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Variación latitudinal del tamaño corporal de ***Tegula atra*** (Lesson, 1830) (Gasterópodo: Trochidae) en aguas someras del sur de Chile

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RESUMEN

La gran variabilidad de los ambientes marinos en Chile está asociada a la longitud de su costa, la cual está regulada por diversos procesos oceanográficos que perfilan la distribución, abundancia y morfología de las especies marinas. *Tegula atra* es un gasterópodo marino de gran distribución en el Pacífico sur, cualidad que le permite ser un buen modelo de estudio para evaluar la variación de su tamaño corporal respecto a su distribución latitudinal. Un total de 236 individuos fueron recolectados en seis sitios de muestreo entre 41,6 ° ~ 53,6 °S. La relación entre el peso, la talla (media geométrica) y su distribución latitudinal fue evaluada de acuerdo con regresiones de Pearson y de cuantiles. En relación con la latitud, se observó una correlación positiva y sustancial (Pearson) entre el peso y la talla ($p > 0,05$) al desplazarse hacia el sur. Los resultados de la regresión de cuantiles reflejaron que tanto la pendiente como el valor R^2 son significativos para la latitud con las dos variables analizadas (peso, media geométrica). Entre los factores que afectan al tamaño corporal de *T. atra*, se sugiere una diferenciación adaptativa de este género a diferentes temperaturas -lo que ya se ha observado en especies antárticas-. Esto revela una interacción entre la latitud, la fertilidad y el suministro de alimento, condición que se refleja en *T. atra* en la ecorregión subantártica. Sin embargo, el estudio de las zonas intermedias en el sur de Chile y la interacción con otros factores abióticos (por ejemplo, la profundidad) puede dilucidar estas variaciones en el tamaño corporal.

Palabras clave: Tamaño corporal, sur de Chile, latitud, *Tegula atra.*

Latitudinal variation of *Tegula atra* body size (Lesson, 1830) (Gastropod: Trochidae) in shallow waters from southern Chile

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ABSTRACT

The great variability of sea environments in Chile is associated with the length of its coastline, which is regulated by several oceanographic processes that outline the distribution, abundance, and morphology of marine species. *Tegula atra* is a marine gastropod greatly distributed in the southern Pacific, quality that allows it to be a good study model to evaluate the variation of its body size regarding its latitudinal distribution. A total of 236 individuals were collected in six sampling sites between 41.6° ~ 53.6°S. The relationship between weight, height (geometric mean) and its latitudinal distribution was evaluated according to Pearson and to quantile egressions. Related to the latitude, it was noted a positive and substantial correlation (Pearson) between weight and height ($p > 0.05$) moving southward. The results from the quantile regression reflected that both the slope and the R^2 value are significant to the latitude with both of the analyzed variables (weight, geometric mean). Among the factors that affect the body size of the *T. atra*, it is suggested an adaptive differentiation of this genus to different temperatures- which has already been observed in Antarctic species. This reveals an interaction between latitude, fertility and food supply, condition that is reflected by *T. atra* in the Subantarctic eco-region. However, the study of intermediate areas in southern Chile and the interaction with other abiotic factors (*e.g.*, depth) may elucidate these variations in the body size.

Keywords: Body size, Southern Chile, latitude, *Tegula atra*.

INTRODUCTION

Body size is considered as one of the most important characteristics in organisms (Peters, 1983; West *et al.* 1997), hence the growing interest in understanding the processes that generate spatial patterns in the body size in marine environment, especially in main gradients, such as those associated to latitude (Blackburn *et al.* 1999; Rex *et al.* 1999; Roy & Martien, 2001).

There are several remarks about the latitudinal variations in the physical and reproductive condition that can be related to marine invertebrates. For instance, Thorson (1936) suggests an increase of egg size in marine invertebrates as its latitudinal distribution increases (Marshall & Keough; Laptikhovsky; Lardies & Castilla). Thus, he directly relates egg production by female and the offspring size, creating a latitudinal cline. The latter relates body size and its latitudinal increase, which has also been tested with "*Bergmann's rule*" (Blackburn *et al.* 1999). This distributional pattern of the body size has been confirmed in a variety of terrestrial organisms, such as mammals, reptiles and birds (Blackburn & Gaston; McQueen *et al.*; Miller; Silva & Downing; Olalla-Tarraga *et al.*; Olson *et al.*; Rodríguez *et al.*) while in marine environments it has been tested in fish, crustacean and molluscs (Da Rocha & Silva; Defeo & Cardoso; Domínguez-Petit *et al* Frank; Lonsdale & Levinton; Marquet *et al.*; Monaco *et al.;* Roy & Martien; Spicer & Gaston). In Chile, there are a small number of studies describing the existence of this kind of associations, in spite of the particular geomorphology and extension of its coast by more than 55.000 linear kilometres, where the 95% belongs to a set of archipelagos, islands and canals, which allows evaluating possible tendencies in the body size of some marine invertebrate.

In southern Chile (between 42° ~ 56°S) lays the Patagonian Canals and Fjords System (PCFS) (Montiel *et al.;* Montiel & Rozbaczylo; Spalding *et al.*). This coastline extension fosters a great variety of habitats affected by different oceanographic processes that condition the latitudinal distribution, abundance, and morphology of some invertebrate species (Avise; Avise *et al.*; Dawson; Wares *et al.*). Considering this habitat variability from PCFS, it is possible to observe, in marine invertebrates, that morphological features can present high morphologic variations as a response to environmental changes (Sánchez *et al.* 2011). For example, some investigations using muricid gastropod *Acanthina monodon* as study model identified a pattern into the geometric morphology of the shell, which was closely associated to its genetic divergence, especially in southern PCFS (Sánchez *et al.* 2011).

Tegula atra (Lesson, 1830) is a gastropod from Trochidae family, which is characterized for its wide distribution in Southeast Pacific, from Pacasmayo, Peru to southernmost Strait of Magellan, Chile (54°S) (Reid & Osorio, 2000) and only in Falkland /Malvinas Island (51°S) in the Atlantic (Carcelles & Williamson, 1951; Linse, 1999). Besides, *T. atra* presents a bathymetric distribution from the intertidal to 10 m deep (Häussermann & Försterra, 2010), where its habitat is normally related to intertidal zones, associated to rocky bottoms (rock mass, cobble) and to populations of brown macroalgae, especially *Lessonia nigrescens*, currently indicated as *L. spicata* and *L. berteroana* (González *et al.* 2012). In Northern Chile, in rocky shallow low-tidal water, it is related to *L. trabeculata* holdfasts (Veliz & Vásquez, 2000; Villegas *et al.* 2008). This association with macroalgae places it as a strong benthic herbivore, in addition to be considered as one of the most abundant and frequent organisms in exposed rocky environments in northern Chile (Vásquez & Buschmann, 1997; Vásquez *et al.* 1998; Veliz & Vásquez, 2000). Regarding its morphology, it can be stated that it has a semi-flat base, non-umbilicated, with smooth rounded, half convex whorls, of purplish black colour and a pearl white interior (Aldea & Valdovinos, 2005 ; Veliz & Vásquez 2000).

Considering previous information, it is important to determine the existence of body size modifications in species that have a wide latitudinal distribution range and how these are capable to affect its auto-ecology. Olabarria and Thurston (2003) studied a buccinid gastropod, *Troschelia berniciensis*, describing an increase in body size in relation to the latitude, which can be reflected in changes in the community structure, such as the growth in small-sized populations, while the opposite happens in populations with larger heights. According to this, the relationship between body size and abundance reveals how populations are distributed in the ecological systems (Marquet *et al.* 2005; White *et al.* 2007). This condition emphasises body size variations as an essential aspect in ecology, with important consequences for the community structure and biodiversity.

In this context, *T. atra* has been selected as a suitable research model to evaluate if the patterns described for the northern hemisphere occur in southernmost Chile, and how this variation might change across the latitudinal distribution of the species.

MATERIALS AND METHODS

Tegula atra individuals were randomly collected in seven sampling areas between 42°S and 54°S, which comprises two political regions in Chile: Los Lagos (north) and Magellan (south). In the former two places were selected: Metri Bay (41.6°S) and Calbuco (41.8°S), while in the latter four collecting areas were determined: Mornington Island (49.2°S), Fuente Sound (50.4°S), Andres Channel (50.5°S), and Punta Santa Ana (53.6°S). This latitudinal distribution covers a range of ~12° (Table 1, Fig. 1).

The samples were collected by scuba diving in depths that range from 1 to 10 metres. Live individuals were placed in containers with seawater at ambient temperature. Containers were marked, classified by study area, and moved while being hermetically sealed to the Subantarctic Marine Resources Investigation Center of Magallanes University in Punta Arenas city, for subsequent analysis. Once in the laboratory, each *T. atra* specimen was used to obtain the morphometric information required for the research.

The variables described on body size for this species were height and width of the shell (cm), which were registered with help of a digital calliper to 0.01 mm precision, along with the individual total weight (g), which was determined using an analytical balance (0.0001 g).

Statistical analysis

To evaluate the association between body size and latitudinal distribution of *T. atra* population in a direct form, it was used the Pearson product-moment correlation coefficient as descriptive statistics to the height and weight distribution, according to each sample area. In addition to this, the analytical protocol suggested by Olabarria and Thurston (2003) was used. This analysis method considers, initially, the determination of the geometric mean of the

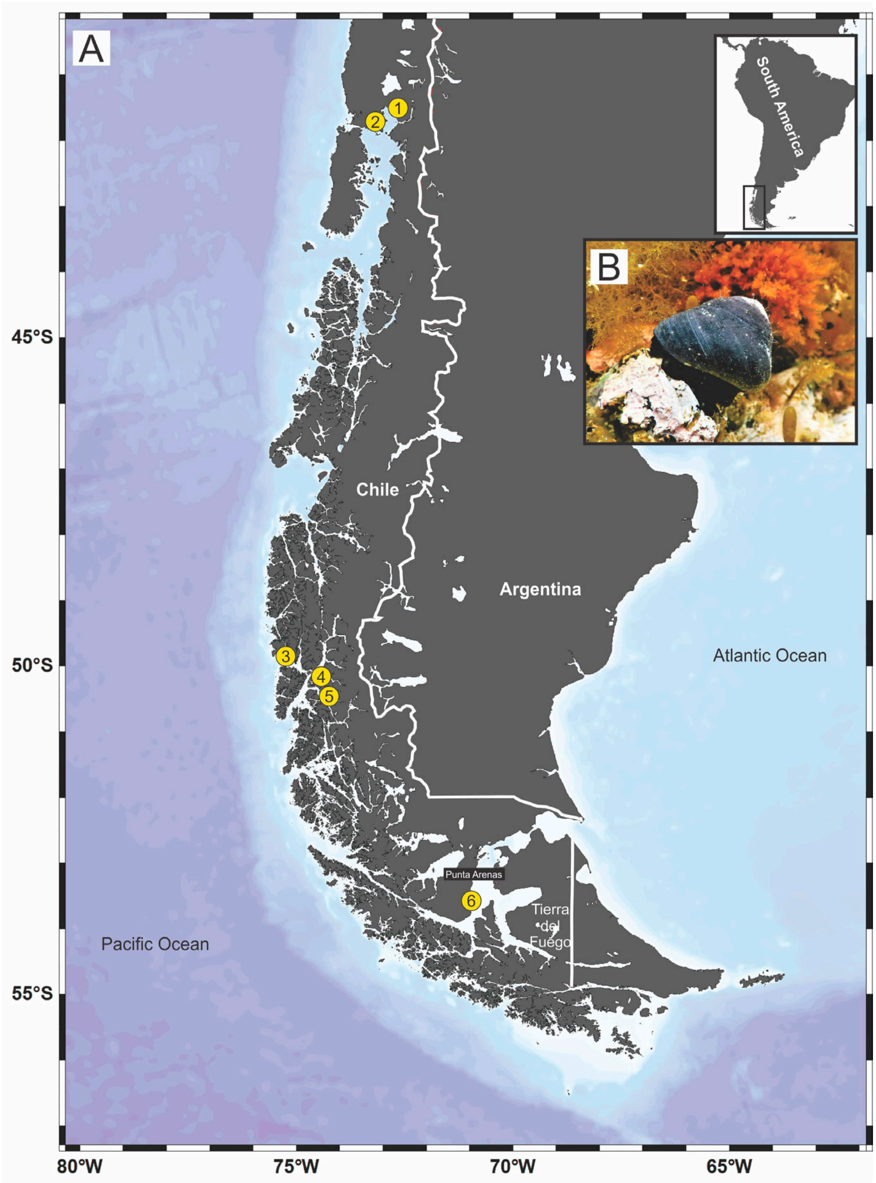

Fig. 1. (**A**) Geographical distribution of sampling sites *T. atra* in the Los Lagos region (41.3°S ~ 41.4°S); 1: Metri Bay (**MB**) and 2: Calbuco (**CB**), and Magellan region (49.1°S ~ 53.3°S); 3: Mornington Island (**MI**), 4: Fuente Sound (**FS**), 5: Andrés Channel (**ACh**) and 6: Punta Santa Ana (**PSA**). (**B**) Individual of *T. atra* from natural populations of PSA Magellan region. (Underwater photograph by Mauricio Palacios).

Table 1. Sites surveyed and number of specimens collected from *T. atra* by location in the Los Lagos and Magellan regions.

Sites	code	Latitude (°S)	Length (°W)	regions	No. individuals (*n* = 226)
Metri Bay	MB	41°35'42.2”	72°42'16.5”	LL	27
Calbuco	CB	41°46'52.3”	73°08'01.2”	LL	41
Mornington Is.	MI	49º10'44.9”	75°23'52.9”	M	20
Fuente Sound	FS	50°23'02.3"	74°20'17.8”	M	47
Andrés Channel	ACh	50°28'15.9”	74°16'59.7”	M	50
Punta Santa Ana	PSA	53°37'17.6”	70°58'09.4”	M	41

maximum height and width, which represents the body size in two dimensions. Accordingly, it gives a normalization degree of the specific differences found in the shape of the shell. Moreover, the geometric mean is able to correlate accurately the body mass and the linear dimensions of the shell in gastropod molluscs (Jackson *et al.* 1996; Roy & Martien, 2001; Stanley, 1986). Moreover, the geometric mean is able to correlate accurately the body mass and the linear dimensions of the shell in gastropod molluscs (Roy, 2002). The data on height and weight were previously transformed into Log_{10} to lessen the heteroscedasticity (Olabarria & Thurston, 2003).

Subsequently, quantile regressions were carried out; this technique is characterised by its tolerance to extreme values from the dependant variable and the data variability, giving an objective evaluation to the body size tendency, regardless of the sample size (Scharf *et al.* 1998; McClain & Rex, 2001). Also, it must be stated that the *T. atra* measured individuals were extracted at random, without considering their stage as adults or juveniles; in consequence, the quantile regressions take in account the variability introduced with the age component (factor) (Cade & Noon, 2003; Koenker & Machado, 1999). This kind of regression has a coefficient of determination R^2, obtained by subtracting value 1 from the absolute height of the original model's deviation, by the absolute deviations of the null model (Cade & Richards, 2001). The effect of the latitude in the maximum heights of each individual was directly assessed using quantile regressions between the latitude and several size measures from 5 to 95 quantiles, five by five.

Finally, a two-way of analysis of variance (ANOVA) was applied to evaluate the differences between the described variables (total weight and geometric mean) and the latitudinal distribution of the populations. When significant differences were observed, Tukey's HSD tests were applied *a posteriori,* as pair-wise tests. Figures were generated using the R library factoextra, and the fviz_pca_var and fviz_pca_biplot functions. All analyzes were performed with the routines defined in the R version 3.6.1 platform (R Core Team, 2020).

RESULTS

It was observed that individuals from the southernmost study area (*i.e.,* Magellan region) averaged the heaviest weight (g) and height (cm) in relation to those found in the northernmost study area (*i.e.,* Los Lagos region, Fig. 2). Total weight (g) is the variable in which more differences were observed between the northerner and southern populations of the study area. For example, in MB, *T. atra* individuals averaged 13.27 ± 1.27 g and in PSA 31.15 ± 2.68 g (Fig. 2a). At the shell length the pattern is lost, since the specimens collected in MB (north) presented heights of 3.55 ± 0.13 cm, whereas the specimens from PSA reached 4.49 ± 1.32 cm (Fig. 2b). Lastly, for the shell diameter, this tendency is repeated with 2.37 ± 0.11 cm in MB (north) and with 3.14 ± 0.14 cm in PSA (south) (Fig. 2c).

Pearson correlation coefficient shows a positive and significant correlation (t= 7.2582, *d.f*= 224, $p < 0.0001$) between the total weight (g) in *T. atra* individuals and latitude (Fig. 3a). To the same degree, this tendency is repeated on the height (geometric mean) with a positive and significant (t= 6.6805, *d.f*= 224, $p < 0.0001$) slope north southward (Fig. 3b). The analysis of variance shows significant differences in the total weight (ANOVA, *d.f*= 5, F= 25.93, $p < 0.0001$) and geometric mean of the height (ANOVA, *d.f*= 5, F= 28.81, $p < 0.0001$), in all six sampling sites. The subsequent HSD-Tukey test for the total weight (g) variable identified that the PSA

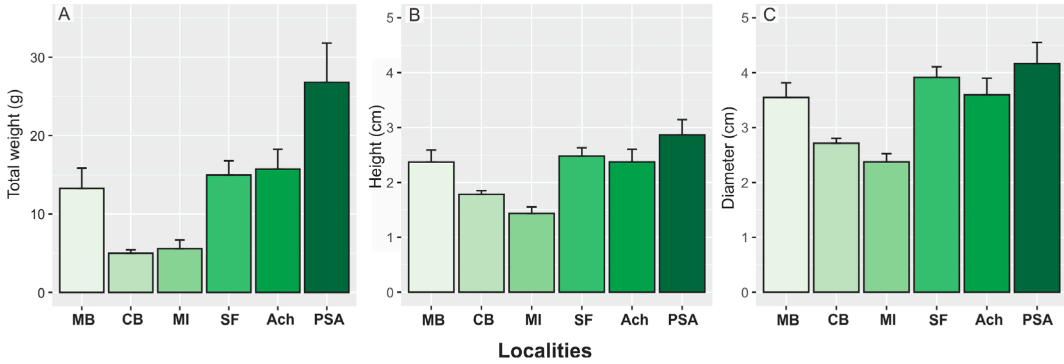

Fig. 2. Variation in body size (± CI) of *T. atra* populations in southern Chile. A) Total weight (g), B) height (cm) and C) diameter (cm). The localities are arranged from north to south. Metri Bay (**MB**) and Calbuco (**CB**), and Magellan region; Mornington Island (**MI**), Fuente Sound (**FS**), Andrés Channel (**ACh**) and Punta Santa Ana (**PSA**).

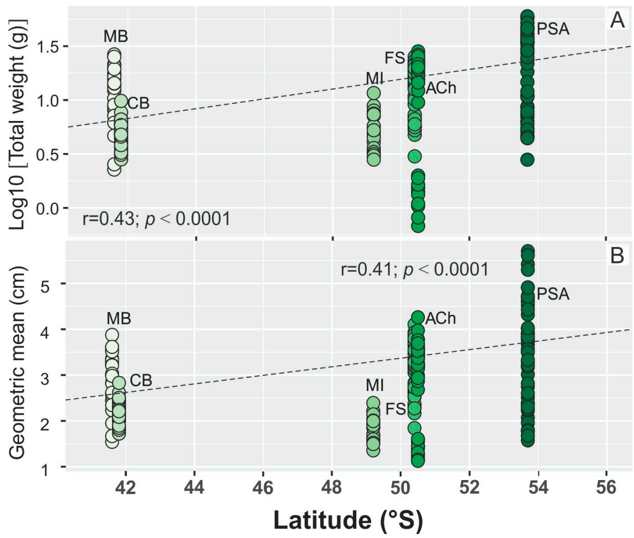

Fig. 3 Latitudinal variation in body size of T. atra in southern Chile. A) Log10 total weight (g), B) geometric mean as a measure of waist (length - height). Metri Bay (MB) and Calbuco (CB), and Magellan region; Mornington Island (MI), Fuente sound (FS), Andres channel (Ach) and Punta Santa Ana (PSA)..

Table 2. Results of Tukey's HSD post hoc test for Log_{10} total weight (g) and Geometric mean (cm) from *T. atra* between localities in the Los Lagos and Magellan regions. Significant *p-values* are in bold.

Localities	code	Log_{10} total weight (g) *p- value*	Geometric mean (cm) *p- value*
MB	CB	<**0.0001**	**0.0016**
	MI	**0.0044**	<**0.0001**
	FS	0.9392	0.8348
	ACh	0.9997	0.9998
	PSA	**0.0002**	<**0.0001**
CB	MI	0.9993	0.4499
	FS	<**0.0001**	<**0.0001**
	ACh	<**0.0001**	<**0.0001**
	PSA	<**0.0001**	<**0.0001**
MI	FS	<**0.0001**	<**0.0001**
	ACh	**0.0013**	<**0.0001**
	PSA	<**0.0001**	<**0.0001**
FS	ACh	0.8203	0.7823
	PSA	**0.0009**	**0.0005**
ACh	PSA	<**0.0001**	<**0.0001**

Table 3. Values the R squared and *p- values* for an ordinary linear regression for every dependent variable against latitude, significant *p- values* are in bold (n= 226).

	R^2	*p-value*
Log_{10} total weight (g)	0.1455	<**0.0001**
Geometric mean	0.1372	**0.0023**

Table 4. Values of slope and *p-value* for quantile regressions for every dependent variable compared to latitude, significant *p- values* are in bold (n= 236).

	Quantile			
Variables	10%	50%	85%	90%
Logarithm of biomass	0.0009	0.0526	0.0352	0.0329
p-value	(0.9275)	(**<0.0001**)	(**<0.0001**)	(**<0.0001**)
Geometric mean	0.0232	0.1013	0.0836	0.0981
p-value	(0.2126)	(**<0.0001**)	(**<0.0001**)	(**<0.0001**)

population scores the biggest differences, in relation to the populations in northern study areas (MB and CB, $p < 0.0001$), and even with the other *T. atra* southern populations ($p < 0.0001$) (Table 2). Regarding the geometric mean as an integration measure of the length and height of the shell, it can be stated that the PSA population remains as the one that contributed in a larger proportion to the differences in respect of the northern populations (MB, $p < 0.0001$; CB, $p < 0.0001$), and among the rest of the southern populations (MI, $p < 0.0001$; FS, $p = 0.0005$; ACh, $p =$ $p < 0.0001$) (Table 2). Furthermore, it is observed that populations from MI, FS and ACh as a set, statistically differ from both northern populations of the study area ($p < 0.0001$). Furthermore, it is observed that populations from FS and ACh, statistically differ from the population of CB ($p < 0.0001$ and $p < 0.0001$ respectively), but not with the population of MB ($p > 0.05$) (Table 2).

Quantile regression analysis

The quantile regression shows the existence of a significant and positive relationship in both of analysed variables (Log_{10} weight and geometric mean) and the latitude. For all linear regressions, both the slope and the R^2 value were significant. From these, the weight (g) is the variable that shows the highest R^2 value (0.1455, Table 3). The quantile regression of this variable shows high and significant slope values in high, and significant quantile values for slopes in the 50%, 85% and 90% quantile, where each of them is greater than 1. The same happens to the simple linear regression slope (Table 4, Fig. 4a).

All quantile regressions have positive and significant slopes in 50%, 85% and 90% quantile, and non-significant in 10% quantile ($p > 0.0001$). Moreover, it is observed that the slope grows along the quantile, which means that the largest organisms (presumably the adults) in each latitude show greater differences than those with medium size, and that the smallest organisms do not have any difference in height (Table 4, Fig. 4b). This would determine that differences in size are given by differences in growth rate rather than by the initial size.

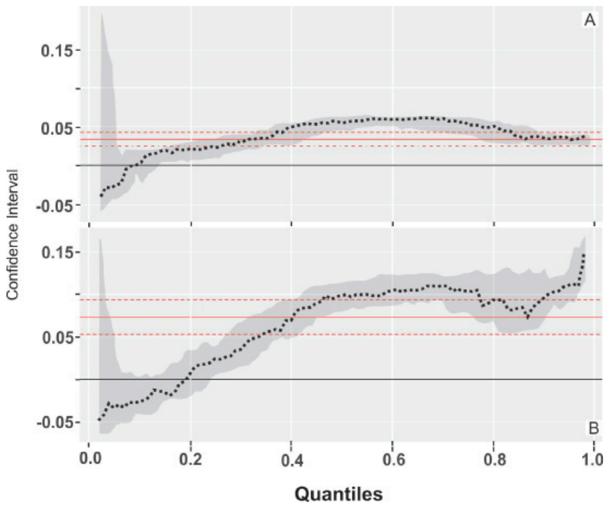

Fig. 4. Graphs showing in the black line and grey shadow the estimation of the slope and its respective confidence interval for every percentile in a quantile regression, and in red the slope and confidence interval for a linear regression with latitude as independent variable and **A)** Log_{10} total weight and **B)** Geometric mean as a measure of waist (length - height).

DISCUSSION

This investigation is the first study made on the body size variation of molluscs from Southeast Pacific shallow waters. On this respect, the comparative analysis using data from shallow sea is important to acquire a better understanding of the processes that controls the body size distribution of ocean species (Roy, 2002). The results present an increase in height and weight along with a latitudinal increase. Nonetheless, even when the increment was considerable, there was no important relationship between the southern Otway Sound and the other three northern areas of study (MB, CB and MI). The study of intermediate areas, particularly in Aysen region -located between 45° ~ 48°S- would clarify the correlation between body size and latitude, two important components when describing the distribution of the species' life history (Olabarria & Thurston, 2003; Roy & Martien, 2001).

Lately, research concerning phenotypical variation in relation to latitude in a large spatial scale has been strongly biased to land ecosystems (*e.g.*, Reaka, 1980; Roy & Martien, 2001). Studies carried out in terrestrial invertebrates (*e.g.*, butterflies), indicate that there is no relevant relationship between body size and latitude (Hawkins & Lawton, 1995; Miller, 1991), the same has been observed in marine invertebrates (*e.g.*, bivalve, Roy & Martien, 2001). Nevertheless, other studies have shown a body size increase with latitude, particularly in marine gastropods (Frank, 1975; Olabarria & Thurston, 2003). Moreover, body size increment with latitude has been also demonstrated in terrestrial invertebrates, such as flies and nematodes (James *et al.* 1995; Van Voorhies, 1996). On the other hand, in this study area it was evaluated how the geometric morphology of muricid molluscs such as *Acanthina monodon* varies with its latitudinal distribution; then, this variation is an answer to the marked genetic diversity of the populations (Sánchez *et al.* 2011), pattern that might be valid to *T. atra*, as well.

Some factors that might explain the gradients of corporal size in invertebrates are centred on the temperature effects over body size and cell number, or on mortality patterns (*e.g.*, Van Voorhies, 1996; Spicer & Gaston, 1999), along with the dispersal ability of the species (Frank

1975). In that regard, in bivalves with planktotrophic larvae it seems that environmental barriers are important components in the latitudinal distribution of body size (Roy & Martien, 2001). Notwithstanding, there is no evidence that demonstrate if geographic environmental barriers may hold any importance to determine the latitudinal patterns in the gastropods body size (Olabarria & Thurston, 2003). Species lacking larval dispersal mechanisms can be more vulnerable to body size variations than species with a long pelagic larval stage. This was registered for the buccinidae *Troschelia berniciensis*, which is a species with direct development (Olabarria & Thurston, 2003). However, coastal species with planktonic larvae as *Tegula funebralis,* have shown a significant increase in their height, together with latitude (Frank, 1975).

Sea snails from the *Tegula* genus present a slow, sporadic growth (Peppard, 1964). Thus, *T. atra* would not successfully grow in the south were it not for its longevity, which allows it to reach a bigger size. On the contrary, in the northernmost area, the growth rate is high enough as to ensure an appropriate reproduction and to maintain abundant populations with smaller specimens. The same observation was indicated for *T. funebralis* in the northern hemisphere (Frank, 1975), which double its own size in a 36.5 to 48.8°N gradient.

There are different factors that would affect *T. atra* body size, including temperature, predation, population density bounded to food supply, and rate of juvenile recruitment. The measurement of each of these factors is essential to infer which has or have a greater influence over the specie body size.

In relation to temperature, it has been described that intertidal environment present higher variations. These variations directly affect the physiological behaviour of organisms. Investigations from several *Tegula* species suggest an adaptive differentiation to diverse temperatures, which is observed in the differences in protein synthesis (Somero, 2002), demonstrating the genus acclimatisation to diverse distribution ranges (Salas *et al.* 2014; Tomanek, 2002). Furthermore, other studies in Antarctic species from the Trochidae family- specifically *Margarella antarctica*- reveal a positive correlation with latitude; variable that is also related with fertility and food availability (Linse *et al.* 2006). The condition latter described is reproduced by *T. atra* in the Subantarctic eco-region, taking into account the wide environmental variability of the area.

Another factor that could be conditioning body size differences in *T. atra* in southernmost Chile (in relation to the populations located in 42°S) is the low predatory incidence found in the south, particularly by organisms identified as predators of this species. For example, the starfish *Stichaster striathus* has been proclaimed as an important predator of macro-invertebrate's communities, especially of those which are associated to *Lessonia* holdfasts (Vásquez, 1993), as in the case of the *T. atra*; however, this predator species has not been observed in southernmost Chile. Conversely, those starfish found in Subantarctic waters, such as *Cosmasterias lurida*- which includes 25 invertebrate species in its diet (Ríos & Mutschke, 2009) do not interact directly with *T. atra* populations, and it is a minor specie in its diet (Garrido, 2012). Besides, some studies carried out in the Atlantic Patagonian coastline indicate that the main dietary items of the *C. lurida* are composed by several species of Mytilidae (Zaixso, 2004), organisms that are largely found in the *T. atra* range of distribution in southern Chile.

Considering the dietary habits of *T. atra*, the main food resource is brown algae, especially from the order Laminariales (González *et al.* 2012; Vásquez & Buschmann, 1997; Vásquez *et al.* 1998; Veliz & Vásquez, 2000; Villegas *et al.* 2008). It is important to highlight that these macroalgae species present a distinctive seasonality in Los Lagos region (Buschmann *et al.* 2004), with a strong decrease of biomass in wintertime (*e.g.*, 100% adult mortality of *Macrocystis pyrifera*), which would be restricting the supply of food for invertebrate herbivores. This situation forces them to utilize their energetic resources during those periods of low algae abundance, which would affect their physical condition. This seasonal nature of the kelp forests does not occur in southernmost Chile (*i.e.*, Magellan region), where the populations have annual stability (Palacios, 2012).

In many species of marine gastropods, there have been described strong morphological variations throughout an environmental gradient (Sepúlveda *et al.* 2012), a situation that could be reflected in the large environmental heterogeneity of the PCFS, producing isolation and a morphological differentiation among the populations (Lee & Boulding, 2009). Similarly, it would affect the body size variation of *T. atra*, as a recruitment determinant, and contributing new individuals to the population. Also, it has already been reported a differentiation in the reproductive strategies of some gastropods throughout a latitudinal gradient. For instance, in southern Chile, it has been observed a change in *Creppipatella dilatata* larval development, recognizing an indirect development cycle and a second alternative of direct development, presenting nurturing eggs and less, but bigger juveniles (Gallardo, 1977). This pattern would be replicated by *T. atra,* and thus explaining the body size differences exhibited between the populations from southernmost regions and those from MB and CB (*i.e.*, Los Lagos region).

Finally, it is important to evaluate intermediate areas, and the interaction with other abiotic factors (*e.g.*, depth), which may elucidate even more this pattern of body size variation in populations of *T. atra* distributed throughout Southern Chile.

REFERENCES

Aldea, C. & Valdovinos, C. (2005). Rockyshore mollusks of the South-Central Chile (36° - 38°S): Taxonomy and key of identification. *Gayana*, *69*(2), 364-396. http://dx.doi.org/10.4067/S0717-65382005000200014

Avise, J.C. (1992). Molecular population structure and the biogeographic history of a regional fauna: a case study with lessons from conservation biology. *Oikos*, *63*, 62-76. https://doi.org/10.2307/3545516

Avise, J.C., Reeb, C.A. & Saunders, N.C. (1987). Geographic population structure and species differences in mitochondrial DNA of mouthbrooding marine catfishes (Ariidae) and demersal spawning toadfishes (Battrachoididae). *Evolution*, *41*, 991-1002.

Blackburn, T.M., Gaston, K.J. & Loder, N. (1999). Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions*, *5*, 165-174. https://doi.org/10.1046/j.1472-4642.1999.00046.x

Blackburn, T.M. & Gaston K.J. (1996). Spatial patterns in the body size of bird species in the New World. *Oikos 77*, 436-446. https://doi.org/10.2307/3545933

Buschmann, A., Vásquez, J., Osorio, P., Reyes, E., Filun, L., Hernández-González, M. & Vega, A. (2004). The effect of water movement, temperature and salinity on abundance and reproductive patterns of *Macrocystis* spp. (Phaeophyta) at different latitud in Chile. *Marine Biology, 145*, 849-862. https://doi.org/10.1007/s00227-004-1393-8

Cade, B.S. & Noon, B.R. (2003). A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment 1*, 412-420. https://doi.org/10.1890/1540-9295(2003)001[0412:AGITQR]2.0.CO;2

Cade, B.S. & Richards, J.D. (2001). User manual for Blossom statistical software. Midcontinental Ecological Science Center. U.S. Geological Survey. Fort Collins 124pp.

Carcelles, A. & Williamson, S. (1951). Catálogo de los moluscos marinos de la provincia Magallánica. *Revista del Instituto Nacional de Investigación y Ciencias Naturales. Buenos Aires (Argentina)*, *2*, 225-383.

Core Team R. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org

Da Rocha, R.F. & Silva, R. (2011). Biogeography and connectivity between western South American and Antarctic marine molluscs. *Oecologia Australis*, *15(1)*, 111-123. https://doi.org/10.4257/oeco.2011.1501.09

Dawson, M.N. (2001). Phylogeography in coastal marine animals: a solution from California? *Journal of Biogeography*, *28*, 723-736. https://doi.org/10.1046/j.1365-2699.2001.00572.x

Defeo, O. & Cardoso, R.S. (2002). Macroecology of population dynamics and life history traits of the mole crab *Emerita brasiliensis* in Atlantic sandy beaches of South America. *Marine Ecology Progress Series*, *239,* 169-179. https://doi.org/10.3354/meps239169

Domínguez-Petit, R., García-Fernández, C., Leonarduzzi, E., Rodrigues, K. & Macchi, G.J. (2022). Parental Effects and Reproductive Potential of Fish and Marine Invertebrates: Cross-Generational Impact of Environmental Experiences. *Fishes 7 (4)*, 188. https://doi.org/10.3390/fishes7040188

Frank, P.W. (1975). Latitudinal variation in life history features of the black turban snail *Tegula funebralis* (Prosobranchia: Trochidae). *Marine Biology*, *27,* 219-223. https://doi.org/10.1007/BF00391630

Gallardo, C.S. (1977). Two modes of development in the morphospecies *Crepidula dilatata* (Gastropoda: Calyptraeidae) from southern Chile. *Marine Biology*, *39,* 241-251. https://doi.org/10.1007/BF00390998

Garrido, I.A. (2012). *Ecología trófica del asteroideo* ***Cosmasterias lurida*** (Phillips, 1858) en el seno del Reloncaví (Sur de Chile): distribución, abundancia, alimentación y movimiento. Tesis de Grado de Biología Marina, Universidad Austral de Chile, Valdivia. 86 pp.

González, A.V., Beltran, J., Hiriart-Bertrand, L., Flores, V., de Reviers, B., Correa, J.A. & Santelices, B. (2012). Identification of cryptic species in the *Lessonia nigrescens* complex (Phaeophyceae, Laminariales). *Journal of Phycology*, *58,* 1153-1165. https://doi.org/10.1111/j.1529-8817.2012.01200.x

Häussermann, V. & Försterra, G. (2010). *Fauna Marina Bentónica de la Patagonia Chilena Guía de identificación ilustrada*. 1ª Edición.

Hawkins, B.A & Lawton, J.H. (1995). Latitudinal gradients in butterfly body sizes: is there a general pattern? *Oecologia*, *102,* 31-36. https://doi.org/10.1007/BF00333307

Jackson, J.B., Jung, C.P. & Fortunato, H. (1996). Paciphilia revisited: transisthmian evolution of the Strombina group. In: Jackson J. B. C., Budd A. F., Coates A. G. (Eds.) Evolution and environment in tropical America, University of Chicago Press, Chicago 234-270.

James, A.C., Azevedo, B.R. & Partridge, L. (1995). Cellular basis and developmental timing in a size cline of *Drosophila melanogaster*. *Genetics*, *140,* 659-666. https://doi.org/10.1093/genetics/140.2.659

Koenker, R. & Machado, J.A. (1999). Goodness of fit and related inference processes for quantile regression. *Journal of the American Statistical Association*, *94,* 1296-1310. https://doi.org/10.2307/2669943

Laptikhovsky, V. (2006). Latitudinal and bathymetric trends in egg size variation: a new look at Thorson's and Rass's rules. *Marine Ecology*, *27,* 7-14. https://doi.org/10.1111/j.1439-0485.2006.00077.x

Lardies, M.A. & Castilla, J.C. (2001). Latitudinal variation in the reproductive biology of the commensal crab *Pinnaxodes chilensis* (Decapoda: Pinnotheridae) along the Chilean coast. *Marine Biology*, 139, 1125-1133. https://doi.org/10.1007/s002270100661

Lee, H.J. & Boulding, E.G. (2009). *Spatial and temporal population genetic structure of four northeastern Pacific littorinid gastropods: the effect of mode of larval development on variation at one mitochondrial and two nuclear DNA markers. Molecular Ecology, 18,* 2165-2184. https://doi.org/10.1111/j.1365-294X.2009.04169.x

Linse, K. (1999). Mollusca of the Magellan region. A checklist of the species and their distribution. In: Magellan-Antarctic: Ecosystems that drifted apart. Arntz W. E. and Ríos C. (Eds.). *Scientia Marina*, *63* (Supl. 1), 399-407. https://doi.org/10.3989/scimar.1999.63s1399

Linse, K., Barnes, D.K.A. & Enderlein, P. (2006). Body size and growth of benthic invertebrates along an Antarctic latitudinal gradient. *Deep-Sea Research II*, *53,* 921-931. https://doi.org/10.1016/j.dsr2.2006.03.006

Lonsdale, D.J. & Levinton, J.S. (1985). Latitudinal differentiation in copepod growth: an adaptation to temperature. *Ecology*, *66,* 1397-1407. https://doi.org/10.2307/1938002

Marquet, P.A., Navarrete, S.A. & Castilla, J.C. (1990). *Scaling population density to body size in rocky intertidal communities. Science 250,* 1125-1127. https://doi.org/10.1126/science.250.4984.1125

Marquet, P.A., Quiñones, R.A., Abades, S., Labra, F., Tognelli, M., Arim, M. & Rivadeneira, M. (2005). Scaling and power-laws in ecological systems. *The Journal of Experimental Biology*, *208,* 1749-1769. https://doi.org/10.1242/jeb.01588

Marshall, D.J. & Keough, M. (2007). The Evolutionary Ecology of Offspring Size in Marine Invertebrates Advances. *Marine Biology*, *53,* 1-60. https://doi.org/10.1016/S0065-2881(07)53001-4

McClain, C.R. & Rex, M.A. (2001). The relationship between dissolved oxygen concentration and maximum size in deep-sea turrid gastropods: an application of quantile regression. *Marine Biology*, 139: 681-685. https://doi.org/10.1007/s002270100617

McQueen, A., Klaassen, M., Tattersall, G.J., Atkinson, R., Jessop, R., Hassell, C.J., Christie, M., Victorian Wader Study Group, Australasian Wader Studies Group, Symonds, M.R.E., (2022). *Thermal adaptation best explains Bergmann's and Allen's Rules across ecologically diverse shorebirds. Nature Communications*, *13,* 4727. https://doi.org/10.1038/s41467-022-32108-3

Miller, W.E. (1991). Body size in North American Lepidoptera as related to geography. *Journal of the Lepidopterists Society*, *45,* 158-168.

Monaco, C.J., Brokordt, K.B. & Gaymer, C.F. (2010). Latitudinal thermal gradient effect on the cost of living of the intertidal porcelain crab *Petrolisthes granulosus*. *Aquatic Biology*, 9: 23-33. https://doi.org/10.3354/ab00223

Montiel, A. & Rozbaczylo, N. (2009). Poliquetos. In: V. Häussermann & G. Försterra (Eds.) *Fauna Marina Bentónica de la Patagonia. Nature in Focus*, Santiago, Chile. pp 543-581.

Montiel, A., Quiroga, E. & Gerdes, D. (2011). Diversity and spatial distribution patterns of polychaete assemblages in the Paso Ancho, Straits of Magellan Chile. *Continental Shelf Research*, *31,* 304-314. https://doi.org/10.1016/j.csr.2010.11.010

Olabarria, C. & Thurston, M.H. (2003). Latitudinal and bathymetric trends in body size of the deep-sea gastropod *Troschelia berniciensis* (King). *Marine Biology*, *143,* 723-730. https://doi.org/10.1007/s00227-003-1116-6

Olalla-Tárraga, M.A., Rodríguez, M.A. & Hawkins, B.A. (2006). *Broad-scale patterns of body size in squamate reptiles of Europe and North America.* ***Journal of Biogeography*** *33,* 781-793. https://doi.org/10.1111/j.1365-2699.2006.01435.x

Olson, V.A., Davies, R.G., Orme, C.D.L., Thomas, G.H., Meiri, S., Blackburn, T.M., Gastón, K.J., Owens, I.P.F. & Bennett, P.M. (2009). *Global biogeography and ecology of body size in birds. Ecology Letters, 12:* 249-259. https://doi.org/10.1111/j.1461-0248.2009.01281.x.

Palacios, M. (2012). Algae. In: Aldea, C. (Eds.), *A Biodiversity guide representing the seabeds of Magallanes*. Ediciones Fundación CEQUA.

Peppard, M.C. (1964). Shell Growth and repair in the Gastropod *Tegula funebralis*. *The Veliger 6* (Suppl.): 59-63.

Peters, R.H. (1983). *The ecological implications of body size.* Cambridge University Press.

Reaka, M.L. (1980). *Geographic range, life history patterns, and body size in a guild of coral-dwelling mantis shrimps. Evolution 34,* 1019-1030.

Reid, D. & Osorio, C. (2000). The shallow-water marine Mollusca of the Estero Elefantes and Laguna San Rafael, southern Chile. *Bull. Natural History Museum*, London. (Zool.) *66 (2)*, 109-146.

Rex, M.A., Etter, R.J., Clain, A.J. & Hill, M.S. (1999). *Bathymetric patterns of body size in deep-sea gastropods.* ***Evolution*** *53,* 1298-1301. https://doi.org/10.2307/2640833

Ríos, C. & Mutschke, E. (2009). Contribution to the knowledge of *Macrocystis pyrifera*: bibliographic review of the kelp forests distributed in the Magellan region. *Anales del Instituto de la Patagonia*, *37(1),* 97-102. http://dx.doi.org/10.4067/S0718-686X2009000100009

Rodríguez, M.A., Olalla-Tárraga, M.A. & Hawkins, B.A. (2008). Bergmann's rule and the geography of mammal body size in the Western Hemisphere. *Global Ecology and Biogeography*, *17,* 274-283. https://doi.org/10.1111/j.1466-8238.2007.00363.x

Roy, K. & Martien, K.K. (2001). Latitudinal distribution of body size in north-eastern Pacific marine bivalves. *Journal of Biogeography*, *28,* 485-493. https://doi.org/10.1046/j.1365-2699.2001.00561.x

Roy, K. (2002). Bathymetry and body size in marine gastropods: a shallow water perspective. *Marine Ecology Progress Series*, *237,* 143-149. https://doi.org/10.3354/meps237143

Sánchez, R., Sepúlveda, R.D., Brante, A. & Cárdenas, L. (2011). Spatial pattern of genetic and morphological diversity in the direct developer *Acanthina monodon* (Gastropoda: Mollusca). *Marine Ecology Progress Series* *434,* 121-131. https://doi.org/10.3354/meps09184

Salas, A., Díaz, F., Denisse-Re, A., Galindo-Sánchez, C.E., Sánchez-Castrejon, E., González, M., Licea, A., Sanchez-Zamora, A. & Rosas, C. (2014). Preferred Temperature, Thermal Tolerance, and Metabolic response of *Tegula regina* (Stearns, 1892). *Journal of Shellfish Research*, *33 (1),* 239-246. https://doi.org/10.2983/035.033.0123

Scharf, F.S., Juanes, F. & Sutherland, M. (1998). Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. *Ecology* *79,* 448-460. https://doi.org/10.1890/0012-9658(1998)079[0448:IERFTE]2.0.CO;2

Sepúlveda, R., Jara, C.G. & Gallardo, C. (2012). Morphological analysis of two sympatric ecotypes and predator-induced phenotypic plasticity in *Acanthina Monodon* (Gastropoda: Muricidae). *Journal of Molluscan Studies*, 78: 173-178. https://doi.org/10.1093/mollus/eyr058

Silva, M. & Downing, J.A. (1995). CRC handbook of mammalian body masses. CRC Press. New York 359 pp.

Somero, G.N. (2002). Thermal Physiology and Vertical Zonation of Intertidal Animals: Optima, Limits, and Costs of Living. *Integrative and Comparative Biology*, *42,* 780-789.

Spalding, M., Fox, H., Allen, G., Davidson, N., Ferdaña, Z., Finlayson, M., Halpern, B., Jorge M., Lombana, A., Lourie, S., Martin, K., McManus, E., Molnar, J., Recchia, C.& Robertson, J. (2007). Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. *BioScience*, 57(7): 573-583. https://doi.org/10.1641/B570707

Spicer, J.I. & Gaston, K.J. (1999). Amphipod gigantism dictated by oxygen availability? *Ecology Letters*, *2,* 397-403. https://doi.org/10.1046/j.1461-0248.1999.00105.x

Stanley, S.M. (1986). Population size, extinction and speciation: the fission effect in Neogene Bivalvia. *Paleobiology* *12,* 89-110.

Thorson, G. (1936). The larval development, growth and metabolism of arctic marine bottom invertebrates compared with those of other seas. *Meddelelser om Grø nland*, *100,* 1-55.

Tomanek, L. (2002). The Heat-Shock Response: Its Variation, Regulation and Ecological Importance in Intertidal Gastropods (genus *Tegula*). *Integrative and Comparative Biology*, *42,* 797-807. https://doi.org/10.1093/icb/42.4.797

Van Voorhies, W.A. (1996). Bergmann size clines: a simple explanation for their occurrence in ectotherms. *Evolution*, *50,* 1259-1264.

Vásquez, J.A., Camus, P. & Ojeda, F. (1998). Diversity, structure and functioning of rocky coastal ecosystems in northern Chile. *Revista Chilena de Historia Natural* *71,* 479-499.

Vásquez, J.A. & Buschmann, A. (1997). Herbivore-kelp interactions in Chilean subtidal communities: a review. *Revista Chilena de Historia Natural*, *70,* 41-52.

Vásquez, J.A. (1993). Patrones de distribución de poblaciones submareales de *Lessonia trabeculata* en el norte de Chile. Facultad de Ciencias del Mar. Universidad Católica del Norte. Coquimbo. Chile. *Serie Ocasional* *2,* 187-211.

Veliz, D. & Vásquez, J.A. (2000). The trochidae family (Mollusca: Gastropoda) in northern Chile: taxonomic and ecological considerations. *Revista Chilena de Historia Natural*, *73 (4),* 757-769. http://dx.doi.org/10.4067/S0716-078X2000000400018

Villegas, M.J., Laudien, J., Sielfeld, W. & Arntz, W.E. (2008). *Macrocystis integrifolia* and *Lessonia trabeculata* (Laminariales; Phaeophyceae) kelp habitat structures and associated macrobenthic community off northern Chile. *Helgoland Marine Research*, 62 (Suppl 1): 33-43. https://doi.org/10.1007/s10152-007-0096-1

Wares, J.P., Gaines, S.D. & Cunningham, C.W. (2001). A comparative study of asymmetric migration events across a marine biogeographic boundary. *Evolution*, *55,* 295-306.

West, G.B., Brown, J.H. & Enquist, B.J. (1997). A general model for the origin of allometric scaling laws in biology. *Science*, 276:122-126. https://doi.org/10.1126/science.276.5309.122

White, E.P., Ernest, S.K.M., Kerkoff, A.J. & Enquist, B.J. (2007). Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution*, *22 (6),* 323-330. https://doi.org/10.1016/j.tree.2007.03.007

Zaixso, H.E. (2004). Ribbed mussel *Aulacomya atra atra* (Molina) (Bivalvia: Mytilidae) beds of the San José Gulf (Chubut, Argentina): Diversity and relationships with related facies. *Revista de Biología Marina y Oceanografía*, 39 (2): 61-78. http://dx.doi.org/10.4067/S0718-19572004000200003.

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