

Toward a Better Understanding of the Native–Nonnative Status of *Mytilus* Mussels in the Southwestern Atlantic: Comparing Pre-European Middens and Modern Populations



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ABSTRACT

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The aim of this study is to determine the degree of similarity of the *Mytilus* mussels currently found along the Patagonian coast of Argentina to those found in pre-European colonization middens, in order to approach an understanding of whether the former are native or not. An elliptic Fourier analysis between pre-European archaeological (native) and modern mussels (cryptogenic) was performed, and the resulting data were analyzed with multivariate approaches (principal component analysis, discriminant function analysis, and cluster analysis). Our results showed that when all samples belonging to the Patagonian coast were included on a single analysis, modern and archaeological mussels were clustered in two major groups, matching the macroregional marine biogeographic scheme. In addition, morphometric differences were detected when modern and archaeological mussels from similar latitudes were compared. We discuss these results in light of the natural and anthropogenic changes that occurred along the Argentinean coast together with the environmental changes occurring between the biogeographic provinces along the SW Atlantic coast.

ADDITIONAL INDEX WORDS: *Elliptic Fourier analysis, marine invasion.*



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INTRODUCTION

Biological invasions (*i.e.* the successful establishment and spread of species through human activities outside their native range) are increasingly frequent and are considered to be one of the major threats to biodiversity conservation worldwide (Carlton, 1989; Elton, 1958) and a barrier to the knowledge of biogeography (Bortolus and Schwindt, 2007; Crisci, Katinas, and Posadas, 2003). The spread of nonnative species has led to a breakdown of traditional faunal boundaries and contributed to the homogenization of flora and fauna around the world and sometimes to the extinction of native species (McKinney and Lockwood, 1999). The study of biological invasions have been mainly focused in terrestrial environments; however, invasions in marine systems are of such magnitude that marine invasions may be leading to profound ecological changes in the ocean (Carlton and Geller, 1993).

Mytilus is a cosmopolitan marine genus distributed in cold temperate seas of both northern and southern hemispheres (Hilbish *et al.*, 2000; McDonald, Seed, and Koehn, 1991; Seed, 1992). Taxonomists consider the blue mussels to be a group of three closely related taxa of mussels with similar shell morphology known as the *Mytilus edulis* complex. It first appeared in the North Atlantic during the Middle Pliocene, 3.1–4.8 million years before the present (YBP; Rawson and Harper, 2009; Riginos and HENZLER, 2008) and reached the Southern

Hemisphere, presumably, through a migration event *via* an Atlantic route during the late Pleistocene *circa* 0.84 million YBP (Gérard *et al.*, 2008; Hilbish *et al.*, 2000). The presence of *Mytilus* fossils in the Southern Hemisphere was considered to support the native origin for the *Mytilus* complex in this region (Doello Jurado, 1922; Fleming, 1959; Gardner, 2004). Nevertheless, it is currently known that as a result of human shipping activities throughout history, different species of this complex have spread aggressively worldwide, including in the Southern Hemisphere (Carlton and Geller, 1993; Carlton and Ruiz, 2003; Gardner 2004). Considering that the extinction of native *Mytilus* species may go unnoticed (Geller 1999), it is unclear whether modern mussel populations within the Southern Hemisphere are of native or introduced origin, or both.

Mytilus spp. are among the most common coastal organisms in Southern Brazil, Uruguay, and Argentina. They are present across the Argentine and Magellanic marine biogeographic provinces with different environmental and biological conditions (Balech and Ehrlich, 2008). Within each of these marine provinces, *Mytilus* mussels inhabit a variety of environments, including rocky shores, mudflats, salt marshes, brackish and marine areas, intertidal and shallow subtidal waters, displaying a great spectrum of variations in morphology and physiology (Kautsky, Johannesson, and Tedengren, 1990; Petes, Menge, and Murphy, 2007). In spite of being a common organism along the Argentine coast, where it is a common fishery (Ciocco, Lasta, and Bremec, 1998; Morsan and Zaidman, 2008) and aquaculture resource (Pascual and Castaños, 2008), its native or invasive status is still under discussion (Savoya 2012).

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Ethnographic and archaeological records showed that mussels were also an important food supply for pre-European cultures in the Patagonian coast of Argentina (Gómez Otero, Lanata, and Prieto, 1998; Moreno, 2008; Orquera, 1999; Zubimendi, Castro, and Moreno, 2004). Middens (*i.e.* heaps of refuse characterized by mollusk shells and bones of guanacos, pinnipeds, fish, birds, and other animals of nutritional value for the native people; Figure 1, Cruz and Caracotche, 2008) are distributed throughout the Patagonian coast, and many of them date to pre-European times. Assuming that marine invasions in eastern America started with the arrivals of the Europeans (Carlton 1989, 1999), all species present in pre-European middens belong to native fauna.

Shell morphometry is a taxonomic trait tool that has been used to discriminate among species of *Mytilus* (Beaumont *et al.*, 2008; Gardner, 2004; Innes and Bates, 1999; Krapivka *et al.*, 2007; McDonald, Seed, and Koehn, 1991; Valladares, Manríquez, and Suárez-Isla, 2010). In that sense, a comparative morphometric study between mussels from pre-European middens and modern mussels presents as an exceptional opportunity to study the native or invasive status of the mussels *Mytilus* in the Patagonian coast of Argentina. Thus, the aim of this study is to determine the degree of similarity of the *Mytilus* mussels currently found along the Patagonian coast of Argentina to those found in pre-European colonization middens, in order to approach an understanding of whether the former are native or not. We discuss the results in the light of the natural and anthropogenic changes that occurred along the SW Atlantic (SWA) coast.

METHODS

Study Area

The study area covered both marine biogeographic provinces from Argentine continental shelf: the Argentine province extends from 30°S–32°S to 41°S–44°S, and the Magellanic from 44°S to the southern extreme (Figure 2; Balech and Ehrlich, 2008). Archaeological shells dated as pre-European colonization were collected from three locations: Faro San Matías (FSM, 2910 ± 90 YBP; Río Negro; Favier Dubois and Borella, 2007), Barranca Norte (BN, 2960 ± 60 YBP, 3060 ± 80 YBP; Chubut; Gómez Otero, 2006), and Monte León (ML arch, 970 ± 50, 1830 ± 70 YBP; Santa Cruz; Muñoz, Caracotche, and Cruz, 2009; Figure 2). Each archaeological sample had a modern counterpart collected from a site as close as possible to the archaeological site in order to minimize the influence of environmental variation on the shell morphology. Modern shells were collected from Punta Mejillón (PM, close to FSM, Río Negro), San José gulf (GSJ, close to BN, Chubut), and Monte León (ML mod, close to ML arch, Santa Cruz; Figure 2), covering a wide area of the intertidal within each location in order to include small spatial morphology variation. In total 240 shells were included. Considering the absence of mussels from middens in the northern part of the coast of Argentina, neither archaeological nor modern shells from this area were included in this study (Bonomo, 2007).

Outline Analysis

Although shell morphology may be affected by the environment, the absence of genetic material in the mussels from the

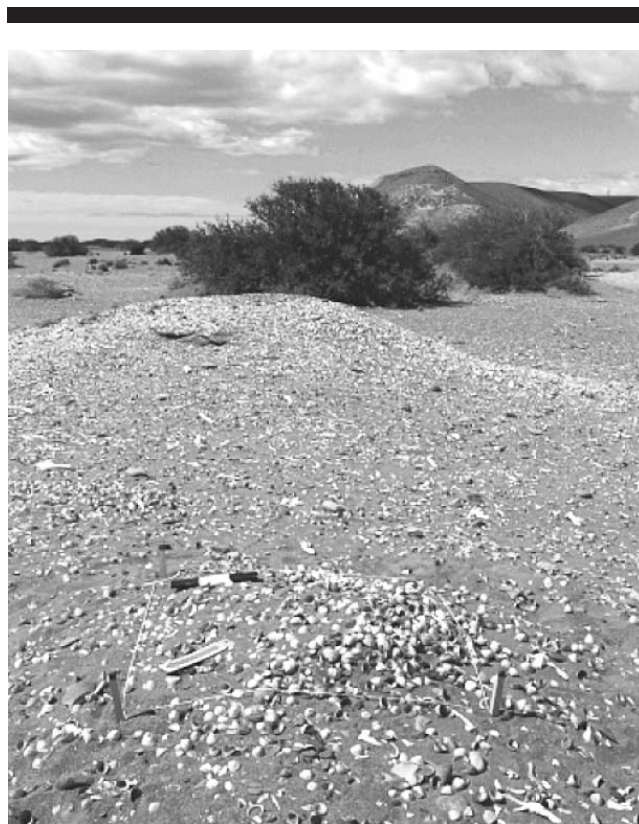


Figure 1. Midden from Santa Cruz province. Middens are archaeological sites characterized by the accumulation of mollusk shells and bones of animals, as a consequence of human consumption. Commonly, these accumulations consist of bones of guanacos, pinnipeds, fish, birds, and other prey of nutritional value to the native people diet, and to lithic artifacts (picture obtained from Cruz, Muñoz, and Caracotche, 2009).

middens makes morphometry the best approach to conduct this investigation. The shell shape variation was studied by elliptic Fourier analysis, which consists of decomposing a curve into a sum of harmonically related ellipses (Lestrel, 1997). In order to minimize the introduction of variability by measuring different valves (*i.e.* right and left) in the different mussels studied, only the right valves were used. For each valve, images with 1 × 1 cm of scale were taken with a digital camera (Sony Cybershot 10M pixel resolution). For getting the best possible outline of the inner surface of the shell, valves were positioned upward and the outer surface was settled on a piece of clay in order to avoid movement during the capture of the photograph; thus, the plane delimited by the shell outline was perfectly parallel to the camera. The closed contours of each shell outline were obtained as chain-coded data from the digital images (Freeman, 1974). Following Crampton (1995), we found in a visual estimation that 10 harmonics were appropriate to describe mussel shell shape in accordance with other studies (Ferson, Rohlf, and Koehn, 1985; Innes and Bates, 1999). The orientation, size, and starting point of the different outlines were standardized (Kuhl and Giardina, 1982) so that three of the four elliptic Fourier coefficients describing the first harmonic ellipse were constant for all outlines. In this sense,

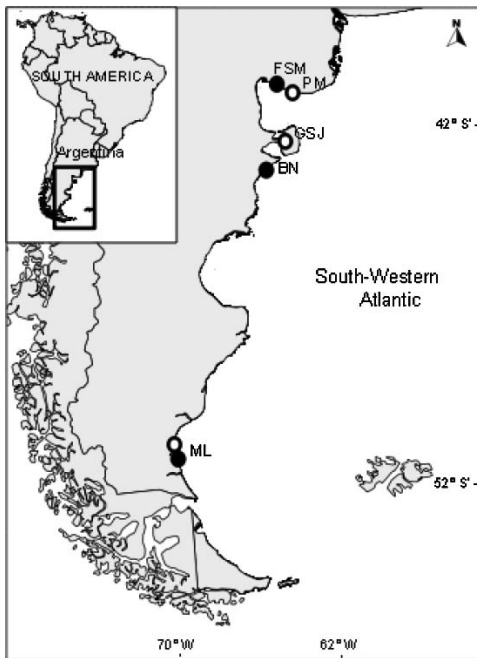


Figure 2. Map including sampling locations. Modern shells were collected from Punta Mejillón, PM; San José gulf, GSJ; Monte León, ML (white circles). Archaeological shells were collected from Faro San Matías, FSM; Barranca Norte, BN; Monte León, ML (black circles).

the Fourier normalized space was composed of 37 morphometric variables. The software Shape v.1.2 (Iwata and Ukai, 2002) was used for all the analyses.

Statistical Analysis

Three principal component analyses (PCA) of the variance-covariance matrix, based on individuals, were performed for each archaeological-modern pair of shells from a single region (*i.e.* FSM/PM, BN/GSJ, ML arch/ML mod) in order to summarize the shape variations and to study the relationship between them. Discriminant function analysis (DFA) was used to determine what percent of each location, *a priori* classified as modern or archaeological, could be correctly assigned to their location of origin by a discriminant function (*i.e.* cross validation analysis). Differences in the Fourier's coefficients between modern and archaeological shells for each pair were tested using multivariate analysis of variance (MANOVA; Manly, 1986). To evaluate spatial variations of the shell shape, a cluster analysis was applied using an unweighted pair group method with arithmetic mean (UPMGA) in order to show the distances and the relationship (*i.e.* Mahalanobis) among all samples (*i.e.* modern and archaeological). Before performing the analyses explained above, shell area was related with the principal components through a linear multiple regression (Costa *et al.*, 2008; De Maesschalck *et al.*, 1999) in order to assess allometry (association between size and shape).

RESULTS

The multiple linear regression of the principal components involved the four first principal components, which summa-

rized 90% of the total variation. The regression analysis between the PCA and the shell area was negligible ($R^2 = 0.13$); considering that only 13% of the shells' variation was explained by the first four components, no allometric correction was performed before the statistical analyses. All PCAs explained 75–76% of total variation (Figure 3). The pair of modern and archaeological shells from the three localities of Patagonia showed statistically significant differences (Río Negro Wilks' $\lambda = 0.25$, $p < 0.0001$; Chubut Wilks' $\lambda = 0.22$, $p < 0.0001$; Santa Cruz Wilks' $\lambda = 0.38$, $p < 0.025$; respectively).

The cross validation analysis obtained from DFA showed that 92.5% and 97.5% of the shells from FSM and PM, respectively, were correctly assigned to their category of origin, while these percentages were 95% for shells from BN and GSJ. Finally, 90% and 92.5% of the shells from ML arch and ML mod, respectively, were correctly allocated to their category of origin. The UPMGA performed among all samples showed two major groups (Figure 4). One of them grouped PM and FSM (the northernmost Argentinean modern and archaeological samples) and the other grouped GSJ, BN, ML mod, and ML arch; modern and archaeological samples from Chubut and Santa Cruz (Figure 4). In the latter group, two subgroups were detected, one included archaeological samples (BN and ML arch) and the other included the modern samples (Figure 4).

DISCUSSION

Our results showed that the shape of the shells of modern and archaeological mussels along the Patagonian coast of Argentina are consistently different. Shell morphometry has been a useful taxonomic tool to discriminate among species of *Mytilus* mussels, in particular in those cases where genetic studies cannot be performed, as happens with fossil and many archaeological records (Gardner, 2004). Different multivariate analyses, such as PCA, MANOVA, and UPMGA together, are commonly and widely applied to summarize the shape variations on Fourier descriptors. On the other hand, recent works, primarily applied to agriculture industry, have shown that the modeling approaches might give efficient results with the advantage of making the results and procedures comparable among disciplines (see Costa *et al.*, 2011 and the references therein).

In the study of morphology, it is important to consider that morphology is a plastic character affected by the kind of environment (Gardner, 2004; Gordillo, Bayer, and Martinelli, 2010; Kautsky, Johannesson, and Tedengren, 1990; Ruffino *et al.*, 2013; Seed, 1992), coastal geomorphology (Moeser, Leba, and Carrington, 2006; Steffani and Branch, 2003), wave force (Bell and Gosline, 1997; Denny, Daniel, and Koehl, 1985), and community structure (Caro and Castilla, 2004; Norberg and Tedengren, 1995), among others. Thus, differences between modern and archaeological mussels could support differences in the taxonomy only if they lived under similar environmental conditions. For southern South America, the existent knowledge of the coastal archaeology and paleoclimatology give us the opportunity to study the differences in shape between the mussels from archaeological sites and modern environments and to discuss the potential causes of these differences.

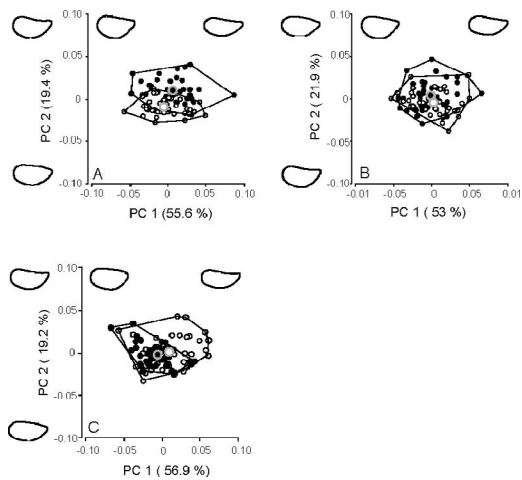


Figure 3. Principal component plots based on 37 Fourier coefficients for modern (white circles) and archaeological (black circles) *Mytilus* from three locations of the Argentine coast (A, FSM/PM; B, BN/GSJ; C, ML mod/ML arch). Reconstructions of the extreme shell shapes (mean $-2SD$ and mean $+2SD$) are shown along PC1 and PC2. Larger circles with gray outlines indicate the average for each group. The black lines link the extreme points from each group.

It is known that mussels living in the subtidal zones have thicker shells and a wider posterior muscle than the mussels living in intertidal environments (Beadman *et al.*, 2003; Savoya, 2012). The modern mussels here studied were collected from intertidal rocky shores as experts support the idea that archaeological mussels were also collected from the intertidal (Cruz and Caracotche, 2008; Gómez Otero, Lanata, and Prieto, 1998; Orquera and Piana, 2006; Zubimendi, Castro, and Moreno, 2004). First, the coast of Patagonia is characterized by a large tidal range, which, together with the null intertidal slope, leaves hundreds of meters of intertidal exposed for many hours for the harvest of mussels. Second, the ear osteoma (*i.e.* a typical cranial piece within the marine hunter-gatherers of south and western Patagonian channels and islands, generated as a consequence of diving in cold waters; Gaete *et al.*, 2004; Ocampo and Rivas, 2004; Orquera and Piana, 2006) has not been registered in native people from the continental Patagonian Atlantic coast, suggesting that they did not dive to collect seafood. This evidence supports the hypothesis that mussels from middens were harvested at the intertidal of rocky shores rather than at the subtidal or other environments (Gómez Otero, 2006; Gómez Otero, Lanata, and Prieto, 1998). Within this scenario, the methods we applied were highly appropriate and led us to reasoned and realistic conclusions.

Wave force has been reported as another factor influencing the characteristics of the shape of intertidal organisms, including mussels (Bell and Gosline, 1997; Denny, Daniel, and Koehl, 1985). For example, mussels from wave-sheltered sites were reported as taller, wider, and with a ventral edge more concave than mussels from wave-exposed sites (Seed, 1968; Steffani and Branch, 2003). In addition, coastal geomorphology directly affects the intensity of the wave force, and

therefore the differences between modern and archaeological mussels could be a response to the geomorphologic changes taking place over time in each study site. However, expert geologists and geomorphologists agreed that the coast of Argentina has not changed significantly during the last 3000 years, which is within the time period of this study (Codignotto and Aguirre, 1993; Ponce *et al.*, 2011). Therefore, the morphological variations we found between modern and archaeological mussels (see Figure 3) would not respond to environmental changes.

Previous morphological studies of several bivalves addressed with elliptic Fourier analysis were able to discriminate among different closely related species (Gordillo *et al.*, 2011; Innes and Bates, 1999; Puillandre *et al.*, 2009). Innes and Bates (1999), for instance, found morphological differences between *Mytilus edulis* and *Mytilus trossulus* from a sympatric population, proving the existence of variations in shell morphology and genotype of the mussels even under identical environmental conditions. Indeed, considering similitude between present and past environments where the modern and archaeological mussels were collected, it is likely that the observed morphological variations respond to genetic differences. Until now, no study had been specifically focused on detecting mussel invasions in the SW Atlantic; however, the maritime navigation between east America and the rest of the world started at least five centuries ago. Until the opening of the Panama Canal in 1914, the traffic between Europe and the countries in the Pacific Ocean was very intense through the Magellan Strait and Cape Horn. For centuries the countries along the east coast of South America served as way stations for ship traffic. Considering some biological traits of mussels such as planktonic larvae, the presence of byssal threads to attach to hard substrate, high tolerance to adverse environmental conditions, and high phenotypic plasticity (Carlton, 1999; Carlton and Geller, 1993; Kautsky, Johannesson, and Tedengren, 1990; Seed, 1992), these organisms are likely to have been transported on the hull of ancient vessels, as well as in the ballast water of the modern ships. In consequence, the invasion of mussels in different regions of the world, including the SWA, is highly probable (Beaumont *et al.*, 2008; McDonald, Seed, and Koehn, 1991; Wonham, 2004). The morphometric differences between modern and pre-European archaeological mussels, together with similar environmental conditions in which modern and archaeological mussels lived, support the occurrence of mussel invasions in the SWA.

The spatial segregation observed in the UPMGA belongs to a latitudinal segregation among samples. Mussels from the Argentine marine province (*i.e.* FSM, PM) were discriminated from those from the Magellanic marine province (F, BN, ML mod, ML arch). These two biogeographic provinces are different in several ways. The intertidals of the Argentine marine province are characterized by movable sandy bottoms, the prevalence of northern winds, and the alternation of warm and temperate-cold coastal waters with microtidal to mesotidal amplitudes. In contrast, the shore of the Magellanic province is characterized by macrotidal amplitudes, with hard bottoms, cold SW strong winds, and a net predominance of sub-Antarctic waters from the Malvinas/Falkland current (Balech and Ehrlich, 2008). In this sense, the macroscale differences

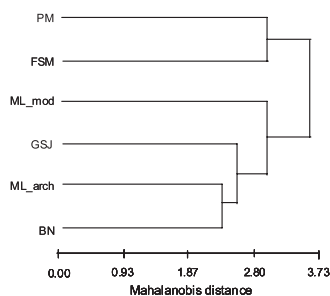


Figure 4. Tree from UPMGA analysis showing shell shape relationship among pre-European archaeological mussels and modern mussels included in this study. See Figure 2 for location abbreviations.

observed in shell morphology of modern and archaeological mussels could respond to the biogeographic scheme of the Argentine shelf, reflecting the strong heterogeneity of the Argentine coast in terms of the oceanography, climate, and topography, which has stayed almost unchanged since middle Holocene times (Ponce *et al.*, 2011).

In short, although a (native) species may vary its morphology over a geologic time scale, the fact that *Mytilus* spp. were recently recorded aggressively invading several regions worldwide poses serious doubts on the native status of the SW Atlantic populations. Our results provided valuable and conclusive evidence showing that in spite of their similarity, modern populations of *Mytilus* are morphologically different from pre-European ones. In addition to the morphologic variations owed to macroenvironmental heterogeneity (maritime biogeographic regions), our results show a distinctive morphology that allows a clear differentiation between modern and pre-European populations. These findings are consistent with a hypothetical introduction of invasive *Mytilus* spp. in this region and urge the performance of complementary molecular phylogenetic comparisons that include *Mytilus* populations worldwide. Cryptic invasions are constantly capturing the attention of more researchers because they can seriously confound the way we see natural systems and, more importantly, because they can inadvertently hamper management and conservation decisions.

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LITERATURE CITED

- Balech, E. and Ehrlich, M.D., 2008. Esquema biogeográfico del mar argentino. *Revista de Investigación y Desarrollo Pesquero*, 19, 45–75 [in Spanish].
- Beadman, H.A.; Caldwell, R.W.G.; Kaiser, M.J., and Willows, R.I., 2003. How to toughen up your mussels: using mussel shell morphological plasticity to reduce predation losses. *Marine Biology*, 142(3), 487–494.
- Beaumont, A.R.; Hawkins, M.P.; Doig, F.L.; Davies, I.M., and Snow, M., 2008. Three species of *Mytilus* and their hybrids identified in Scottish loch: natives, relicts and invaders? *Journal of Experimental Marine Biology and Ecology*, 367(2), 100–110.
- Bell, E.C. and Gosline, J.M., 1997. Strategies for life in flow: tenacity, morphometry and probability of dislodgment of two *Mytilus* species. *Marine Ecology Progress Series*, 159, 197–208.
- Bonomo, M., 2007. El uso de los moluscos marinos por los cazadores-recolectores pampeanos. *Chungara, Revista de Antropología Chilena*, 39(1), 87–102 [in Spanish].
- Bortolus, A. and Schwindt, E., 2007. What would have Darwin written now? *Biodiversity and Conservation*, 16(2), 337–345.
- Carlton, J.T., 1989. Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. *Conservation Biology*, 3(3), 265–273.
- Carlton, J.T., 1999. The scale and ecological consequences of biological invasions in the world's oceans. In: Sandlund, O.T.; Schei, P.J., and Viken, A., (eds.), *Invasive Species and Biodiversity Management*. Dordrecht, The Netherlands: Kluwer, pp. 195–212.
- Carlton, J.T. and Geller, J.B., 1993. Ecological roulette: the global transport and invasion of non indigenous marine organisms. *Science*, 261(5117), 78–82.
- Carlton, J.T. and Ruiz, G.M., 2003. *Invasive Species: Vectors and Management Strategies*. Washington, DC: Island, 600p.
- Caro, A.U. and Castilla, J.C., 2004. Predator-inducible defences and local intrapopulation variability of intertidal mussel *Semimytilus algosus* in Central Chile. *Marine Ecology Progress Series*, 276, 115–123.
- Ciocco, N.F.; Lasta, M.L., and Bremec, C., 1998. Pesquerías de bivalvos: mejillón, vieiras (tehuélche y patagónica) y otras especies. In: Boschi, E., (ed.), *El Mar Argentino y Sus Recursos Pesqueros*. Tomo 2. Mar del Plata, Argentina: INIDEP, Secretaría de Agricultura, Ganadería, Pesca y Alimentación, pp. 143–166 [in Spanish].
- Codignotto, J.O. and Aguirre, M.L., 1993. Coastal evolution, changes in sea level and molluscan fauna in northeastern Argentina during the late Quaternary. *Marine Geology*, 110(1–2), 163–175.
- Costa, C.; Aguzzi, J.; Menesatti, P.; Antonucci, F.; Rimatori, V., and Mattocchia, M., 2008. Shape analysis of different populations of clams in relation to their geographical structure. *Journal of Zoology*, 276(1), 71–80.
- Costa, C.; Antonucci, F.; Pallottino, F.; Aguzzi, J.; Sun, D.W., and Menesatti, P., 2011. Shape analysis of agricultural products: a review of recent research advances and potential application to computer vision. *Food and Bioprocess Technology*, 4(5), 673–692.
- Crampton, J.S., 1995. Elliptic Fourier shape analysis of fossil bivalves: some practical considerations. *Lethaia*, 28(2), 179–186.
- Crisi, J.V.; Katinas, L., and Posadas, P., 2003. *Historical Biogeography: an Introduction*. Cambridge, Massachusetts: Harvard University Press, 250p.
- Cruz, I. and Caracotche, M.S., 2008. *Arqueología de la Costa Patagónica: Perspectivas para la Conservación*. Río Gallegos: Universidad Nacional de la Patagonia Austral, 260p [in Spanish].
- Cruz, I.; Muñoz, A.S., and Caracotche, M.S., 2009. Zooarqueología y patrimonio de la costa al sur de la Patagonia. *Desde la Patagonia Difundiendo Saberes*, 6(9), 18–24 [in Spanish].

- De Maesschalck, R.; Estienne, F.; Verdú-André, S.J.; Candolfi, A.; Centner, V.; Despaigne, F.; Jouan-Rimbaud, D.; Walczak, B.; Massart, D.L.; DeJong, S.; De Noord, O.E.; Puel, C., and Vandeginste, B.M.G., 1999. The development of calibration models for spectroscopic data using principal component regression. *Internet Journal of Chemistry*, 2(19), 1.
- Denny, M.W.; Daniel, T.L., and Koehl, M.A.R., 1985. Mechanical limits to size in wave-swept organisms. *Ecological Monographs*, 55(1), 69–102.
- Doello Jurado, M., 1922. Un nuevo *Mytilus* fósil del terciario de la Patagonia. *Anales de la Sociedad Científica Argentina*, 94, 86–90.
- Elton, C.S., 1958. *The Ecology of Invasions by Animals and Plants*. London: Methuen, 181p [in Spanish].
- Favier Dubois, C.M. and Borella, F., 2007. Consideraciones acerca de los procesos de formación de concheros en la costa norte del golfo San Matías (Río Negro, Argentina). *Cazadores Recolectores del Cono Sur: Revista de Arqueología*, 2, 151–165 [in Spanish].
- Ferson, S.; Rohlf, F.J., and Koehn, R.K., 1985. Measuring shape variation of two-dimensional outlines. *Systematic Zoology*, 34(1), 59–68.
- Fleming, C.A., 1959. Notes of New Zealand recent and tertiary mussels. *Transactions and Proceedings of the Royal Society of New Zealand*, 87, 165–178.
- Freeman, H., 1974. Computer processing of line drawing image. *Surveys*, 6(1), 57–97.
- Gaete, N.; Navarro, X.; Constantinescu, F.; Mera, C.; Selles, D.; Solari, M.E.; Vargas, M.L.; Oliva, D., and Durán, L., 2004. Una mirada al modo de vida canoero del mar interior desde Piedra Azul. *Chungara, Revista de Antropología Chilena*, 36 (numero especial 1), 333–346 [in Spanish].
- Gardner, J.P.A., 2004. A historical perspective of the genus *Mytilus* (Bivalvia: Mollusca) in New Zealand: multivariate morphometric analyses of fossil, midden and contemporary blue mussels. *Biological Journal of the Linnean Society*, 82(3), 329–344.
- Geller, J., 1999. Decline of a native mussel masked by sibling species invasion. *Conservation Biology*, 13(3), 661–664.
- Gérard, K.; Bierre, N.; Borsa, P.; Chenuil, A., and Féral, J.P., 2008. Pleistocene separation of mitochondrial lineages of *Mytilus* spp. mussels from Northern and Southern Hemispheres and strong genetic differentiation among southern populations. *Molecular Phylogenetics and Evolution*, 49(1), 84–91.
- Gómez Otero, J., 2006. Recursos, Dieta y Movilidad en la Costa Centroseptentrional de Patagonia Durante el Holoceno Medio y Tardío. Buenos Aires, Argentina: Facultad de Filosofía y Letras (UBA), Ph.D. thesis, 540p [in Spanish].
- Gómez Otero, J.; Lanata, J.L., and Prieto, A., 1998. Arqueología de la costa atlántica patagónica. *Revista de Arqueología Americana*, 15, 107–185 [in Spanish].
- Gordillo, S.; Bayer, M.S., and Martinelli, J., 2010. Moluscos recientes del Canal Beagle, Tierra del Fuego: un análisis cualitativo y cuantitativo de los ensambles de valvas fósiles y actuales. *Anales Instituto Patagonia*, 38(2), 95–106 [in Spanish].
- Gordillo, S.; Márquez, F.; Cárdenas, J., and Zubimendi, M.A., 2011. Shell variability in *Tawera gayi* (Veneridae) from southern South America: a morphometric approach based on contour analysis. *Journal of the Marine Biological Association of the United Kingdom*, 91(4), 815–822.
- Hilbish, T.J.; Mullinax, A.; Dolven, S.I.; Meyer, A.; Koehn, R.K., and Rawson, P.D., 2000. Origin of the antitropical distribution pattern in marine mussels (*Mytilus* spp.): routes and timing of trans-equatorial migration. *Marine Biology*, 136(1), 69–77.
- Innes, D.J. and Bates, J.A., 1999. Morphological variation of *Mytilus edulis* and *Mytilus trossulus* in eastern Newfoundland. *Marine Biology*, 133(4), 691–699.
- Iwata, H. and Ukai, Y., 2002. SHAPE: a computer program package for quantitative evaluation of biological shapes based on elliptical Fourier descriptors. *Journal of Heredity*, 93(5), 384–385.
- Kautsky, N.; Johannesson, K., and Tedengren, M., 1990. Genotypic and phenotypic differences between Baltic and North Sea populations of *Mytilus edulis* evaluated through reciprocal transplantations. I. Growth and morphology. *Marine Ecology Progress Series*, 59, 203–210.
- Krapivka, S.; Toro, J.E., Alcapán, A.C.; Astorga, M.; Presa, P.; Pérez, M., and Guíñez, R., 2007. Shell-shape variation along the latitudinal range of the Chilean blue mussel *Mytilus chilensis* (Hupe 1854). *Aquaculture Research*, 38(16), 1770–1777.
- Kuhl, F.P. and Giardina, C.R., 1982. Elliptic Fourier features of a closed contour. *Computer Graphics and Image Processing*, 18(3), 236–258.
- Lestrel, P.E., 1997. *Fourier Descriptors and Their Applications in Biology*. Cambridge, U.K.: Cambridge University Press, 466p.
- Manly, B.F.J., 1986. *Multivariate Statistical Methods: A Primer*. London: Chapman and Hall, 159p.
- McDonald, J.H.; Seed, R., and Koehn, R.K., 1991. Allozymes and morphometric characters of three species of *Mytilus* in the Northern and Southern hemispheres. *Marine Biology*, 111(3), 323–333.
- McKinney, M.L. and Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution*, 14(11), 450–453.
- Moeser, G.M.; Leba, H., and Carrington, E., 2006. Seasonal influence of wave action on threads production in *Mytilus edulis*. *Journal of Experimental Biology*, 209(5), 881–890.
- Moreno, J.E., 2008. *Arqueología y Etnohistoria de la costa patagónica central en el Holoceno tardío*. Rawson, Chubut: Fondo editorial provincial, Secretaría de Cultura del Chubut, 179p [in Spanish].
- Morsan, E.M. and Zaidman, P., 2008. Scale, dynamic and management in the harvesting of mussel in North Patagonia (Argentina). In: McManus, N.F. and Bellinghouse, D.S., (eds.), *Fisheries: Management, Economics and Perspectives*. New York: Nova, pp. 171–197.
- Muñoz, A.S.; Caracotche, M.S., and Cruz, I., 2009. Cronología de la costa al sur del río Santa Cruz: nuevas dataciones radiocarbónicas en Punta Entrada y Parque Nacional Monte León (provincia de Santa Cruz, Argentina). *Magallania*, 37(1), 19–38 [in Spanish].
- Norberg, J. and Tedengren, M., 1995. Attack behavior and predatory success of *Asterias rubens* L. related to differences in size and morphology of the prey mussel *Mytilus edulis* L. *Journal of Experimental Marine Biology and Ecology*, 186(2), 207–220.
- Ocampo, E. and Rivas, H.P., 2004. Poblamiento temprano de los extremos geográficos de los canales patagónicos: Chiloé e Isla Navarino I. *Chungara, Revista de Antropología Chilena*, 36 (numero especial 1), 317–331 [in Spanish].
- Orquera, L.A., 1999. El consumo de moluscos por los canoeros del extremo sur. *Relaciones de la Sociedad Argentina de Antropología*, 24, 307–327 [in Spanish].
- Orquera, L.A. and Piana, E.L., 2006. El poblamiento inicial del área litoral sudamericana sudoccidental. *Magallania*, 34(2), 21–36 [in Spanish].
- Pascual, M. and Castaños, C., 2008. *Acuicultura Estado de conservación del mar patagónico y áreas de influencia*, versión electrónica. Puerto Madryn, Argentina: Edición del Foro. <http://www.marpatagonico.org> [in Spanish].
- Petes, L.E.; Menge, B.A., and Murphy, G.D., 2007. Environmental stress decreases survival, growth, and reproduction in New Zealand mussels. *Journal of Experimental Marine Biology and Ecology*, 351(1–2), 83–91.
- Ponce, J.F.; Rabassa, J.; Coronato, A., and Borrromei, A.M., 2011. Palaeogeographical evolution of the Atlantic coast of Pampa and Patagonia from the last glacial maximum to the middle Holocene. *Biological Journal of the Linnean Society*, 103(2), 363–379.
- Puillandre, N.; Baylac, M.; Boisselier, M.C.; Cruaud, C., and Samadi, S., 2009. An integrative approach to species delimitation in *Benthomangelia*. *Biological Journal of the Linnean Society*, 96(3), 696–708.
- Rawson, P.D. and Harper, F.M., 2009. Colonization of the northwest Atlantic by the blue mussel, *Mytilus trossulus* postdates the last glacial maximum. *Marine Biology*, 156(9), 1857–1868.
- Riginos, C. and Henzler, C.M., 2008. Patterns of mtDNA diversity in North Atlantic populations of the mussel *Mytilus edulis*. *Marine Biology*, 155(4), 399–412.
- Ruffino, M.M.; Vasconcelos, P.; Pereira, F.; Fernández-Tajés, J.; Darriba, S.; Méndez, J., and Gaspar, M.B., 2013. Geographical

- variation in shell shape of the pod razor shell *Ensis siliqua* (Bivalvia: Pharidae). *Helgoland Marine Research*, 67(1), 49–58.
- Savoya, V., 2012. *Mytilus* spp. de Ambientes Costeros del Atlántico Sudoccidental: ¿Nativas, Exóticas o Ambas? Córdoba, Argentina: Universidad Nacional de Córdoba, Ph.D. thesis, 121p [in Spanish].
- Seed, R., 1968. Factors influencing shell shape in the mussel *Mytilus edulis*. *Journal of the Marine Biological Association of the United Kingdom*, 48(3), 561–584.
- Seed, R., 1992. Systematics evolution and distribution of mussels belonging to the genus *Mytilus*: an overview. *American Malacological Bulletin*, 9(2), 123–137.
- Steffani, C.N. and Branch, G.M., 2003. Growth rate, condition, and shell shape of *Mytilus galloprovincialis*: responses to wave exposure. *Marine Ecology Progress Series*, 246, 197–209.
- Valladares, A.; Manríquez, G., and Suárez-Isla, B.A., 2010. Shell shape variation in populations of *Mytilus chilensis* from southern Chile: a geometric morphometric approach. *Marine Biology*, 157(12), 2731–2738.
- Wonham, M.J., 2004. Mini review: distribution of Mediterranean mussel *Mytilus galloprovincialis* (Bivalvia: Mytilidae) and hybrids in the Northeast Pacific. *Journal of Shellfish Research*, 23(2), 535–543.
- Zubimendi, M.A.; Castro, A.S., and Moreno, J.E., 2004. El consumo de moluscos en la costa norte de Santa Cruz. *Intersecciones en Antropología*, 6, 121–137 [in Spanish].

□ RESUMEN □

El objetivo del presente trabajo es realizar un estudio morfológico entre valvas de mejillones *Mytilus* actuales y arqueológicos de la costa patagónica de Argentina, a fin de brindar una nueva perspectiva que permita mejorar el conocimiento sobre el origen nativo o invasor de los mejillones *Mytilus* actuales. Valvas arqueológicas (nativas) y actuales (criptogénicas) se estudiaron mediante el análisis elíptico de Fourier, y los datos obtenidos se analizaron con análisis multivariados (análisis de componentes principales, análisis de función discriminante, análisis de conglomerados y MANOVAs). Por un lado, los resultados muestran que en un análisis conjunto de todas las muestras (*i.e.* actuales y arqueológicas) éstas se agruparon siguiendo el esquema biogeográfico del mar argentino. Por otro lado, las valvas actuales y arqueológicas procedentes de latitudes similares de la costa patagónica se diferenciaron morfométricamente. Los resultados se discuten a la luz de los cambios naturales y antropogénicos ocurridos a lo largo de la costa argentina, y considerando además las diferencias ambientales entre ambas provincias biogeográficas del mar argentino.