Connecting pH with body size in the marine gastropod *Trophon geversianus* in a latitudinal gradient along the south-western Atlantic coast

MARIANO E. MALVÉ[1], SANDRA GORDILLO[2] AND MARCELO M. RIVADENEIRA[3]

[1]Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Av. Vélez Sársfield 299 X5000JJC Córdoba, Argentina, [2]Centro de Investigaciones en Ciencias de la Tierra (CICTERRA, CONICET-UNC), Av. Vélez Sársfield 1611 X5016GCA Córdoba, Argentina, [3]Laboratorio de Paleobiología, Centro de Estudios Avanzados en Zonas Áridas (CEAZA) & Universidad Católica del Norte, Av. Bernardo Ossandón 877, C.P. 1781681, Coquimbo, Chile

There is growing concern about the impact of contemporaneous ocean acidification on marine ecosystems, but strong evidence for predicting the consequences is still scant. We have used the gastropod Trophon geversianus *as a study model for exploring the importance of oceanographic variables (sea surface temperature, chlorophyll* a, *oxygen, calcite and pH) on large-scale latitudinal variation in mean shell length and relative shell weight. Data were collected from a survey carried out in 34 sites along ~1600 km. Neither shell length nor relative shell weight showed any monotonic latitudinal trend, and the patterns of spatial variability were rather complex. After correcting for spatial autocorrelation, only pH showed a significant correlation with mean shell length and relative shell weight, but contrary to expectations, the association was negative in both cases. We hypothesize that this could mirror the negative effect of acidification on growth rate, which may cause larger asymptotic size. Latitudinal trends of body size variation are not easy to generalize using ecogeographic rules, and may be the result of a complex interaction of environmental drivers and life-history responses.*

INTRODUCTION

The biological consequences of global warming are already affecting species physiology, distribution and phenology, and this will inevitably alter competitive and other interactions between species, which in turn will affect local abundance and geographic ranges (Hughes, 2000). During the 20th century, increasing $[CO_2]$atm has driven an increase in the global oceans' average temperature of $0.74°C$ and in acidity by 0.1 pH unit (Solomon, 2007). Ocean acidification (OA) is increasingly recognized as a major global problem and is rapidly changing the carbonate system of the world's oceans. Past mass extinction events have been linked to OA and the current rate of change in seawater chemistry is unprecedented (Beerling & Berner, 2002). The combustion of fossil fuels has enriched levels of CO_2 in the world's oceans and decreased ocean pH (Talmage & Gobler, 2010).

This altered seawater chemistry has been far more rapid than the Earth has previously experienced (Kurihara, 2008). The CO_2-driven OA leads to a decrease in the calcium carbonate ($CaCO_3$) saturation state of the ocean surface waters and has potentially negative impacts on marine taxa, particularly those that build skeletons, shells and biogenic calcium carbonate tests, commonly known as calcifiers (Guinotte & Fabry, 2008; Kurihara, 2008). Several analyses have used molluscs as a study model to understand the effects of ocean acidification (Narita *et al.*, 2012), yet these studies are still scant and results cannot be generalized. In this respect, OA may be inhibiting the development and survival of larval shellfish and contributing to global declines of some bivalve populations (Talmage & Gobler, 2010). In addition, several experiments have shown a decrease in growth, calcification, survival, development and abundance of organisms at decreased pH levels, in response to OA across a broad range of marine organisms (Gazeau *et al.*, 2010; Kroeker *et al.*, 2013).

Body size is probably the most studied trait in ecological and evolutionary literature, because it has profound consequences on the structure and function of natural systems (Schmidt-Nielsen, 1984). Studying spatial and temporal patterns of variation in body size is therefore crucial to understanding biotas on ecological and evolutionary timescales. Bergmann's rule is a classic conceptual framework for geographic variations in body size, and predicts that body size increases towards polar regions (Meiri, 2011). In a recent review of Bergmann's rule by Watt *et al.* (2010), an overview of 57 studies was carried out. Twenty of the 57 studies were on ectothermic organisms (vertebrates, invertebrates, protozoans

Corresponding author:
M.E. Malvé
Email: marianomalve@gmail.com

1

and plants) and only nine of these 20 corresponded to invertebrates, of which only one marine invertebrate, a snow crab from the northern hemisphere, was included. Of these nine studies, four followed Bergmann's rule and the other five did not. Indeed, Bergmann's rule remains poorly described for marine invertebrates (Berke *et al.*, 2013). Given that Bergmann's rule was originally proposed for endotherms, its use with ectotherms has been criticized; yet the name still prevails, either by inertia or tradition (Heinze *et al.*, 2003; Fisher *et al.*, 2010; Berke *et al.*, 2013). Here we use the term 'Bergmann's pattern' to refer to the existence of a latitudinal increase in body size towards higher latitudes, irrespective of the driving mechanisms.

As size and temperature increased, growth became increasingly constrained due to oxygen shortage in aquatic and water-saturated habitats (Atkinson, 1994). In this respect, high temperatures may impose constraints on growth that only arise later on during ontogeny; this simple and potentially general explanation is supported by the fact that thermal optima for growth efficiency and growth rate decrease as individuals grow (Angilletta & Dunham, 2003). Ultimately, higher temperatures result in faster growth to a smaller final size. In other words, most ectotherms mature at a larger size at lower developmental temperatures. This pattern of wide taxonomic prevalence has been coined the temperature-size rule.

Trophon geversianus (Pallas, 1774) is a common and widespread inhabitant of intertidal and shallow subtidal environments. On the south-west Atlantic coast this species is reported from 35°S to 56°S (including the Malvinas/Falkland Islands), while on the south-east Pacific coast it ranges from 42°S to 56°S (Griffin & Pastorino, 2005; Pastorino, 2005). This species is dioecious, with internal fertilization and intra-capsular embryonic development (Zaixso, 1973; Penchaszadeh, 1976). For this genus, planktonic larvae are not known (Pastorino, 2005), neither is there evidence of external sexual dimorphism, and the sex ratio is different from 1:1 (with a bias towards females) (Cumplido *et al.*, 2010). The shell size (up to 100 mm) is extremely variable, as can be appreciated from the large number of names proposed for the different morphological variants of this species (Pastorino, 2005). In Southern Chile, this carnivorous gastropod is also one of the commercially harvested benthic species because productivity is significantly correlated with body size (P/B ratio) (Andrade *et al.,* 2009).

Here, we used death assemblages (sets of dead, taxonomically identifiable organic remains that are encountered in still largely unburied form on landscapes and seafloors, Kidwell & Tomasovych, 2013) as a source of biological information whose most important feature is that they are time-averaged, temporally coarse accumulations in which non-contemporaneous individuals co-occur. The living assemblages can vary from year to year due to vagaries of recruitment and mortality, so the death assemblages provide a better record of the organisms that usually inhabit an environment. Therefore, molluscan death assemblages capture a strong signal of relative abundance of living species (Kidwell, 2002).

The aim of this study is to assess patterns and possible processes driving latitudinal variation of body size in the gastropod *Trophon geversianus*, and in particular to: (a) evaluate the existence of a poleward increase in body size and identify conformance to Bergmann's rule or the temperature-size rule and (b) determine the role of oceanographic variables as drivers of the latitudinal trends in body size.

MATERIALS AND METHODS

Study area

The Argentinean coast is an interesting case study given its extension towards polar latitudes and the presence of two different biogeographic provinces: the Argentine and the Magellanic. The different physiographic characteristics allow the distinction of movable sandy bottoms in the former, and gravel bottoms where large algae grow in the latter. Climatic differences explain the prevalence of northern winds in the Argentine province, where warm and temperate-cold coastal waters alternate, while in the Magellanic province there are strong westerly winds with a predominance of subantarctic waters from the Malvinas Current. These factors explain the faunal composition differences between provinces: the Argentine is characterized by the considerable heterogeneity of its components and the Magellanic by its homogeneity and endemic taxa (Balech & Ehrlich, 2008). The boundary between these provinces varies seasonally between 41°S and 43°S with the northward fluctuations of the cold Malvinas Current in the winter (Balech & Ehrlich, 2008). In this respect, the Patagonian coast provides an opportunity to collect and examine mollusc shell assemblages due to their relative abundance and high preservation potential (Gordillo *et al.*, 2014). Empty shells, mostly bivalves and gastropods, are found along the coast on the active beach and in adjacent deposits in marine terraces (Gordillo & Archuby, 2014).

Data collection and analyses

Biological data were obtained from field surveys in 34 beaches (Table 1) along the Argentinean coast between Buenos Aires (Los Pocitos) and Tierra del Fuego (Beagle Channel) (Figure 1), encompassing ∼1600 km. At each beach all the dead shells of *Trophon geversianus* deposited above the high tide sea level were collected. Unlike modern living assemblages, death shell assemblages are time averaged (i.e. they include specimens spanning from a few years to hundreds of years; Behrensmeyer *et al.*, 2009), which allows us to include multiple cohorts, thus increasing the robustness of body size estimates. Death shell assemblages potentially contain individuals at various ages including both immature and mature ones. Ideally, size should be compared among individuals at the same age. For that purpose extensive sclerochronological data would be required, which is far beyond the scope of this study.

Taphonomic processes such as fragmentation, dissolution, abrasion and bioerosion can affect shells' traits. However, most of the shells retain the usual ornamentation suggesting that abrasion and bioerosion were negligible. Other taphonomic attributes were taken into account and minimized when possible, such as fragmentation since only entire (unbroken) shells were used in the analyses. Shell length was measured along an axis passing through the apex to the bottom of the shell with a digital caliper (precision 0.01 mm) and shells were cleaned and weighed using a digital scale (precision 0.01 g). All analyses were performed on log-transformed data given the great spatial variability in the dataset.

For each site climatological information was compiled on five oceanographic variables that could potentially be related to body size: (a) sea surface temperature, (b) concentration

Table 1. Detail of the 34 study sites (N = 1348). A indicates Argentine province and M corresponds to the Magellanic province. The asterisk indicates the Transition Zone (41°S – 43°S) between the Argentine and Magellanic biogeographic provinces.

Site	Latitude (°S)	Longitude (°W)	Biogeographic province	Sample size	Mean shell length (mm)	Standard error (mm)
Los Pocitos	−40.43	−62.42	A	2	35.02	4.96
Punta Colorada	−40.84	−65.12	A	6	23.78	7.70
El Cóndor	−41.06	−62.84	A*	7	35.22	12.02
Caleta de los Loros	−41.05	−63.58	A*	120	44.54	8.75
Playas Doradas	−41.63	−65.02	A*	51	21.68	7.04
Puerto Lobos	−41.99	−65.07	A*	447	22.47	5.08
Puerto Pirámides	−42.35	−64.17	A*	50	19.41	4.37
El Doradillo	−42.66	−64.99	A*	1	38.74	0
Puerto Madryn	−42.78	−65.04	A*	89	18.14	6.11
Playa Unión	−43.31	−65.03	M	11	21.25	5.47
Playa Elola	−44.84	−65.73	M	37	31.25	10.40
Bahía Bustamante	−45.13	−66.54	M	31	33.48	5.76
Rada Tilly	−45.94	−67.56	M	40	32.12	9.17
Caleta Olivia	−46.49	−67.48	M	45	36.36	6.56
Cabo Blanco	−47.20	−65.74	M	7	28.38	4.31
Puerto Deseado	−47.76	−65.89	M	2	40.81	1.63
San Julián	−49.20	−67.45	M	1	39.54	0
Makenke	−49.33	−67.37	M	103	20.8	6.05
Monte León	−50.21	−68.52	M	16	34.82	5.80
Punta Loyola	−51.37	−69.01	M	26	22.23	3.28
Faro Vírgenes	−52.20	−68.21	M	15	36.79	13.33
Strait of Magellan 3	−52.32	−69.49	M	11	65.82	9.34
Strait of Magellan 2	−52.34	−69.49	M	9	32.85	14.23
Strait of Magellan 1	−52.34	−69.49	M	3	24.41	10.96
Strait of Magellan 5	−52.58	−70.15	M	7	30.81	10.02
Río Chico	−53.59	−67.98	M	17	29.18	7.99
Cabo Domingo	−53.69	−67.84	M	13	28.42	14.92
Río Grande	−53.80	−67.66	M	39	24.74	5.76
Punta María	−53.94	−67.50	M	14	27.21	5.04
Cabo Auricosta	−54.05	−67.31	M	70	32.44	7.34
Cabo San Pablo	−54.28	−66.71	M	24	37.79	5.89
Bahía Brown	−54.48	−68.14	M	3	60.33	7.65
Bahía Golondrina	−54.50	−68.21	M	30	49.07	8.66
Puerto Williams	−54.55	−67.37	M	1	61.1	0

of chlorophyll *a*, (c) concentration of oxygen, (d) concentration of calcite, (e) pH and (f) wave height. For variables a – e, information corresponds to long-term climatological annual means, and was obtained from rasters created by the BioOracle database (Tyberghein *et al.*, 2012, available at http://www.oracle.ugent.be/), with a resolution of 9.2 km. Wave height was included as a proxy of wave exposure along the study area, and data were obtained from the Hexacoral/LOICZ database (http://hercules.kgs.ku.edu/hexacoral/envirodata/hex_modfilt_firststep3dev1.cfm) at 0.5° grid cell resolution.

The relationship between different body size proxies and oceanographic variables was analysed. Two body size proxies were used: (a) mean shell length and (b) relative weight (cubic root of shell weight/shell length). These values were associated to oceanographic variables using a Pearson moment-product correlation. In order to reduce bias introduced by spatial autocorrelation, a frequent problem in ecological data affecting the significance rates of the statistical analyses (Dale & Fortin, 2009), P-values were corrected for spatial structure using Dutilleul's method. Analyses were carried out using SAM freeware application (Rangel *et al.*, 2010).

RESULTS

Oceanographic variables show differing latitudinal trends (Figure 2); sea surface temperature varied ∼2-fold, decreasing by around 7°C along the latitudinal gradient. The concentration of oxygen increased towards higher latitudes, particularly around the Tierra del Fuego archipelago (52° – 54°S). Both chlorophyll *a* and calcite concentration were much more variable, with lower values observed around mid-latitudes and increasing towards the north and south. In contrast, pH showed a hump-shaped latitudinal pattern with maximum values found around 46°S, declining towards the Buenos Aires and Tierra del Fuego provinces. On the other hand, wave height increased towards higher latitudes.

The body size of *Trophon geversianus* did not show any monotonic latitudinal trends (Figure 3, Table 2), and had a rather complex spatial pattern, with higher values around southern Buenos Aires (41°S), Peninsula de Valdés (47°S) and Tierra del Fuego (54°S) (Figure 3). Despite the lack of latitudinal trends, body size showed strong spatial variation. Mean shell length showed a 3-fold difference between the smallest and largest sites, while for relative weight this difference was 10-fold.
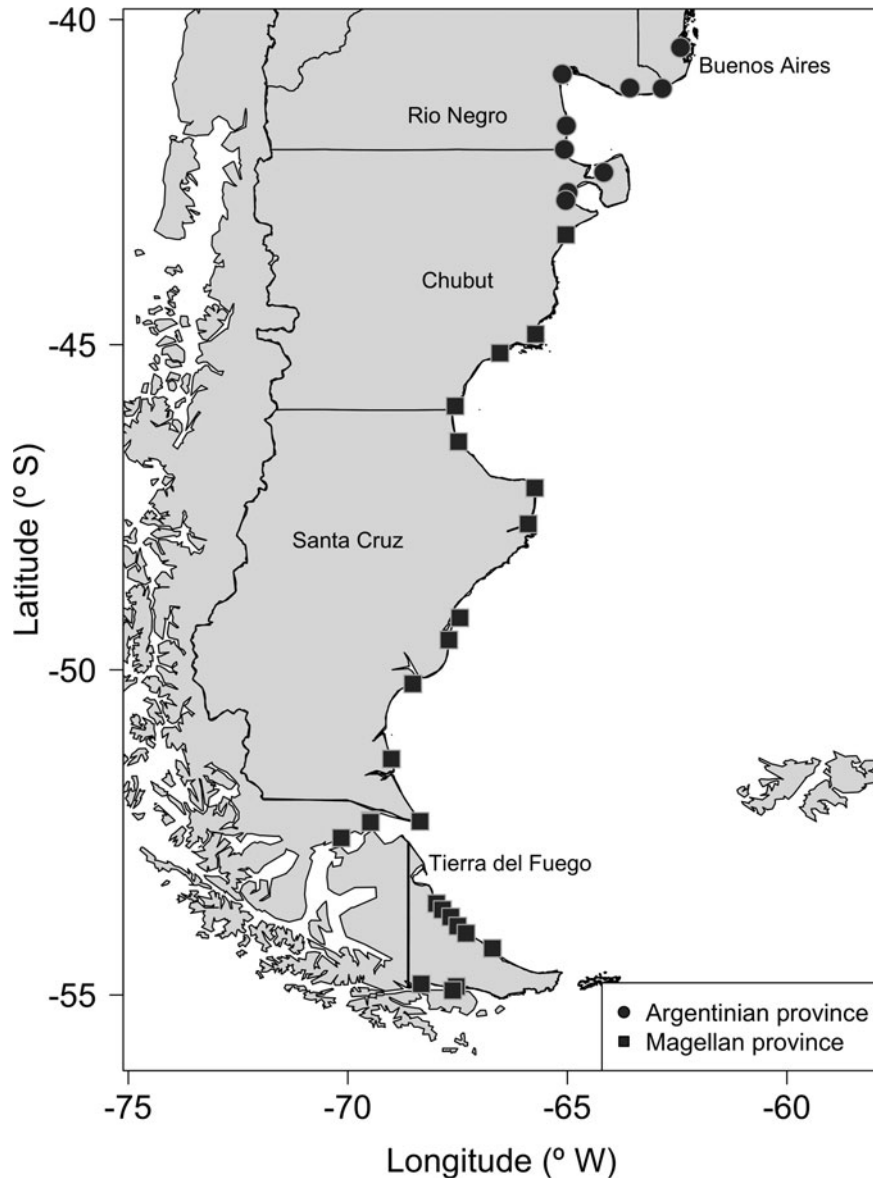
**Fig. 1.** Map of the study region, showing the sampled sites.

No oceanographic variables, except pH, were correlated to any proxy for body size (Table 2). In the case of pH, this was negatively and significantly correlated to mean shell length ($r = -0.38$, $P = 0.046$) and relative shell weight ($r = -0.50$, $P = 0.015$) (Table 2 and Figure 3). The negative relationship remained significant even without correcting for spatial auto-correlation in both cases (Table 2). Because the number of shells was very variable among beaches (Table 1), analyses were re-ran using only sites with N > 20 shells, in order to account for possible bias in sampling effort. The trends remained unchanged (data not shown).

DISCUSSION

The analysis of a high number of shells (>1000) from several locations (>30) encompassing 14 degrees of latitude covering two distinct biogeographic regions showed no support for the existence of an increase towards higher latitudes, and no

association with sea surface temperature, as expected by Bergmann's rule and the temperature-size rule. In contrast, the spatial variability in body size can be linked to a variation in ocean pH. However, the body size of *Trophon geversianus* shows high spatial variability throughout the study area. Extremely large individuals were collected at three sites (outliers, see Figure 3A) in high latitudes corresponding to the Magellan Region and Beagle Channel. These areas are unlike the other sites along the Atlantic coast because of the limited exchange of waters with the Atlantic Ocean resulting in different environmental conditions, and its recent geological history strongly influenced by glaciations (Gordillo *et al.*, 2005).

Studies aimed at evaluating the existence of Bergmann's rule in marine molluscs are rather scant (e.g. Frank, 1975; Cardoso *et al.*, 2006; Linse *et al.*, 2006; Lee & Boulding, 2010; Watson *et al.*, 2012; Briones *et al.*, 2014). At intraspecific level, there is no consensus about the latitudinal trend followed by the body size of mollusc species, and either positive (Frank, 1975; Lee & Boulding, 2010), negative (Watson *et al.*,
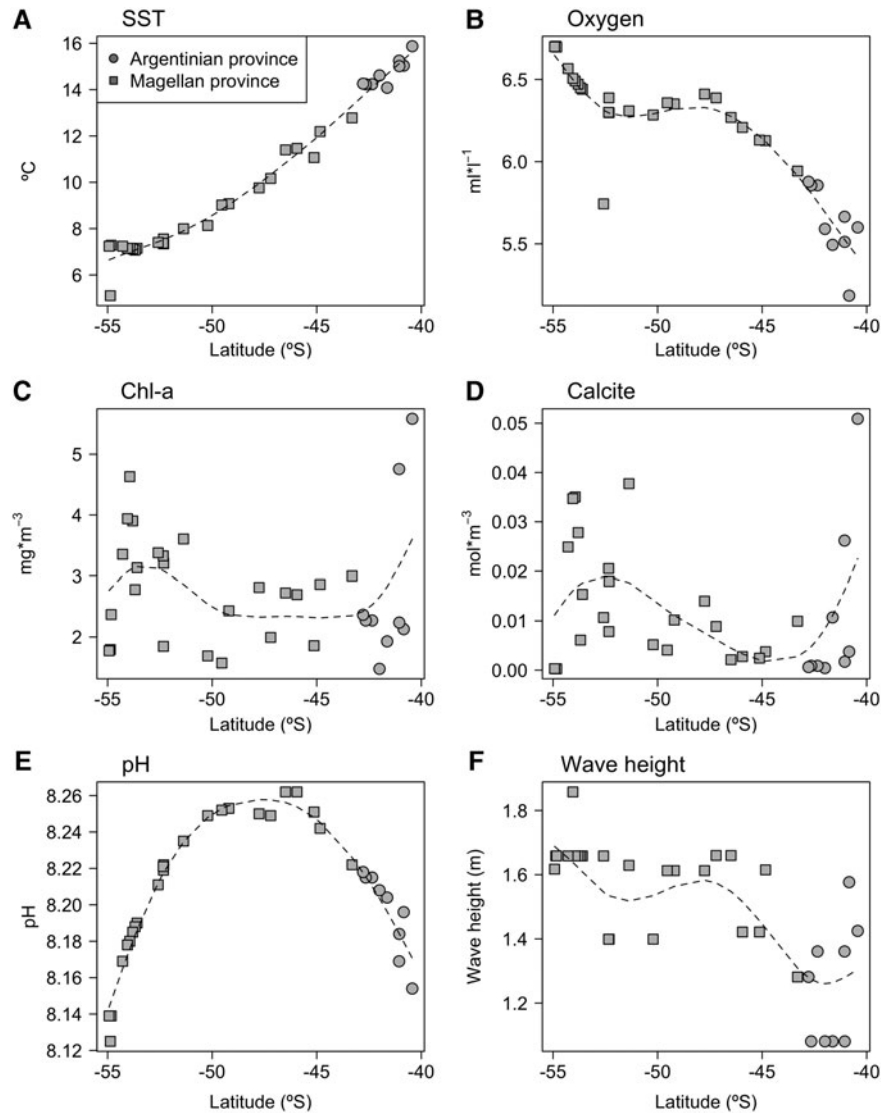
Fig. 2. Latitudinal variation of oceanographic variables. (A) Sea surface temperature; (B) Oxygen concentration; (C) Chlorophyll *a* concentration; (D) Calcite concentration; (E) pH; (F) Wave height. The dotted line corresponds to a lowess smoothing line.

2012) or no correlation (Linse *et al.*, 2006; Briones *et al.*, 2014) have been reported. A recent analysis carried out at interspecific level showed no support for Bergmann's rule across 59 bivalve families and 4845 species (Berke *et al.*, 2013). Similarly, Cardoso *et al.* (2006) found a weak trend for increasing shell length in bivalves at higher latitudes. Given this evidence, and despite the slight poleward increase in mean shell length, our results showed no support of the existence of Bergmann's rule in *T. geversianus*.

Empirical evidence shows that the relationship between body size and sea temperature is also extremely variable among species (Frank, 1975; Linse *et al.*, 2006; Watson *et al.*, 2012; Briones *et al.*, 2014). Hence, contrary to ecophysiological experiments which show a clear relationship between body size and rearing temperature in ectotherms and thus support the temperature-size rule (Atkinson, 1994; Irie *et al.*, 2013), our study shows no significant effect of sea surface temperature on the body size of *T. geversianus*.

Furthermore, other oceanographic variables may help explain large-scale patterns of invertebrate body size, for

example oxygen concentration (Chapelle & Peck, 1999) and chlorophyll *a* (a proxy for food availability; Ho *et al.*, 2010). These variables showed no correlation with the body size of *T. geversianus*. Calcium carbonate ($CaCO_3$) solubility is driven by different factors including sea temperature, pressure and pH (Watson *et al.*, 2012). It is expected that increasing acidification will increase $CaCO_3$ solubility, thus making the calcification process more difficult. Indeed, meta-analyses of experimental studies show drastic impacts of acidification on different physiological and ecological processes in molluscs (Kroeker *et al.*, 2013). The potential impact of acidification on body size *per se* is less understood. For instance, Watson *et al.* (2012) found that the shell mass of five mollusc species increased when living in waters with higher aragonite saturation. On the other hand, in our study both proxies for body size were negatively correlated to pH. We suspect that this apparent contradictory result may arise from the negative relationship between growth rate and the asymptotic body size observed in other molluscs (e.g. Cardoso *et al.*, 2006). Additional studies addressing the latitudinal variation in
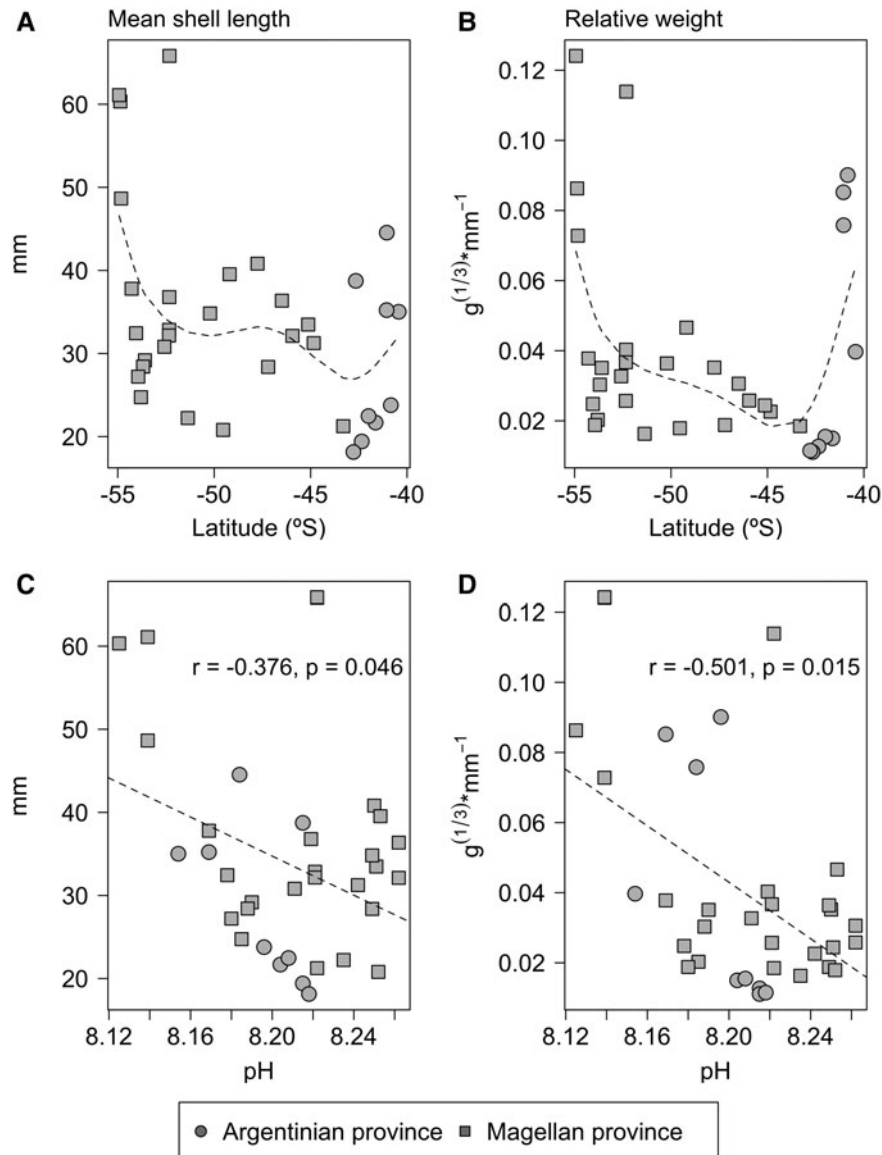
Fig. 3. Latitudinal variation of mean shell length and relative weight and its correlation with pH.

growth parameters may shed light on this hypothesis. Alternatively, our results may be influenced by the comparatively high values of pH observed across the south-west Atlantic coast (8.13–8.26) compared with the global ocean

Table 2. Correlation (Spearman's product-moment) between mean shell length and the relative shell weight vs. latitude, sampled shells and oceanographic variables. In parentheses are shown P-values (uncorrected/corrected by Dutilleul's method). Significant values (after correction) are shown in bold.

Variable	Mean shell length	Relative shell weight
Latitude	−0.378 (0.025/0.261)	−0.178 (0.308/0.459)
SST	−0.367 (0.03/0.266)	−0.142 (0.417/0.546)
Chl-a	−0.073 (0.678/0.669)	−0.045 (0.798/0.793)
Calcite	−0.114 (0.514/0.493)	−0.111 (0.526/0.516)
Oxygen	0.399 (0.018/0.187)	0.072 (0.682/0.751)
pH	−0.376 (0.026/**0.046**)	−0.501 (0.002/**0.015**)
Wave height	0.131 (0.454/0.638)	0.107 (0.542/0.600)

(7.95–8.38; Takahashi et al., 2014). In this sense, the functional relationship between body size and pH may be non-linear, and so other responses may be observed in regions with a different pH range.

Additionally, genetic studies will probably improve our understanding of this species given that T. geversianus shows direct development, suggesting that morphological variation is more likely to be caused by genetic differentiation rather than phenotypic plasticity, compared with species with planktonic larvae. Recently, phylogenetic analysis of COI gene fragments showed no consistent differences among individuals sampled in intertidal and subtidal habitats at three sites in Northern Patagonia (Márquez et al., 2015).

Also, biological interactions may also contribute to shaping latitudinal patterns in the body size of T. geversianus. For instance, the presence of the voracious, invasive crab Carcinus maenas, which lives along Chubut province in the south-west Atlantic coast (Hidalgo et al., 2005), may be inducing phenotypic responses from T. geversianus. Trussell (2000) found that gastropod shells that have been exposed

to predation by *C. maenas* for a longer time period (∼100 years) were heavier, thicker and stronger. Aquarium experiments confirm that *C. maenas* feed on slow-moving and sessile animals including *T. geversianus* (Hidalgo *et al.*, 2007). A taphonomic analysis of shells around the introduced/invasive range of this species (Chubut province, 45°S) (Malvé *et al.*, unpublished data) shows that thicker shells also tend to have a higher repair frequency (probably produced by crabs), thus suggesting a direct link between predation risk and body size.

The inertia of death assemblages to short-term changes in species composition thus turns them into good proxies for long-term or regional-scale studies of benthic assemblages. Our results show that body size has a complex spatial trend of variability that cannot be easily encapsulated by ecogeographic rules (e.g. Bergmann's rule and the temperature-size rule). Molluscan death assemblages can be used to predict climate change effects on marine biodiversity (Warwick & Turk, 2002), and our study highlights the potential usefulness of biogeographic studies for anticipating the impacts of global change (i.e. ocean warming and acidification) on marine biodiversity. This may be of particular interest in socio-economically important species, such as *T. geversianus*. Insights into the resolution, fidelity and dynamics of death assemblages' accumulation now provide a confident basis for using them to evaluate the recent history of modern-day systems representing a valuable resource for understanding our present and future (Kidwell & Tomasovych, 2013). Finally, a more complete analysis of the latitudinal variation of life-histories (i.e. growth rates based on sclerochronological analyses), complemented with laboratory experiments and phylogeographic analyses, may provide a much more robust basis for unveiling the patterns and processes which explain the structure and dynamics of *T. geversianus* along the southwestern Atlantic coast.

REFERENCES

Andrade C., Montiel A. and Quiroga E. (2009) Estimación de producción secundaria y productividad para una población intermareal de *Trophon geversianus* (Bahía Laredo, Estrecho de Magallanes). *Anales del Instituto de la Patagonia* 37, 73–84.

Angilletta M.J. Jr and Dunham A.E. (2003) The temperature-size rule in ectotherms: simple evolutionary explanations may not be general. *American Naturalist* 162, 332–342.

Atkinson D. (1994) Temperature and organism size: a biological law for ectotherms? *Advances in Ecological Research* 25, 1–54.

Balech E. and Ehrlich M.S. (2008) Esquema biogeográfico del mar Argentino. *Revista de Investigación y Desarrollo Pesquero* 19, 45–75.

Beerling D.J. and Berner R.A. (2002) Biogeochemical constraints on the Triassic-Jurassic boundary carbon cycle event. *Global Biogeochemical Cycles* 16, 1–13.

Behrensmeyer A.K., Kidwell S.M. and Gastaldo R.A. (2009) Taphonomy and paleobiology. *Paleobiology* 26, 103–147.

Berke S.K., Jablonski D., Krug A.Z., Roy K. and Tomasovych A. (2013) Beyond Bergmann's rule: size–latitude relationships in marine Bivalvia world-wide. *Global Ecology and Biogeography* 22, 173–183.

Briones C., Rivadeneira M.M., Fernández M. and Guiñez R. (2014) Geographical variation of shell thickness in the mussel *Perumytilus purpuratus* along the Southeast Pacific Coast. *Biological Bulletin* 227, 221–231.

Cardoso J.F., van der Veer H.W. and Kooijman S.A. (2006) Body-size scaling relationships in bivalve species: a comparison of field data with predictions by the Dynamic Energy Budget (DEB) theory. *Journal of Sea Research* 56, 125–139.

Chapelle G. and Peck L.S. (1999) Polar gigantism dictated by oxygen availability. *Nature* 399, 114–115.

Cumplido M., Averbuj A. and Bigatti G. (2010) Reproductive seasonality and oviposition induction in *Trophon geversianus* (Gastropoda: Muricidae) from Golfo Nuevo, Argentina. *Journal of Shellfish Research* 29, 423–428.

Dale M.R. and Fortin M.J. (2009) Spatial autocorrelation and statistical tests: some solutions. *Journal of Agricultural, Biological and Environmental Statistics* 14, 188–206.

Fisher J.A., Frank K.T. and Leggett W.C. (2010) Breaking Bergmann's rule: truncation of Northwest Atlantic marine fish body sizes. *Ecology* 91, 2499–2505.

Frank P.W. (1975) Latitudinal variation in the life history features of the black turban snail *Tegula funebralis* (Prosobranchia: Trochidae). *Marine Biology* 31, 181–192.

Gazeau F.P.H., Gattuso J.A., Dawber C., Pronker A.E., Peene F., Peene J., Heip C.H.R. and Middelburg J.J. (2010) Effect of ocean acidification on the early life stages of the blue mussel *Mytilus edulis*. *Biogeosciences* 7, 2051–2060.

Gordillo S. and Archuby F. (2014) Live-live and live-dead interactions in marine death assemblages: the case of the Patagonian clam *Venus antiqua*. *Acta Palaeontologica Polonica* 59, 429–442.

Gordillo S., Bayer M.S., Boretto G. and Charó M. (2014) *Mollusk shells as bio-geo-archives: evaluating environmental changes during the Quaternary*, 1st edition. Berlin: Springer-Verlag.

Gordillo S., Coronato A.M.J. and Rabassa J.O. (2005) Quaternary molluscan faunas from the island of Tierra del Fuego after the Last Glacial Maximum. *Scientia Marina* 69, 337–348.

Griffin M. and Pastorino G. (2005) The genus *Trophon* Monfort, 1810 (Gastropoda: Muricidae) in the Tertiary of Patagonia. *Journal of Paleontology* 79, 296–311.

Guinotte J.M. and Fabry V.J. (2008) Ocean acidification and its potential effects on marine ecosystems. *Annals of the New York Academy of Sciences* 1134, 320–342.

Heinze J., Foitzik S., Fischer B., Wanke T. and Kipyatkov V.E. (2003) The significance of latitudinal variation in body size in a holarctic ant, *Leptothorax acervorum*. *Ecography* 26, 349–355.

Hidalgo F.J., Barón P.J. and Orensanz J.M.L. (2005) A prediction come true: the green crab invades the Patagonian coast. *Biological Invasions* 7, 547–552.

Hidalgo F.J., Silliman B.R., Bazterrica M.C. and Bertness M.D. (2007) Predation on the rocky shores of Patagonia, Argentina. *Estuaries and Coasts* 30, 886–894.

Ho C.K., Pennings S.C. and Carefoot T.H. (2010) Is diet quality an overlooked mechanism for Bergmann's rule? *American Naturalist* 175, 269–276.

Hughes L. (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* 15, 56–61.

Irie T., Morimoto N. and Fischer K. (2013) Higher calcification costs at lower temperatures do not break the temperature-size rule in an intertidal gastropod with determinate growth. *Marine Biology* 160, 2619–2629.

Kidwell S.M. (2002) Time-averaged molluscan death assemblages: palimpsests of richness, snapshots of abundance. *Geology* 30, 803–806.

Kidwell S.M. and Tomasovych A. (2013) Implications of time-averaged death assemblages for ecology and conservation biology. *Annual Review of Ecology, Evolution, and Systematics* 44, 539–563.

Kroeker K.J., Kordas R.L., Crim R., Hendriks I.E., Ramajo L., Singh G.S., Duarte C.M. and Gattuso J.P. (2013) Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Global Change Biology* 19, 1884–1896.

Kurihara H. (2008) Effects of CO2-driven ocean acidification on the early developmental stages of invertebrates. *Marine Ecology-Progress Series* 373, 275–284.

Lee H.J. and Boulding E.G. (2010) Latitudinal clines in body size, but not in thermal tolerance or heat-shock cognate 70 (HSC70), in the highly-dispersing intertidal gastropod *Littorina keenae* (Gastropoda: Littorinidae). *Biological Journal of the Linnean Society* 100, 494–505.

Linse K., Barnes D.K. and Enderlein P. (2006) Body size and growth of benthic invertebrates along an Antarctic latitudinal gradient. *Deep Sea Research Part II: Topical Studies in Oceanography* 53, 921–931.

Márquez F., Vilela R.A.N., Lozada M. and Bigatti G. (2015) Morphological and behavioral differences in the gastropod *Trophon geversianus* associated to distinct environmental conditions, as revealed by a multidisciplinary approach. *Journal of Sea Research* 95, 239–247.

Meiri S. (2011) Bergmann's Rule – what's in a name? *Global Ecology and Biogeography* 20, 203–207.

Narita D., Rehdanz K. and Tol R.S. (2012) Economic costs of ocean acidification: a look into the impacts on global shellfish production. *Climatic Change* 113, 1049–1063.

Pastorino G. (2005) A revision of the genus *Trophon* Montfort, 1810 (Gastropoda: Muricidae) from southern South America. *The Nautilus* 119, 55–82.

Penchaszadeh P.E. (1976) Reproducción de gasterópodos prosobranquios del Atlántico suroccidental: el género *Trophon*. *Physis* 35, 69–76.

Rangel T.F., Diniz-Filho L.V.B. and Bini L.M. (2010) SAM: a comprehensive application for Spatial Analysis in Macroecology. *Ecography* 33, 46–50.

Schmidt-Nielsen K. (1984) *Scaling: why is animal size so important?* 1st edition. Cambridge: Cambridge University Press.

Solomon S. (ed.) (2007) *Climate change 2007 – the physical science basis: Working group I contribution to the fourth assessment report of the IPCC (Vol. 4)*, 1st edition. Cambridge: Cambridge University Press.

Takahashi T., Sutherland S.C., Chipman D.W., Goddard J.G., Ho C., Newberger T., Sweeney C. and Munro D. (2014) Climatological distributions of pH, pCO_2, total CO_2, alkalinity, and $CaCO_3$ saturation in the global surface ocean, and temporal changes at selected locations. *Marine Chemistry* 164, 95–125.

Talmage S.C. and Gobler C.J. (2010) Effects of past, present and future ocean carbon dioxide concentrations on the growth and survival of larval shellfish. *Proceedings of the National Academy of Sciences USA* 107, 17246–17251.

Tyberghein L., Verbruggen H., Pauly K., Troupin C., Mineur F. and De Clerck O. (2012) Bio-ORACLE: a global environmental dataset for marine species distribution modelling. *Global Ecology and Biogeography* 21, 272–281.

Trussell G.C. (2000) Phenotypic clines, plasticity, and morphological trade-offs in an intertidal snail. *Evolution* 54, 151–166.

Warwick R.M. and Turk S.M. (2002) Predicting climate change effects on marine biodiversity: comparison of recent and fossil molluscan death assemblages. *Journal of the Marine Biological Association of the United Kingdom* 82, 847–850.

Watson S.A., Peck L.S., Tyler P.A., Southgate P.C., Tan K.S., Day R.W. and Morley S.A. (2012) Marine invertebrate skeleton size varies with latitude, temperature and carbonate saturation: implications for global change and ocean acidification. *Global Change Biology* 18, 3026–3038.

Watt C., Mitchell S. and Salewski V. (2010) Bergmann's rule; a concept cluster? *Oikos* 119, 89–100.

and

Zaixso H.E. (1973) Observaciones sobre el desove y embriología de *Trophon geversianus* (Pallas) 1974 (Gastrópoda, Muricidae). *Contribución Científica* 101, 156–162.

Correspondence should be addressed to:
M.E. Malvé
Facultad de Ciencias Exactas, Físicas y Naturales. Universidad Nacional de Córdoba, Av. Vélez Sársfield 299 X5000JJC Córdoba, Argentina
email: marianomalve@gmail.com