identified to the lowest possible taxonomic level. The total cover of each species in the plot was obtained directly by the sum of their intersection points (Castilla, 1988).

The diversity, cover, and composition of plant species living at terrestrial habitats of each site were assessed. At each site, and every four months, a 100m line was placed parallel to the shoreline. Every 10m along the line, 5 x 5 m plots were placed giving a total of 10 plots per site. Plant species occurring in each of the plots were identified to the lowest possible taxonomic resolution, and their cover was estimated by dividing each plot into 100 equally sized squares (Steubing, Godoy & Alberdi 2001).

For both intertidal (algae) and terrestrial (plant) primary producer species with highest covers, an area corresponding to 10% of the cover was tilled on each sampling date to estimate biomasses from cover data. Considering that the objective of this study is to compare the situation of primary producers geographically (i.e., between sites) at intertidal and terrestrial areas, the information on primary producers at both habitats recorded on each sampling date was pooled.

M. atacamensis ABUNDANCE PATTERNS

The abundance of *M. atacamensis* at intertidal and terrestrial areas was assessed by visual censuses. Every four months different observers walking parallel to the shoreline and covering both intertidal and terrestrial habitats recorded the number of individuals occurring at each site. Observers did their censuses at 900, 1100, 1300, 1500 and 1700 hours, walking for one hour on each occasion. Within this hour, the total number of individuals observed was recorded every 10 minutes. Each census covered the same distance (approximately 1 km of coast). According to previous studies, the ectothermic nature of *M. atacamensis* restricts their activity to daytime hours with substrate temperatures above 22°C (Heisig 1973, Fariña et al. 2003). Considering this, the abundance patterns were characterized excluding the data of censuses where no individuals were recorded (i.e., when substrate temperatures were below 22□C).

M. atacamensis DIET

Individuals of *M. atacamensis* were caught using air-compressed guns (hunting permit # 98 from the Chilean Agricultural and Livestock Service, SAG). The captured individuals were sexed, weighed (TW=total weight of the individual in grams), measured (SVL=snout-vent length in centimeters), and their digestive tracts were extracted. In order to characterize the dietary composition, we analyzed the contents of the digestive tracts identifying prey taxa to the lowest possible taxonomic unit. The minimum number of digestive tracts needed for a reliable analysis was calculated using the rarefraction curve of the taxa occurring in each analyzed tract. The curve was drawn following the agglomeration of taxa generated by randomly re-sampling the original data matrix 1,000 times (using EstimateS, Colwell & Codington 1994). This analysis showed that the minimum number of tracts were 19, 15 and 12 for Taltal, Zenteno, and Huasco, respectively. Considering this data, it was necessary to pool all of the individuals captured during the entire study period at each site.

STABLE ISOTOPIC ANALYSIS

To analyze the relative contribution of marine and terrestrial prey, we analyzed $\delta^{13}C$ and $\delta^{15}N$ stable isotopes contents of *M. atacamensis* from each site. Values of $\delta^{13}C$ and $\delta^{15}N$ are higher for marine organisms and/or for terrestrial plants and consumers of localities with high marine inputs of marine-derived energy and nutrients, than for terrestrial producers and consumers without marine input (Chrisholm, Nelson & Schwarez 1982, Mizutani & Wada 1988, Catenazzi & Donnelly 2006).

Following standard procedures (Sabat et al. 2006, Catenazzi & Donnelly 2006) tissue samples were collected from the captured individuals at each site, lipids were extracted; the remaining tissue was dried and ground into a powder. Treated samples were then submitted to the University of Arkansas Stable Isotope Laboratory for analysis.

Trophic level (T.L.) of *M. atacamensis* from each site was calculated using the formulas (Post 2002) for one-source (for Zenteno and Huasco) or for two-source food webs (for Taltal):

One source:

$\text{T.L.} = \lambda + (\delta^{15}\text{N}_{lizard} - \delta^{15}\text{N}_{source\ 1}\ \text{X}\ \text{frec}_{source\ 1})/\Delta_{\text{n}}$

$\text{T.L.} = \lambda + (\delta^{15}\text{N}_{lizard} - [\delta^{15}\text{N}_{Ulva}\ \text{X}\ \text{frec}_{Ulva} + \delta^{15}\text{N}_{Porphyra}\ \text{X}\ (1 - \text{frec}_{Ulva})])/\Delta_{\text{n}}$

where λ is the trophic level of the basal resource (=1 for *Ulva* and *Porphyra*) and Δ_{n} (=3.4) is the mean trophic fractionation of δ^{15}N for each trophic level (Post 2002).

Considering their importance in diet, both by weight and frequency (Table 3), we assumed that main primary producer sources were: *Ulva* sp and *Porphyra columbina* in Taltal (a two-source model), *Porphyra columbina* in Zenteno, and *Ulva* sp in Huasco (a one-source model in each case). In every case the equations were calculated using the sources'δ^{15}N values and the lizards for each particular site.

For each site, contribution of each prey item to *M. atacamensis* was evaluated by using a linear mixing model (*IsoSource*, Phillips and Gregg 2003), considering three sources in every case (i.e., the signatures of the three most important prey from each site) and two isotopic signatures (δ^{13}C and δ^{15}N). In these models, all possible combinations of each source (i.e., prey) contribution (in proportions from 0 to 1) are examined in small increments (0.1 in our case) and the combinations that make up the observed mixture (i.e., consumer isotopic signature) within a small tolerance (± 0.01 in our case) are considered to be feasible solutions. The frequency and range of potential source contributions are reported as the distribution of feasible solutions for each source (prey). The breadth of the isotopically determined ranges depends on the geometry of the mixing space and the similarity of source and mixture isotopic signatures. In this analysis, the model was run with the mixture (*M. atacamensis* isotopic signature) adjusted for $\delta^{13}C$ and $\delta^{15}N$ trophic fractionation (+ 0.4 and +3.4 for $\delta^{13}C$ and $\delta^{15}N$/trophic level, respectively *sensu* Post 2002) in accordance with its calculated trophic level (see above).

STATISTICAL ANALYSIS

Total cover of plants occurring at terrestrial habitats, abundance patterns of *M. atacamensis* and the proportion of *M. atacamensis* recorded at intertidal and terrestrial areas were compared between sites using one-way Analysis of Variance (ANOVA) models (Winer 1971). In these cases, Site was considered a unique and random factor because no a priori hypothesis about it was stated and because its levels represented one of the several potential combinations over which the study could be done (Underwood 1997). In the case of algae cover at high and mid intertidal zones, the results were compared between sites using two-way Analysis of Variance models. Site and Intertidal levels were considered as random factors, with 3 and 2 levels, respectively. After this was done, a Tukey (HSD) multiple-comparison test was performed to determine which means were significantly different (Day & Quinn 1989). Normality of the data was checked by graphical procedures and, when appropriate (i.e., for cover and abundance), the data were transformed (i.e., arcsine square root and log (x+1) for cover and abundance, respectively). Results are reported using the original (i.e., non-transformed) variables. Homogeneity of variances and independence of the data were verified using

Levene's and Durbing-Watson tests, respectively (Wilkinson, Blank & Gruber 1996).

The Bray-Curtis similarity index (Wolda 1981) was used to analyze the similarity in the species composition observed at the intertidal habitats of each site. Patterns of species composition similarities were contrasted using a cluster diagram of the Bray-Curtis index calculated for each site and intertidal level (high or mid). The cluster was drawn using un-weighted average linkage methods (Wilkinson et al. 1996) and significant level of similarity was estimated using the distribution of the Bray-Curtis index, calculated after bootstrapping the species abundances matrix (Clarke 1993) 1,000 times.

Dietary compositions of *M. atacamensis* from each site were compared applying the Kendall nonparametric coefficient of concordance (W) on prey percentage of total biomass (Table 3). This coefficient indicates the level of association between the rankings of two or more variables, with a null hypothesis of no association (Siegel & Castellan 1988).

Results

INTERTIDAL AND TERRESTRIAL AREAS

A total of 14 algae and 2 invertebrate species were recognized at the high and mid rocky intertidal zones of each site (Table 1). No significant differences were detected in algal cover among sites ($F_{2,293}$=2.01, p= 0.13). Although algae cover was generally higher at mid than at high intertidal levels ($F_{1,293}$=157.03, p< 0.001), within each site this difference was not statistically significant. At the three sites, high intertidal zones were dominated by the rodophyta *Porphyra columbina* whereas mid intertidal zones showed higher covers of the chlorophyta *Ulva* sp and of the rodophyta *Gelidium chilense*. It is worth noting that this last species occurred as small turf whereas both *Ulva* sp and *Porphyra* occurred as fleshy algae. Transformation of algal cover into biomass gives an estimate of 29.1, 22.1 and 24.5 gr./m^2 for *Porphyra columbina* at high intertidal levels of Taltal, Zenteno and Huasco, respectively. For *Ulva* sp., the estimated biomass corresponded to: 19.0, 19.3 and 19.1 gr./m^2 for the mid intertidal levels of these three sites, respectively.

In the case of terrestrial areas, 12 plant species from 8 families were recognized. *Nolana* (Solanaceae) was the genus with higher species representation (5 species). As expected, no plants were recorded during the entire study period on the northernmost site: Taltal. From this site south, the cover of plants increased (from 24.28 ± 2.1 in Zenteno to 33.35 ± 2.5 in Huasco). Mean plant cover transformed into biomass (Table 2) also increased from north to south with *Nolana* species dominating at the mid-range and at the southernmost site (*N. incana* in Zenteno and *N. crassulifolia* in Huasco). *Tetragonia ovata* was another species with high cover and biomass at both sites.

M. atacamensis abundance and activity

The abundance of *M. atacamensis* was significantly different among sites ($F_{2,1123}$=76.46, p< 0.001, Fig 2a). The highest values occurred at Zenteno (at the mid geographic range), followed by Taltal (north) and Huasco (south). In terms of activity, most of the individuals were recorded at terrestrial habitats in each site (Fig 2b). In spite of this, there were significant differences among sites for this variable ($F_{2,\,1123}$=87.96,

$p < 0.001$). Taltal and Zenteno showed similar proportions of individuals at both intertidal (near 30% on average) and terrestrial habitats (near 70% on average), but the southern-most site, Huasco, showed the lowest proportion at the intertidal (less than 20% on average) and the highest at the terrestrial (above 80% on average).

M. atacamensis diet

A total of 14 prey items were identified (Table 3) in the 66 analyzed digestive tracts (n = 23, 21, and 22 for Taltal, Zenteno and Huasco, respectively). The dietary composition was significantly different between sites ($W_{2,21}$=0.36, $p = 0.5$). Of the 13 prey items identified in Taltal, the algae *Ulva* sp. and *Porphyra columbina* were the dominant items in both biomass and frequency. In Zenteno, a lower number of prey (=6) was recognized and *Porphyra columbina* was the most important item in terms of both biomass and frequency. It is worth mentioning that at this site the terrestrial prey, Diptera and Isopoda, were found high in frequency but not high in biomass. The lowest number of prey items (=5) was observed at the southernmost site (Huasco). At this site the marine *Ulva* sp, and the terrestrial Diptera and Isopods were the most important items in terms of biomass and frequency.

Qualitatively the incidence of marine v/s terrestrial items showed a clear geographic trend (Fig 3). From north to south: in Taltal more than 90% of the diet was composed of marine items, in Zenteno this representation decreased (close to 80%) and in the southernmost site, marine items accounted for less than 55% of the diet. Interestingly, these geographic changes were related to an increase (from north to south) in the representation of terrestrial-animal and a reduction in marine-vegetal (algae) items in the diet. In these terms, from north to south, the diet of *M. atacamensis* changed from herbivory to carnivory-ominivory (Fig 3).

STABLE ISOTOPIC ANALYSIS

In accordance with the dietary composition and with the observed changes in the importance of marine v/s terrestrial prey, in the stable isotope analysis (Fig 4) there were practically no differences in *M. atacamensis* $\delta^{13}C$ signatures, a clear geographic trend for $\delta^{15}N$: significantly higher values (i.e., more enriched) were observed in the individuals from Taltal (northernmost site), followed by Zenteno (mid-range site) and Huasco (southernmost site).

Calculated trophic levels of *M. atacamensis* were 2.0 in Taltal, 2.2 in Zenteno and 2.6 in Huasco, corresponding to herbivory (Taltal) omnivory (Zenteno) and to carnivory-omnivory (Huasco). The analysis of the linear mixing model (Fig 4) confirmed that the most important items observed in the digestive tract analysis (both in weight and frequency) effectively contributed to *M. atacamensis* nutritional balance (at least for nitrogen and carbon). For every site a "constrained solution" (*sensu* Phillips and Gregg 2003) was produced indicating that, of the 3 main sources considered, only two produced feasible solutions. For Taltal, the model produced feasible solutions that included *Ulva* sp (median = 0.38, range: 0.08-0.65) and *Porphyra columbina* (median= 0.57, range: 0.31-0.86) but practically excluded Diptera (median= 0.05, range: 0-14). The graphical representation of the model for this site (Fig 4) shows that the mixture (*M. atacamensis* isotopic signature) fails in the line between *Ulva* sp and *Porphyra* *columbina* signatures, far from the Diptera position confirming the status of herbivore for the individuals of this site. In the case of Zenteno, feasible solutions included *Porphyra columbina* (median= 0.6, range: 0.54-0.82) and Diptera (median= 0.3, range: 0.18-0.46) but excluded Isopoda (median= 0.05, range: 0-0.16). For this site, *M. atacamensis* signature failed in the line between *Porphyra columbina* and Diptera (Fig 4), indicating omnivory (with preferences for algae). In Huasco, solutions included Diptera in high proportions (median= 0.74, range: 0.47-1), Isopoda in lower proportions (median= 0.19 range: 0-0.38), and practically excluded *Ulva* sp (median= 0.07, range: 0-0.15). The graphic representation of these solutions located *M. atacamensis* in the line between Isopoda and Diptera, but closest to the Diptera position, indicating carnivory with preferences towards this last prey.

Discussion

Habitat use and trophic patterns of *M. atacamensis* at the Atacama Desert coast are in agreement with observed changes in primary productivity along its geographical range. Two main features represented these changes: a) Primary productivity at intertidal zones seems to be equivalent, but terrestrial plant representation increases from north to south. The rocky intertidal habitats along the entire study area showed similar patterns of species composition and biomass and the only difference detected within this assemblage was the change in species dominance at mid (*Ulva* sp.) and high (*Porphyra columbina*) intertidal levels. In contrast, terrestrial habitats showed conspicuous geographic changes that corresponded with variations in total precipitation (see Introduction). b) Primary consumers, especially animal prey of *M. atacamensis*, showed important differences in species composition and abundance among sites. Studies on Deserts of Baja California (Polis & Hurd 1995), Peru (Catenazzi and Donnelly 2006) and Chile (Jerez 2000, Cepeda-Pizarro, Pizarro-Araya & Vásquez 2005a) have shown that primary consumers and detritivores strongly track their abundance to the standing-stock of both *in situ* (e.g., plant production) and/or *ex-situ* (e.g., subsidies) primary producers. Considering this, for our study area, we expected an increment in the abundance of the terrestrial associated fauna from north to south. Preliminary data from pitfall traps (n= 322) run for a year at the terrestrial area of each study site show that the number of arthropods was the lowest at Taltal (0.11 ± 0.03 ind./trap) but increased to the south reaching similar levels in Zenteno (0.70 ± 0.16 ind./trap) and Huasco (0.57 ± 0.19 ind./trap). In the case of biomass, similar low levels were detected at Taltal (5.92 ± 2.09 mg./trap) and Huasco (5.89 ± 2.30 mg./trap) while Zenteno presented the highest levels (29.02 ± 8.34 mg./trap). The geographic differences between these abundance and biomass patterns are due to changes in primary consumers' species composition. At Taltal the reduced number of arthropods corresponded to coleopteran and spiders. In Zenteno the abundance of insects was mostly represented by coleopteran and isopods with large body sizes, whereas in Huasco, where the highest species richness was observed, most of the insects corresponded to hymenoptera (ants), diptera, thysanura and spiders, all with small body sizes. In the case of intertidal areas, preliminary samples of the fauna associated with the algae did not show differences among sites in either number or biomass but did so between intertidal levels. In the high intertidal zones dominated by *Porphyra columbina,* the most abundant fauna were gastropods (recruits of *Nodolittorina peruviana*) and amphipods (Gamaridae) while in the mid intertidal zones dominated by *Ulva* sp, the dominant fauna corresponded to amphipods (Gamaridae) and diptera larvae. It is worth noting that *Ulva* sp supported a higher abundance of animals than *Porphyra columbina*. For example in the case of amphipods, for all the sites, mean abundance in *Ulva* sp was 100-120 ind./cm^2 while for *Porphyra columbina* it was 9-10 ind/cm^2. Several studies have noted that changes in the associated fauna depend on algal species' architecture (Hacker & Steneck 1990), nutritional value (Christie & Kraufvelin 2004), but more importantly on physical factors correlated with algae distribution at intertidal areas (Buschman 1990, Chavanich & Wilson 2000). In our study, since not only amphipods but also most of the associated fauna showed lower abundances in *Porphyra columbina*, differences in physical factors such as humidity, temperature, and solar radiation exposure between high and mid intertidal levels should explain the observed differences in the associated faunal abundances.

Ambient temperature can largely restrict lizard activity (Huey 1974, Huey & Stlakin 1976, Catenazzi, Carrillo & Donnelly 2005) and is a key factor regulating their abundance. For our study, in terrestrial habitats active lizards were observed over the whole range of temperatures indicating that there were no thermal restrictions to their activity. Regarding the averages of these temperatures, it is worth noting that both Taltal and Huasco showed similar levels (19.41 ± 0.09 °C and 18.75 ± 0.21 °C, for Taltal and Huasco, respectively) while Zenteno showed highest values (24.6 ± 0.18 °C). In the case of the intertidal habitats, lizards were not active over the whole range of temperatures recorded at each site. In Taltal with a range of 11.5 to 48.0 °C, they were active just over

14 °C. In Zenteno with a range of 11.5 to 48.0 °C they were active over 12.5 °C and in Huasco with a range 11.5 to 45.5 °C they were active over 16°C. Despite this, there were practically no differences in the mean temperature at which active lizards were recorded at the intertidal habitat of each site (30.24 ± 0.27 °C, 29.37 ± 0.32 °C and 29.88 ± 0.48 °C, for Taltal, Zenteno and Huasco, respectively). Based in this information, it seems that the thermal scenario along the geographic range of *M. atacamensis* does not change at terrestrial habitats from north to south and does not seem to impose restrictions on *M. atacamensis* activity, but shows a peak in the average active temperature at the mid-range site, Zenteno. In the case of intertidal habitats, this scenario decreases smoothly from north to south, possibly restricting lizard activity by lower temperatures.

Considering both the prey availability scenario (assessed from the analysis of primary producer and consumer species composition and abundance) and observed thermal variation among sites, it is possible to understand the pattern of geographic variations of *M. atacamensis* abundance, habitat use, and diet. In terrestrial habitats of Taltal, the northernmost site, practically no producers or prey occurred at low abundance and biomass. Intertidal substrate presents the highest temperatures with a mean close to the average active temperature of the lizards. In relation to this scenario, the diet of *M. atacamensis* is composed mostly of intertidal prey, with a high representation of algae. Regarding habitat use, although lizards spent most of their time in terrestrial habitats (possibly thermoregulating but not feeding) it is highly probable that feeding activities in this site occur mostly in the intertidal zone, where they spend the highest proportion of the time.

In the mid-range site, Zenteno, several primary producer species occurred at terrestrial habitats and fueled a high abundance and biomass of prey, especially those with big body sizes. In terms of temperature, the conditions at intertidal zones are quite similar to those observed in the northernmost site, but at terrestrial habitats in spite of the fact that the range of temperatures is similar to other sites, the average is clearly higher. This scenario defines a site with good temperature conditions at intertidal and terrestrial habitats, with high prey availabilities. In accordance with these conditions *M. atacamensis* effectively uses both habitats for its omnivorous feeding activities.

At the southernmost site, Huasco, in spite of the increase in primary producer cover and biomass, the changes in species composition (with a reduction on *Nolanas'* species richness) are possibly associated with changes in terrestrial prey species composition (with a dominance of small body sized organisms) and richness (the highest diversity was recorded here). In terms of temperature at this site, the lowest mean substrate temperature registered at intertidal levels could be related to the fact that the highest minimum for active animals at intertidal areas was also recorded here. In these terms, this site seems to be a place were *M. atacamensis* use mostly terrestrial habitats, given that it was here where the lowest abundances, the lowest proportion of lizards at intertidal zones, and a diet with a high proportion of terrestrial prey were recorded.

Early studies on the influence of marine subsidies on terrestrial food webs showed that terrestrial animals effectively consumed mostly dead marine materials such as carrion and drift algae driven to shorelines by physical agents in those areas where terrestrial productivity was low and not enough to maintain these trophic webs (Polis 1995; Polis & Hurd 1995). These terrestrial consumers include isopods, amphipods, beetles and flies (Koepcke & Koepcke 1952, Hayes 1974, Griffiths & Stenton-Dozey 1981), which by reaching astounding densities serve as prey for secondary consumers such as scorpions, reptiles and spiders (Koop & Field 1980, Griffiths & Griffiths 1983). Since then, most of the studies highlight the importance of some physical (i.e., landscape) and biotic components (vector and recipient species) that regulate these cross-ecosystem linkages (Sabo & Power 2002 a, b, Catenazzi & Donnelly 2006). Focusing on particular characteristics of physical and biotic components of the cross-ecosystem linkages allowed researchers to recognize that, in cases where consumers living in one habitat consume prey from another, the process could be highly dynamic in space and/or time and it effectively depended on (Polis & Holt 1997): a) the energetic balance of linked habitats, b) the biological characteristics of prey and consumers and c) the nutritional quality of each habitat.

Our study on the trophic ecology and habitat use of *M. atacamensis* at the Atacama Desert coast confirms that the movement of consumers between habitats depends on the energetic balance of linked habitats (intertidal v/s terrestrial primary and secondary productivity) and on some biological characteristics of consumer species that can facilitate or restrict the process (e.g., thermoregulation). More importantly, it shows that within the geographic range of one species it is possible to find a variation in the use of alternative habitats (intertidal in our case) and important changes in trophic status (from herbivory to carnivory, and in the relative importance of marine v/s terrestrial prey). The study presents a new research perspective: *Microlophus atacamensis* is the southernmost species reaching areas where the desert coast gets some precipitation increasing the terrestrial productivity. From this area occupied by *M. atacamensis* to the north there are at least two more species *M. quadrivitattus*, which lives at the coast of the extreme Atacama Desert, and *M. peruvianus,* found in the milder Peruvian Desert, which shows a precipitation gradient to similar to that of our study area. For the island group, at least 6 species live on different islands of the Galapagos archipelago occurring in almost all kinds of habitats from the high volcanoes to the coast (Stebbins, Lowenstein & Cohen 1967, Carpenter 1970, Schluter 1984, Jordan & Snell 2002). Considering the results of our study, it could be interesting to compare the situation of the diverse group of *Microlophus* species experiencing different habitats, productivity levels and thermal regimes, which are nonetheless linked phylogenetically. Recently, Catenazzi, Carrillo & Donnelly (2005) inspired by a pioneer study by Huey (1974) have described seasonal and geographic eurythermy in *M. peruvianus*. Also, many studies at the Galapagos archipelago have also described the basic ecology of the lizards living on these islands (Wright 1983, 1984, Jordan et al. 2005). Thus, these studies will be the basis for future analysis and comparison of the movement of this kind of consumer between different habitats.

Finally, in our study we show that *M. atacamensis* diet and habitat respond to both regional (i.e., gradient of terrestrial productivity) and local (intertidal prey distribution and the thermal regime) processes. Apart from the rich and diverse ecosystem types occurring within the geographical range of coastal and island *Microlophus* species; the region (from Ecuador to central Chile) is severely affected by climatic events (ENSO) that are importantly modulated on local scales. From the perspective of cross-ecosystem linkages, such events are particularly interesting because they reverse the pattern of productivity imbalance between marine and terrestrial ecosystems described in our study, thus providing an outstanding opportunity to explore the temporal and spatial variation of the phenomena (Sears, Holt & Polis 2004). In particular, during the 1997-1998 ENSO event (J.M. Fariña, pers. com.) the occurrence of rainfall in the northernmost sites was associated with the inclusion of ephemeral terrestrial prey in the diet of *M. atacamensis,* whereas the arrival of dead marine mammals and birds to the southernmost sites attracted the lizards towards intertidal areas, reversing the patterns of geographic variation in the use of intertidal rocky shores described here.

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Table 1: Mean cover (± 1 SE) of the sessile species occurring at high and mid intertidal levels of each site. In every case higher values are underlined.

	MEDANO		Zenteno		HUASCO	
	High	Mid	High	Mid	High	Mid
PHAEOPHYTA						
Ralfsia sp.	1.84 (0.9)	17.5 (3.3)	0.02 (0.02)	10.7 (2.6))	0.8 (0.8)	4.9 (1.6)
Lessonia nigrescens				0.06 (0.04)		
Halopteris ordacea		0.2 (0.2)				
CHLOROPHYTA						
Ulva sp	2.34 (0.7)	35.6 (5.4)	8.4 (2.7)	36.1 (5.9)	3.44 (1.3)	35.8 (5.0)
Codium sp				1.0 (1.0)	0.1 (0.1)	1.4 (0.9)
RODOPHYTA						
Porphyra columbina	27.62 (4.9)	3.8 (1.4)	21.0 (3.8)	5.3 (1.3)	23.3 (3.7)	3.4 (1.2)
Gelidium chilense		10.4 (2.4)		22.5 (2.8)	0.04 (0.04)	16.0 (2.8)
Corallina officinalis				0.1 (0.1)		1.3 (0.5)
Gimnogongrus sp.						0.02 (0.02)
Trematocarpus sp						0.9 (0.6)
Ceramiun rubrum		0.3 (0.1)		0.6 (0.2)		2.2 (0.9)
Crustosa		0.3 (0.2)		1.4 (0.5)		4.1 (1.5)
Hildenbrandtia lecanellieri					0.4 (0.4)	0.7 (0.4)
Chondrus sp		0.06 (0.06)				
CRUSTACEA						
Notochtamalus scabrosus	9.4 (2.9)	12.2 (2.5)	8.1 (2,2)	3.9 (1.3)	2.1 (0.6)	5.6 (1.2)
MOLLUSCA						
Perumitlyus purpuratus	0.08 (0.06)				0.3 (0.1)	0.4 (0.4)

Table 2: Mean biomass (± 1 SE) of plant species occurring at the adyacent (~500m) terrestrial areas of each site. In every case underlined numbers represents the highest values per site.

	TALTAL	ZENTENO	HUASCÒ
Solanaceae			
Nolana crassulifolia	-	-	1260.9 (110.5)
Nolana rupicola	-	20.0 (8.5)	-
Nolana incana	-	400.9 (60.4)	-
Nolana sedifolia	-	19.9 (9.6)	20.8 (10.5)
Nolana salsoloides	-	100.5 (60.5)	-
Aizoaceae			
Tetragonia ovata	-	362.9 (93.8)	600.4 (133.3)
Asteraceae			
Polyachyrus sp	-	220.0 (35.7)	381.3 (121.1)
Frankeniaceae			
Frankenia chilensis	-	1.2 (1.2)	23.4 (4.5)
Boraginaceae			
Heliotropium pycnophyllum	-	6.2 (6.2)	19.8 (15.4)
Malvaceae			
Cristaria pinnata	-	2.0 (1.0)	20.0 (10.5)
Amaranthaceae			
Chenopodium petiolare	-	-	6.3 (6.3)
Plumbaginaceae			
Limonum plumosum	-	22.8 (18.3)	-

Table 3: Dietary composition of M. atacamensis at the study sites. Total weight (W. in grams), the Frequency of occurrence (F.O. in guts) and their respective proportions (%) are shown. Underlined numbers corresponded to the highest values.

Dietary items	Taltal		Zenteno		Huasco	
	W (%)	F.O. (%)	W (%)	F.O. (%)	W (%)	F.O. (%)
ALGAE						
Enteromorpha compressa	13.3 (12.1)	3 (3.4)				
Ulva sp.	49.4 (44.9)	21 (23.6)			13.4 (41.2)	19 (31.2)
Porphyra columbina	41.6 (37.8)	13 (14.6)	22.1 (86.5)	13 (31.9)		
MOLLUSCA						
Prisogaster Niger	0.03 (0.03)	1 (1.1)				
Nodilittorina peruviana	0.5 (0.4)	9 (10.1)	0.2 (1.6)	4 (9.8)	0.7 (2.3)	3 (4.9)
CRUSTACEA						
Acanthocyclus hassleri	0.4 (0.4)	2 (2.3)				
Allopetrolisthes punctatus	0.7 (0.6)	2 (2.3)	1.0 (4.1)	4 (9.8)		
Amphipoda-Gamaridae	0.3 (0.3)	9 (10.1)	0.4 (1.7)	4 (9.8)	2.8 (8.6)	12 (19.7)
Leptograpsus variegattus	0.4 (0.4)	3 (3.4)				
INSECTA						
Diptera	0.6 (0.5)	14 (15.7)	0.3 (1.2)	8 (19.5)	9.0 (27.7)	17 (27.9)
Diptera larvae	0.8 (0.7)	6 (6.7)				
Coleoptera	1.9 (1.7)	5 (5.6)				
Isopoda			1.3 (4.9)	8 (19.5)	6.6 (20.3)	10 (16.4)
VERTEBRATA						
Microlophus atacamensis	0.2 (0.2)	1 (1.1)				

Figure legends:

Fig 1. Map of the study area and sites showing (dark box) the geographic distribution of *M. atacamensis* along the Atacama Desert coast.

Fig 2. Geographical variations (from north to south) in the total abundance (a) and in the proportion of active individuals (b) recorded at intertidal (dark bars) and terrestrial (white bars) habitats of each site

Fig 3. Geographical variation on some general aspects of *M. atacamensis* trophic ecology (based on the proportion of prey in the diet).

Fig 4. *M. atacamensis* and its main preys Carbon (d13C) and Nitrogen (d15N) isotopic signatures from the study sites. Lines represents the results of the mixing model and for each prey the diagram of frequency on the possible solutions is included.

Fig 1

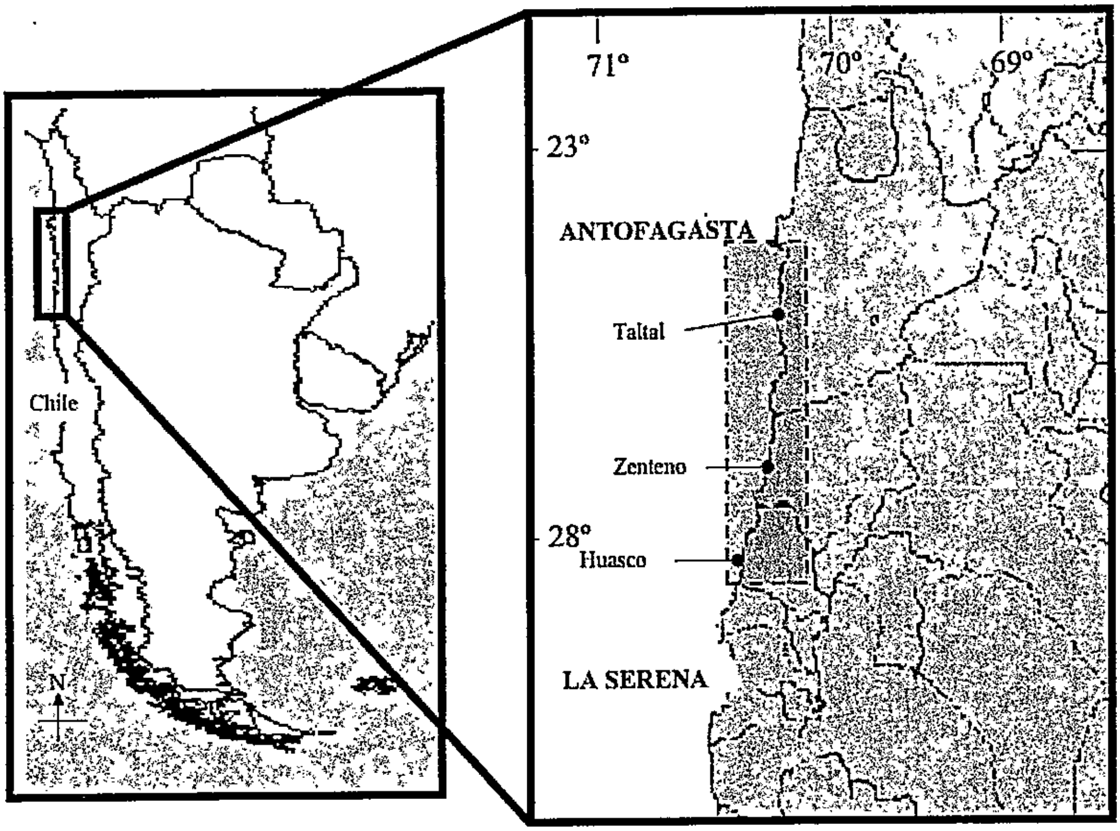
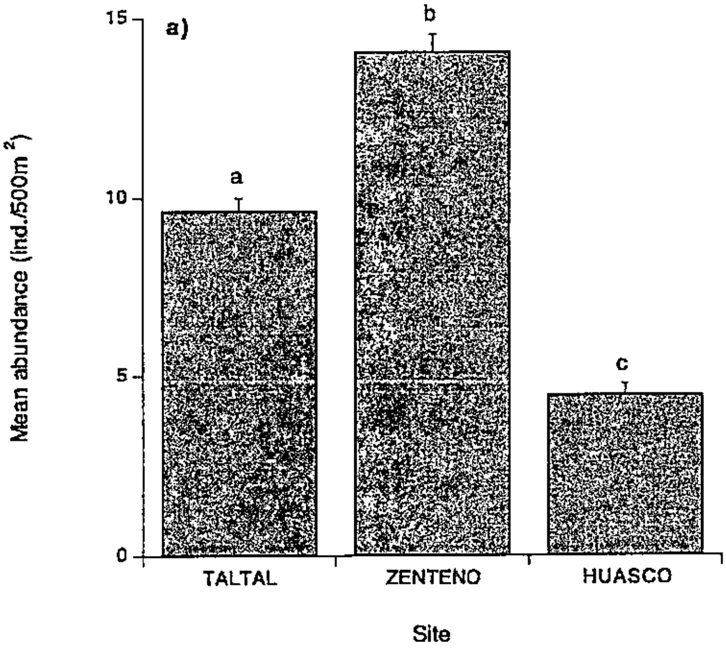

Chile
N
71°
70°
69°
23°
ANTOFAGASTA
Taltal
Zenteno
28°
Huasco
LA SERENA

Fig 2


a)
Mean abundance (ind./500m^2)
15
10
5
0
a
b
c
TALTAL
ZENTENO
HUASCO
Site

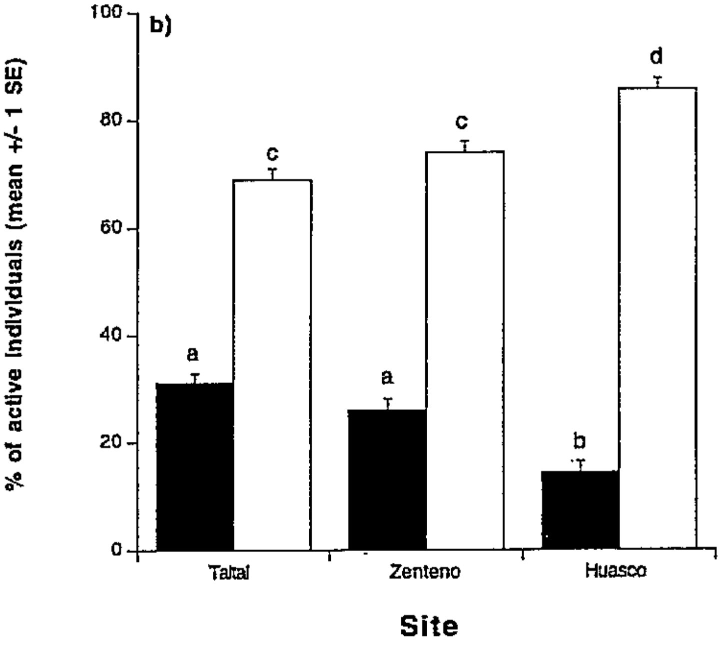

b)
% of active individuals (mean +/- 1 SE)
100
80
60
40
20
0
a
c
a
c
b
d
Taltal
Zenteno
Huasco
Site

Fig 3

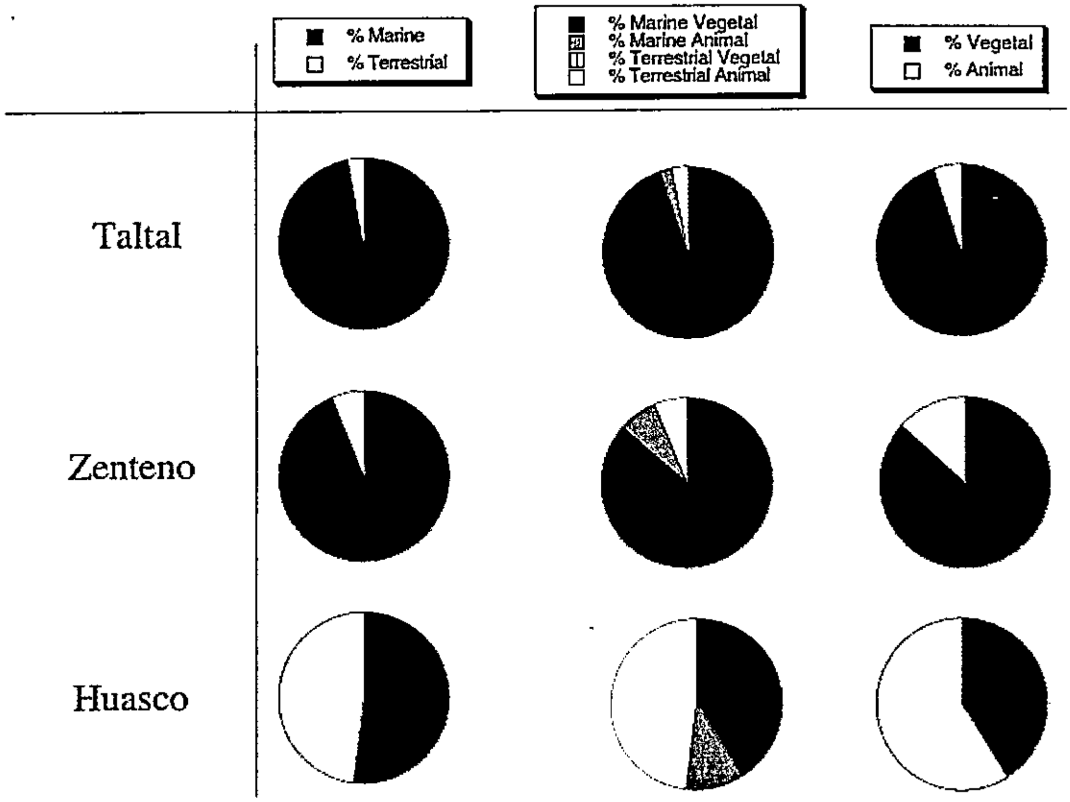
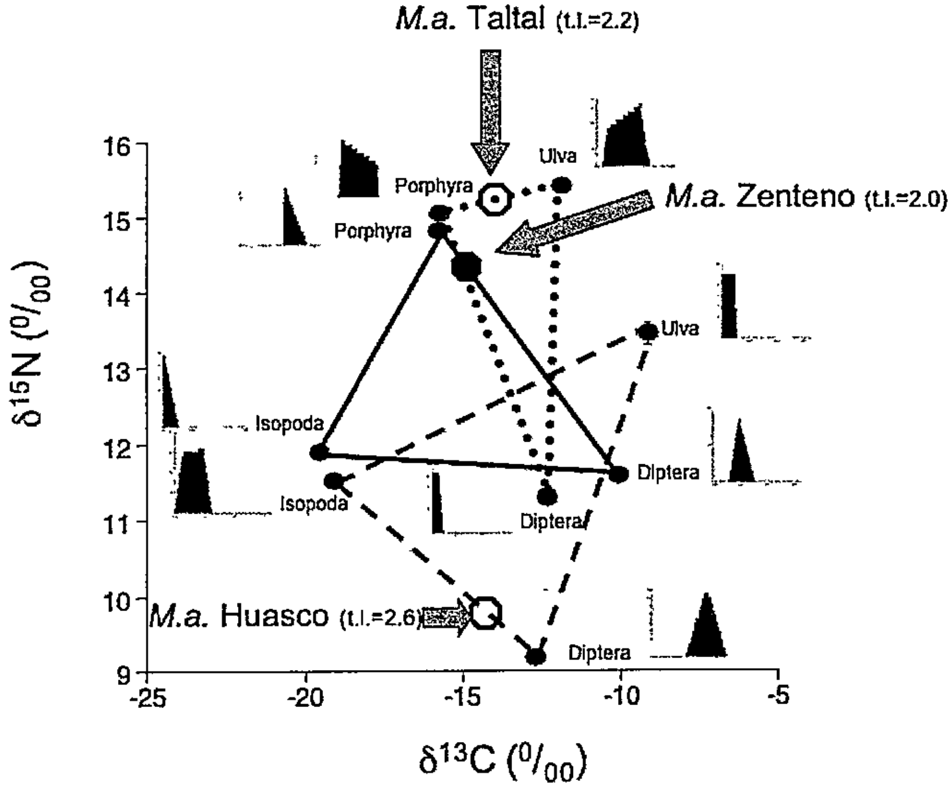

% Marine
% Terrestrial
% Marine Vegetal
% Marine Animal
% Terrestrial Vegetal
% Terrestrial Animal
% Vegetal
% Animal
Taltal
Zenteno
Huasco

Fig 4



M.a. Taltal (t.l.=2.2)
M.a. Zenteno (t.l.=2.0)
M.a. Huasco (t.l.=2.6)
Ulva
Porphyra
Porphyra
Ulva
Isopoda
Isopoda
Diptera
Diptera
Diptera
16
15
14
13
12
11
10
9
-25
-20
-15
-10
-5
$\delta^{15}N$ ($^0/_{00}$)
$\delta^{13}C$ ($^0/_{00}$)

ANEXO 4.

Destino de los ejemplares de *Microlophus atacamensis*

La captura de ejemplares de *M. atacamensis* fue realizada con la autorización del Servicio Agrícola y Ganadero de Chile (SAG), permiso # 98. Los ejemplares que debieron ser sacrificados para los análisis de enzimas, se encuentran almacenados en el laboratorio de Ecofisiología de la Universidad de Chile. Algunos ejemplares serán donados al Museo de esta institución para futuras investigaciones.