

## Morphological plasticity in the Aristotle's lantern of *Arbacia dufresnii* (Phymosomatoida: Arbaciidae) off the Patagonian coast

Lucía Epherra<sup>1</sup>, Augusto Crespi-Abril<sup>1</sup>, Pablo Ezequiel Meretta<sup>2</sup>, Maximiliano Cledón<sup>2</sup> & Enrique Mario Morsan<sup>3</sup>, Tamara Rubilar<sup>1</sup>

1. Centro Nacional Patagonico (CENPAT-CONICET), Puerto Madryn, Chubut, Argentina; epherra@cenpat-conicet.gob.ar; rubilar@cenpat-conicet.gob.ar; crespia@cenpat-conicet.gob.ar
2. Universidad Nacional de Mar del Plata, Buenos Aires, Argentina; pabloemeretta@gmail.com, mcledon@mdp.edu.ar
3. Instituto de Biología Marina y Pesquera "Almirante Storni", San Antonio Oeste, Río Negro, Argentina; qmorsan@gmail.com

Received 19-VI-2014. Corrected 15-X-2014. Accepted 04-XI-2014.

**Abstract:** The relative size of the Aristotle's lantern of most sea urchins varies in relation to the food availability and it is often used to infer the availability of food of the environment. The aim of our study was to evaluate the lantern morphology plasticity of *Arbacia dufresnii* in populations with different environmental characteristics, either mussel beds or disturbed areas, by the invasive alga *Undaria pinnatifida* along the Patagonian Atlantic coast. The test diameter of the sea urchins along with the weight and height of the lanterns, the jaw length and rotula length were measured. Classic and geometric morphometric analyses were performed to test differences among populations. The length of the jaw was the best indicator of relative changes in size of the lantern. The largest length of the jaw was measured in individuals from disturbed areas dominated by the invasive algae *U. pinnatifida*. The rotula shape changed with the increase of the diameter of the sea urchins, it tends to be more elongated with larger sea urchins. Rev. Biol. Trop. 63 (Suppl. 2): 339-351. Epub 2015 June 01.

**Key words:** Echinoidea, *Arbacia dufresnii*, Patagonia, jaw, geometric morphometrics, food availability.

Plasticity in organs is crucial to optimize physiological efficiency and therefore maximize the reproductive output of an organism under changes in food availability and density of individuals (Levitan, 1991). Sea urchins allocate the energy in different organs depending generally on the availability of food (Hill & Lawrence, 2003). Most sea urchins allocate more resources to the Aristotle's lantern (the feeding apparatus) when food is scarce; the lantern becomes relatively larger at a low food availability to increase the strength of scraping. Therefore the difference in the size of the lantern relative to the test diameter is an adaptive morphological plasticity (Ebert, 1980; Ebert et al., 2014). Laboratory studies showed that when food is limiting, more growth occurs in the demi-pyramids (referred to jaw) compared

to the test (Levitan, 1991). On the other hand, when food availability is high, sea urchins present relative small lanterns and large gonads (Black, Codd, Hebbert, Vink & Burt, 1984; Fernández & Boudouresque, 1997; Ebert et al., 2014). However, the relative size of the Aristotle's lantern not always differs between populations (Ebert & Russel, 1992; Lawrence et al., 1996), which could be related to the species life-history strategy since in sea urchins species with stress tolerant strategy the plasticity tends to be minimal (Lawrence, 1990).

To evaluate the changes in the Aristotle's lantern, the frequently chosen method has been the classic morphometric by using the length of the jaw (Ebert, 1980; Levitan, 1991, 1992; Brey, Pearse, Basch, Clintock & Slattery 1995; Lawrence et al., 1996; McShane & Anderson,

1997; Wing, Gibbs & Lamare, 2003; Hagen, 2008; Pederson & Johnson, 2008; Hernández & Russell, 2010; Ebert et al., 2014), the length of the entire lantern (Black et al., 1982, 1984; Arnedo & Ibañez, 1985) or the lantern index (Edwards & Ebert, 1991; Fernández & Boudouresque, 1997; Garrido, 2003; Hill & Lawrence, 2003) as a variable. Classic morphometric focuses on a linear measurement, which impairs analyzing the presence of changes in the shape of the structure (Bookstein et al., 1985; Adams, Rohlf & Slice, 2004; Zelditch et al., 2004). Geometric morphometrics analysis solves these difficulties by analyzing specific points (landmarks) of a structure, making possible to focus on the shape changes (Rohlf, 1998; Richtsmeier et al., 2002; Adams et al., 2004). Given the importance of the structures of the Aristotle's lantern (jaw and rotula) in the feeding process of the sea urchins, it is important to analyze the morphological variation in length and shape of these structures.

*Arbacia dufresnii* (Blainville, 1825) is the most common sea urchin in the South Atlantic Ocean that inhabits both coasts of South America and it is the only species of the genus that it is not distributed exclusively in neotropical regions (Lessios et al., 2012; Wangensteen, 2013). *Arbacia dufresnii* has been described as a carnivore (Penchaszadeh & Lawrence, 1999), as an omnivorous in San Jorge gulf (Díaz de Vivar et al., 2012), and as an herbivore in Nuevo gulf and San José gulf (Galván et al., 2009). The different feeding habits would indicate different food availability along the patagonian coast and behavioral and morphological plasticity in the feeding habit of the species.

The aim of this study was to analyze the morphological plasticity of two structures of Aristotle's lantern (jaw and rotula) of *A. dufresnii* populations inhabiting different patagonian gulfs (San Matías, San José, Nuevo and San Jorge) by using both classic and geometric morphometric to further discuss its relation with different food availability at each environment.

**Study areas:** The study was conducted in the patagonian gulfs of Argentina: San Matías, San José, Nuevo and San Jorge, ranging from 40°50' to 47° S. Selected sites present different environmental characteristics, either mussel beds or disturbed areas by the invasive alga *Undaria pinnatifida*. The San Matías Gulf (SMG) is a semi-enclosed basin, partially connected with the open sea through a shallow sill (60 m depth) (Rivas & Beier, 1990). Its surface is 19 700 km<sup>2</sup> and has a maximum depth of 180 m (Mazio & Vara, 1983). The samplings were made in El Sótano (ES; 40° 56' 30" S - 65° 6' W), on NW coast. Bottom sediment is dominated by sand near the coast line and gradually mixed with shell hash, gravel, and mud (Escofet, Orensanz, Olivier & Scarabino, 1977; Morsan, 2008). This area is characterized by a soft bottom community dominated by bivalves and with scarce algae (Doldan, 2013).

San José Gulf (SJG) is located on the northern margin of Valdés Peninsula. It opens to SMG through a 6.9 km wide mouth located on its northwestern margin. Its surface is 817 km<sup>2</sup> with a mean depth of 40 m and maximum depth of 80 m (Amoroso & Gagliardini, 2010). Two sampling sites were selected in this gulf: Punta Tehuelche (PT; 42° 23' S - 64° 17' W) and Zona 39 (Z39; 42° 23' S - 64° 04' W). Both areas have similar hard bottom communities with abundance of macroalgae, there are shallow rocky reefs of limestone platforms (Zaixso et al., 1998; Boraso de Zaixso, Zaixso & Casas 1999). SJG has been invaded by the alien alga *U. pinnatifida* in 2004 (Irigoyen, 2009). Currently, *U. pinnatifida* dominates the PT area along with small mussels. Instead in Z39 the algae *Codium* sp. is the dominant one (Martelli et al., unpublished).

The Nuevo Gulf (NG), located on the southern margin of Valdés Peninsula, is an elliptical basin with a surface of 2440 km<sup>2</sup> and a maximum depth of 184 m that connects to the continental shelf through a 17 km wide gap (Mouzo et al., 1978). Punta Cuevas (PC, 42° 46' 44" S - 64° 59' 52" W), located near

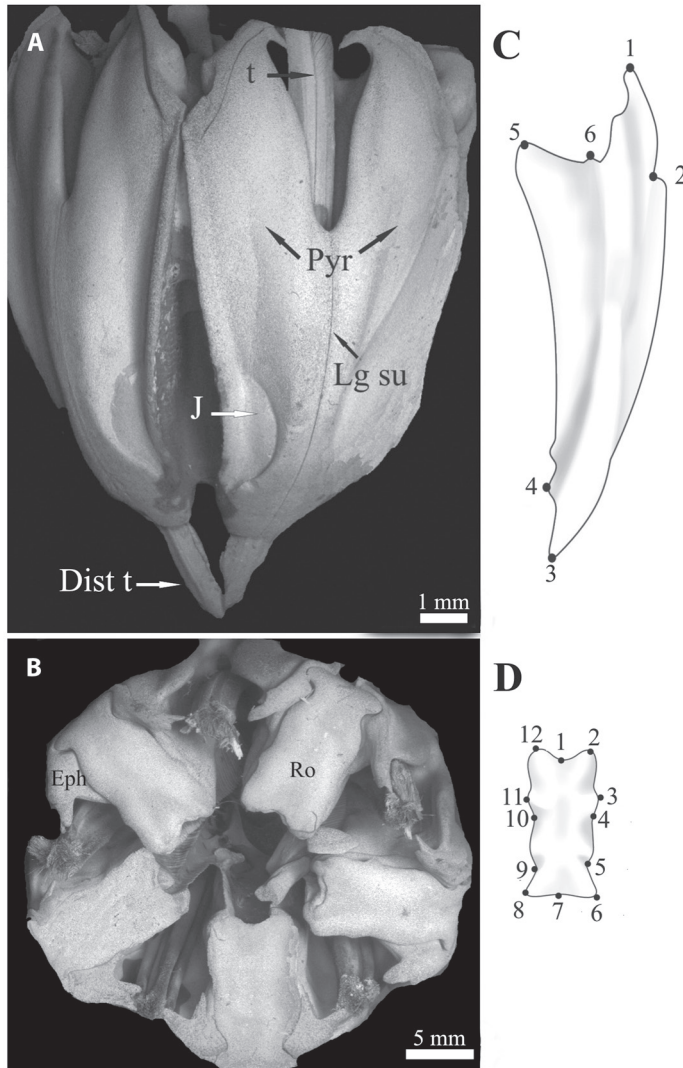
Puerto Madryn city, is a shallow rocky reef of limestone platforms (Irigoyen, Trobbiani, Sgarlatta & Raffo 2011) that has been invaded by *U. pinnatifida* for over 20 year (Casas & Piriz, 1996). Benthic community was dominated by the algae *Codium* spp., *Dyctiota* sp. and *Ulva* spp. before the invasion of *U. pinnatifida* (Piriz et al., 2003). After the invasion, every late winter and spring a dense forest of the invasive alga dominates the rocky reef (Casas et al., 2008). Its presence is associated with a dramatic decrease in species richness and diversity of native seaweeds (Casas, Piriz & Scrosati, 2004).

The San Jorge Gulf (SJOG), it is the southern patagonian gulf, which is the largest one with a surface area of 39340 km<sup>2</sup>. Its maximum depth is almost 110 m (Akselman, 1996) and open to waves entering from the Atlantic Ocean (Isla, Iantanos & Estrada, 2002). La Tranquera beach (LT, 46° 02' 33" S - 67° 35' 52" W) is a high energy rocky coast located in the central area of the gulf. There are extensive kelp forests of *Macrocystis pyrifera* in almost all the rocky sublittoral in the sampling area, with low incidence of the recently introduced *U. pinnatifida* (Zaixso et al., in press).

**Sample Processing:** Sea urchins were randomly collected by scuba diving at each site (ES = 29, PT = 30, Z39 = 41, and PC = 31). In the laboratory, all individuals were narcotized by immersion for 15 min in 5 % MgCl<sub>2</sub> in filtered seawater before dissection. Each sea urchin was blotted dry and wet mass and test diameter were determined. The Aristotle's lantern of *A. dufresnii* (Fig. 1) was dissected out, weighed and measured without disarticulating as proposed by Black et al. (1982). Lantern's soft tissue was removed by immersion in 5 % sodium hypochlorite for 24 h. Then, the lantern elements were thoroughly rinsed in tapwater and air dried. One jaw (ES = 29, PT = 30, Z39 = 41, PC = 31, LT = 31) and one rotula (ES = 18, PT = 30, Z39 = 31, PC = 29, LT = 31) were selected from each lantern to analyze the morphological variation. Photographs were taken on each structure with a digital

camera SONY DSC-W70 (7.2 Megapixels) mounted on a table top to ensure parallelism between the focal plane of the camera and frontal plane of the structure. Each jaw was placed with the inner side facing up to. Each photograph included a scale to standardize the structure sizes. In order to conduct classic morphometric analysis the linear length of jaw and rotula were obtained from the photographs using IMP (Integrated Morphometrics Package) software. Lengths were estimated from landmarks 3 to 6 and from 1 to 7 for jaw and rotula, respectively (see below, Figs. 1C, 1D). In order to conduct geometric morphometric analysis, lanterns from LT were incorporated to the analysis. Individual test diameters of sea urchin collected at LT were not available, however, the lantern were included in the geometric morphometric analysis because the urchins of this population presented almost twice test diameter than the other populations (ca. 50 mm, Epherra et al., 2014). For this analysis, six type-I landmarks arranged in two dimensions were used to characterize jaw shape (Fig. 1C). The rotula was placed with the oral surface facing up and 12 type-I landmarks arranged in two dimensions were selected to characterize structure shape (Fig. 1D). In all cases, landmark coordinates were obtained by using the software TPSDig version 2.

**Data analysis:** To test whether sea urchin Aristotle's lantern morphology measurements (lantern height, lantern weight, length of jaw and length of rotula) (dependent variables) varied between populations, test diameter or the presence of the invasive kelp *U. pinnatifida* (extrinsic variables) a generalized least square (GLS) model was performed. Since the Aristotle's lantern measurements data presented variance heterogeneity per site and in the presence or absence of *U. pinnatifida*, the variance structure with different spread per stratum ("VarIdent" Variance Structure) was included into GLS analyses. Variance structure considers that each factor's stratum has a different spread, modeling it on each case (for more detail see Zuur et al., 2009). Models



**Fig. 1.** *Arbacia dufresnii* Aristotle's lantern of obtained from a Scanning Electron Microscope. Lateral (A) and aboral (B) views of and schematic representations of a jaw, (C) and a rotula (D) with the location of landmarks.

with different number and combinations of the explanatory variables were fitted by Maximum Likelihood and the performance of each model was assessed by Information Theory (IT) procedures. To obtain the best model, Akaike's information criterion (AIC) was applied. AIC differences ( $\Delta_i$ ) and normalized weights of AIC ( $w_i$ ) of all possible models were computed (Burnham, Anderson & Huyvaert, 2011; Symonds & Moussalli, 2011). In addition, the 95% confidence intervals for parameters

estimated in the best model we calculated. Statistical analyses were performed by using the Open Access Software R 3.0.2 (R Development Core Team 2013). The function "gls" from the "nlme" package (Pinheiro et al., 2013) and the "bbmle" library (Bolker and R Development Core Team 2013) were used.

Shape changes in jaw and rotula were visualized through relative warp (RW) analysis. A principal component analysis was performed over the uniform and non-uniform components

of variation, where RW are the principal component orthogonal axis used to describe the main tendencies in shape variation between specimens within a sample (Bookstein, 1998). TpsRelw software Version 1.44 was used to translate, rotate, and scale the landmark configurations for each structure by using the generalized least squares (GLS) superimposition method. Translation and rotation was achieved by superimposing the landmark configurations and adjusting their individual inclination and relative position by minimizing the square root of the sum of squared differences between corresponding landmarks (Rohlf, 1999). Scaling was performed by correcting the landmark configurations in such way that all present the same centroid size. The program was also used to calculate the average individual map (consensus configuration), to derive the uniform (that affecting to the same extent all of the landmarks of the form under study) and non-uniform (all other landmark local differences) components of variation, and to estimate size of structures as the centroid size (the square root of the sum of the squared deviations of landmarks from a centroid point) (Rohlf, 1998; Richtsmeier et al., 2002).

## RESULTS

**Changes in size:** The relations between length of the jaw and the rotula and test diameter at the population are shown in Table 1. The length variation of the jaw and the rotula was best described by the minimal adequate generalized least square model (GLS) that incorporated the population and test diameter as explanatory variables. There were differences between populations for all Aristotle's lantern morphological measurements (lantern height, lantern weight, length of jaw and length of rotula). Moreover, the AIC indicates that the variance structure "*VarIdent*" improved the model compared to the linear regression model.

The jaw length was similar between PC and PT, ES and PT and ES and Z39. The lantern height, lantern weight and the rotula length were similar between ES and Z39 and ES and

TABLE 1

Generalized Least Square Models selection explaining sea urchin Aristotle's lantern morphological measurements variation due to test diameter and between sampled populations

Model	N° par <sub>i</sub>	lantern height			lantern weight			length of jaw			length of rotulae		
		AIC	$\Delta_i$	$w_i$	AIC	$\Delta_i$	$w_i$	AIC	$\Delta_i$	$w_i$	AIC	$\Delta_i$	$w_i$
Pop+ Diam	6	-86.88	10.45	0.01	111.84	6.27	0.04	39.26	2.4	0.22	-203.07	103.19	< 0.001
Pop+ Diam + var	9	-97.34*	0	0.99	105.57*	0	0.94	36.87*	0	0.72	306.26*	0	0.99
Diam + var	6	-82.38	14.96	< 0.001	113.65	8.08	0.02	74.45	37.59	< 0.001	-282.92	23.34	< 0.001
Pop + var	8	66.68	164.02	< 0.001	217.53	111.96	< 0.001	41.8	4.94	0.06	-186.46	119.8	< 0.001
null + var	5	60.94	158.27	< 0.001	223.33	117.76	< 0.001	72.26	35.59	< 0.001	-160.58	145.68	< 0.001
null	2	67.62	164.96	< 0.001	237.4	131.83	< 0.001	75.41	75.41	< 0.001	-149.39	156.87	< 0.001

N° par<sub>i</sub>, number of parameters; AIC, Akaike's information criterion;  $\Delta_i$ , AIC differences;  $w_i$ , normalized weights of AIC.

Pop, population; Diam, test diameter; var, "*VarIdent*" variance structure.

\* indicates the best models.

PT (Table 2). Nonetheless, differences between some populations were found, PC presented larger jaw values than ES and Z39, and PT jaw lengths were larger than Z39 (Table 2; Fig. 2).

The minimal adequate GLS model incorporated the presence of *Undaria pinnatifida* as an explanatory variable to account for the differences in jaw length, lantern height and rotula length between the populations (Table 3). The presence of *U. pinnatifida* was related to larger values of length of jaw (Fig. 2) and lantern height. However, the rotulae were larger in the absence of the invasive alga and the lantern weight did not differ in the presence or absence of *U. pinnatifida* (Table 3).

**Change in shape:** Relative warp analysis showed that the first and second relative warps explained more than 80 % of the total shape variation in both cases (RW1 61 % and RW2 19 % for jaw; RW1 68 % and RW2 17 % for rotula). There was a large overlap in shape of

sea urchins from different populations. As a general pattern, jaw shape changed gradually along RW1 mainly in the aboral region. Negative magnitudes of RW1 were associated to an elongated aboral tip of jaw (Fig. 3A). The shape of the jaw did not change with increasing centroid size (Fig. 3B). The main change in the rotula through the RW1 was along the longitudinal axis of the structure, the positive values were associated to a more elongated rotula (Fig. 4B). The rotula shape changed as centroid size increased (Fig. 4B). Sea urchins from all the populations presented a similar pattern of shape change of the rotula; larger sea urchins presented a more elongated overall shape than smaller sea urchins.

## DISCUSSION

In *Arbacia dufresnii* the relative length of the jaw was the classical measurement that best reflected the changes between populations. The

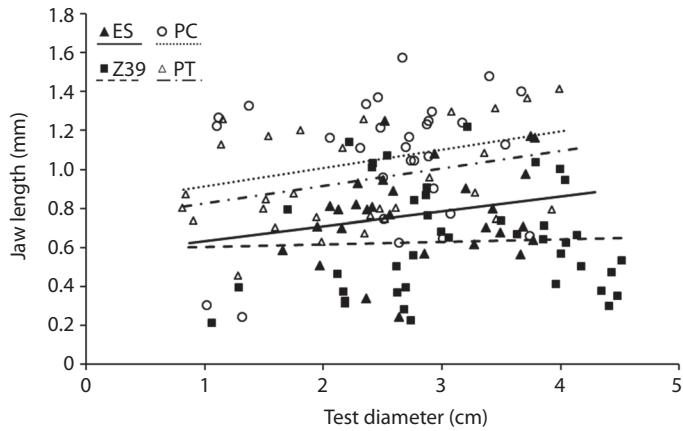
TABLE 2  
Parameter estimations for the selected Generalized Least Square Models explaining sea urchin Aristotle's lantern morphological measurements variation due to test diameter and between sampled populations

Response Variable	Coefficients	Estimate	CI	
		± SE	Lower	Upper
lantern height	Intercept	0.23 ± 0.06	0.11	0.34
	Pop - PT	0.01 ± 0.06	- 0.1	0.12
	Pop - ES	-0.07 ± 0.05	- 0.17	0.03
	Pop - Z39	-0.16 ± 0.05	- 0.26	- 0.06
	Diam	0.30 ± 0.02	0.27	0.33
lantern weight	Intercept	- 0.82 ± 0.11	- 1.04	- 0.6
	Pop -PT	0.43 ± 0.11	0.22	0.64
	Pop -ES	0.17 ± 0.09	- 0.01	0.34
	Pop -Z39	0.09 ± 0.08	- 0.06	0.25
	Diam	0.57 ± 0.04	0.49	0.64
length of jaw	Intercept	0.90 ± 0.09	0.72	1.08
	Pop - PT	- 0.10 ± 0.07	- 0.25	0.04
	Pop - ES	- 0.30 ± 0.07	- 0.45	- 0.16
	Pop - Z39	- 0.47 ± 0.07	- 0.61	- 0.32
	Diam	0.06 ± 0.03	0.01	0.12
length of rotulae	Intercept	0.02 ± 0.01	- 0.004	0.04
	Pop - PT	0.04 ± 0.01	0.02	0.06
	Pop - ES	0.04 ± 0.02	0.01	0.08
	Pop - Z39	0.08 ± 0.03	0.03	0.13
	Diam	0.10 ± 0.004	0.1	0.11

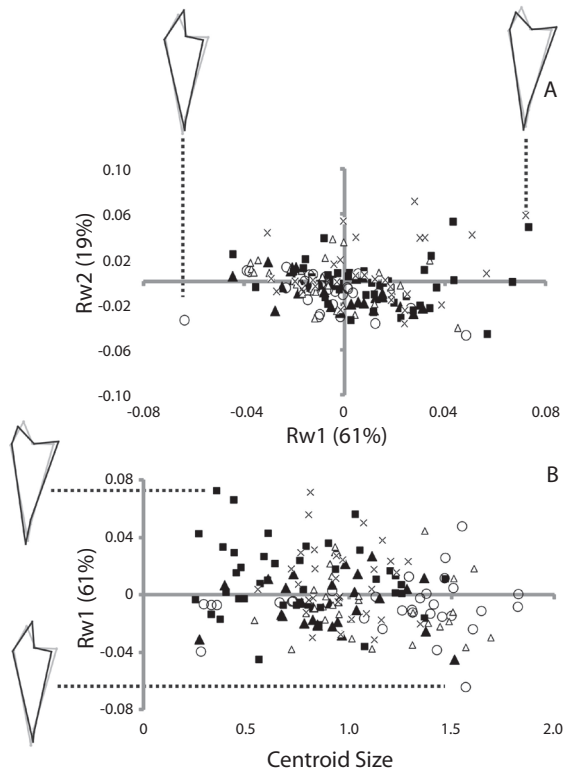
CI, 95 % confidence intervals;

ES, El Sotano; Z39, Zona 39 PT, Punta Tehuelche; PC, Punta Cuevas.

The parameter for Pop (Population) is given as relative to Punta Cuevas population.



**Fig. 2.** Relationship between jaw length (mm) and test diameter (cm) between the selected sites: El Sotano (ES), Zona 39 (Z39), Punta Tehuelche (PT) and Punta Cuevas (PC). White symbols correspond to the presence of *Undaria pinnatifida*; black symbols represent the sampled sites without *U. pinnatifida*. The lines indicate the estimated mean of generalized least square model.



**Fig. 3.** (A) Scatterplots of the first and second components of the relative warp analysis (RW1 and RW2 respectively) using jaw of *Arbacia dufresnii* and (B) of the centroid size and first component of the relative warp analysis. Filled squares correspond to individuals from the location Zona 39, filled triangles correspond to individuals from the location El Sótano, empty triangles correspond to individuals from the location Punta Tehuelche, empty circles correspond to individuals from the location Punta Cuevas, and crosses correspond to individuals from the location La Tranquera. In parenthesis is expressed the percentage of the total shape variation explained by each component or the relative warp analysis. On RW1 axis is represented the shape of jaw at the extremes values of the axis.

TABLE 3  
Generalized Least Square Models selection explaining sea urchin Aristotle's lantern morphology measurements variation due to the presence of invasive algae *Undaria pinnatifida* and test diameter

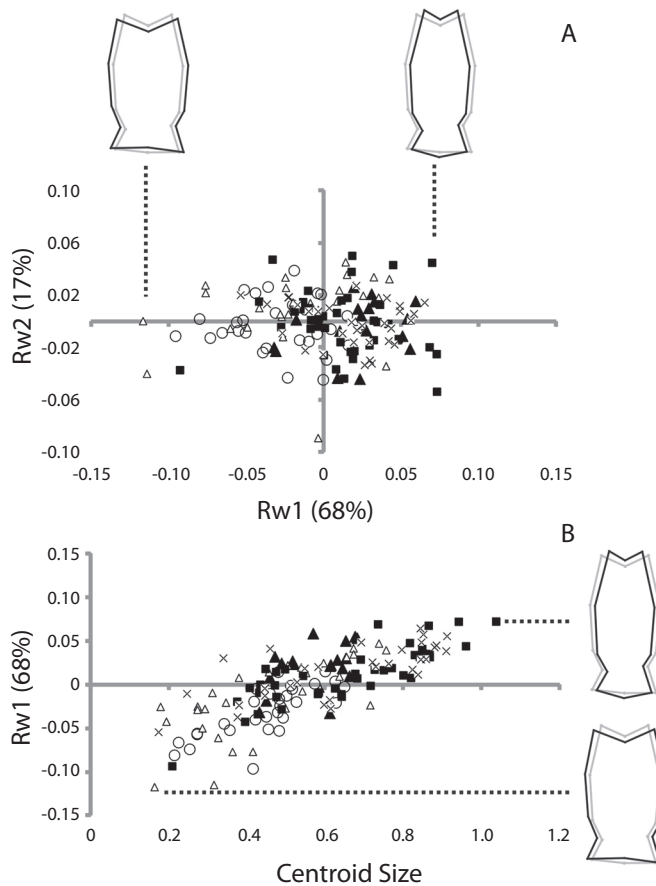
Model	N° par <sub>i</sub>	lantern height			lantern weight			jaw length			length of rotulae		
		AIC	$\Delta_i$	w <sub>i</sub>	AIC	$\Delta_i$	w <sub>i</sub>	AIC	$\Delta_i$	w <sub>i</sub>	AIC	$\Delta_i$	w <sub>i</sub>
Und + Diam	4	-85.85	9.99	0.01	126.6	3.39	0.12	42.65	1.94	0.24	-203.62	60.97	<0.001
Und + Diam + var	5	-95.84	0	0.99	125.42*	2.21	0.22	43.65	2.94	0.14	-264.6*	0	0.79
Diam + var	4	-85.36	1.48	<0.001	123.21	0	0.66	77.91*	37.2	<0.001	-261.91	2.68	0.21
Und + var	4	60.86*	156.7	<0.001	236.26	113.05	<0.001	40.71	0	0.62	-174.28	90.32	<0.001
null + var	3	59.34	155.18	<0.001	237.88	114.67	<0.001	75.41	34.69	<0.001	-148.47	116.13	<0.001
null	2	67.62	163.47	<0.001	237.4	114.19	<0.001	75.95	35.23	<0.001	-149.39	115.2	<0.001

N° par<sub>p</sub>, number of parameters; AIC, Akaike's information criterion;  $\Delta_i$ , AIC differences; w<sub>p</sub>, normalized weights of AIC.  
Pop, *Undaria pinnatifida*; Diam, test diameter; var, "VarIdent" variance structure. \* indicates the best models.

lantern weight and lantern height did not separate populations, because the minimal adequate GLS revealed a large values overlap. The geometric morphometric analysis of the structures of the Aristotle's lantern of *A. dufresnii* showed that the shape of the jaw did not vary among populations or with the increase in diameter of the sea urchins. Given that the jaws grow on all surfaces (Ebert, 1982), it appears that both ends of the lantern of *A. dufresnii* are growing at the same time therefore the shape of the jaw does not change. The rotula shape did not change between populations; however, it did change with the increase of the diameter of the sea urchins. Considering that the rotulae articulate the jaws in the aboral face, bigger jaws should have more elongated rotulae, therefore the changes in shape would be explained by the growth of the lantern.

Energy allocation plasticity in the lantern appears to be related to food availability. A larger lantern would increase the strength of scraping (Ebert, 1980), therefore increasing the grazing potential, which is likely to be of adaptive significance in resource-limited environments (Black et al., 1984). The genus *Arbacia* has been described as omnivorous with a strong tendency to carnivory (Vásquez et al., 1984; Fernández & Boudouresque, 1997; Penchaszadeh & Lawrence, 1999; Hill & Lawrence, 2003; Cobb & Lawrence, 2005; Wangsteen et al., 2011); the sea urchins have a wide range of food item and due to the ability to feed on encrusting algae and protected animals with hard calcareous shells, it has been suggested that their large Aristotle's lantern is indicative of a durophagic habit (Gianguzza & Bonaviri, 2013). Similarly, Hagen (2008) studied two different sympatric species of the genus *Strongylocentrotus* and postulated that the enlargement in size of the lantern is a functional specialization for durophagy (ability to exploit hard shelled prey). More specifically, in the genus *Arbacia*, *A. lixula* may change their feeding habit in relation to the availability of food in the field; when algae are low they can be carnivorous and when algae are abundant are usually omnivorous (Cobb &





**Fig. 4.** (A) Scatterplots of the first and second components of the relative warp analysis (RW1 and RW2, respectively) using rotula of *Arbacia dufresnii* and (B) of the centroid size and first component of the relative warp analysis. Filled squares correspond to individuals from the location Zona 39, filled triangles correspond to individuals from the location El Sótano, empty triangles correspond to individuals from the location Punta Tehuelche, empty circles correspond to individuals from the location Punta Cuevas, and crosses correspond to individuals from the location La Tranquera. In parenthesis is expressed the percentage of the total shape variation explained by each component or the relative warp analysis. On RW1 axis is represented the shape of rotulae at the extremes values of the axis.

Lawrence, 2005). In ES, an area with scarce algal coverage (Doldán, 2013), *A. dufresnii* would feed on the spat of bivalves that are abundant (Penchazadeh & Lawrence, 1999). In fact, a study of its diet in this area indicated that they are predators (Rubilar et al. in prep). On the other hand, sea urchins from ES did not present larger jaws as expected. Therefore, the hypothesis that enlarged lantern size is an adaptation for durophagy may be useful to compare between species rather than among populations. Examples of this can be found in

the data published comparison among species (e.g. Contreras & Castilla, 1987; Hagen, 2008; Bonaviri et al., 2011; Agnetta et al., 2013).

In both SJG and NG populations of *A. dufresnii* present an omnivorous habit with tendency to herbivory (Galvan et al, 2009; Castro, 2014). The analysis of the relative jaws length showed that, although in these three populations the sea urchins tend to have an herbivorous habit, the range of length jaw was large. The relative jaw length has been a useful way to infer the food availability in

field populations of sea urchins (Ebert 1980, Levitan 1991, Fernández & Boudouresque, 1997; McShane & Anderson, 1997; Pederson & Johnson, 2008; Ebert et al., 2014). Therefore, food availability may be responsible for the differences in jaw length among populations of SJG and NG.

Both areas inside GSJ, PT and Z39, are characterized by high abundance of macroalgae (Boraso de Zaixso et al., 1999), however, both populations presented different relative jaw length. Sea urchins with the smallest jaw were found in Z39 population, which would indicate the highest food availability of the populations under study. According to Castro (2014) sea urchins from Z39 present a more diverse and stable diet all year round. Therefore, differences in diet may be responsible for the differences in jaw length found between these two populations.

Sea urchins from areas invaded by *Undaria pinnatifida*, PC and PT, presented similar relative jaw length; these lanterns were the larger ones. This would indicate that these areas presented the lowest food availability among the studied populations of *A. dufresnii*. Even though, *U. pinnatifida* would be a new food item, does not imply that availability of food increases. According to Casas et al. (2004), invasive macroalgae presence is associated with a decrease in species richness and diversity of native macroalgae. In addition, *A. dufresnii* feeds on *U. pinnatifida* only during the summer when the macroalgae is rotten (Teso, Bigatti, Casas, Piriz & Penchaszadeh, 2009; Castro, 2014). Moreover, the presence of *U. pinnatifida* produces an increment in the density of *A. dufresnii* in natural environment (Irigoyen et al., 2011), Therefore, *U. pinnatifida* favors a scenario in which the availability of food is decreased due to the competition between sea urchins and declining of richness of native algae, creating an environment similar to the barrens that are characterized by low food availability (Pederson & Johnson, 2008).

Despite the lack of direct evidence, the differences found in the relative jaw length among the populations under study appear

mainly related to differences in food availability, and indirectly influenced by the presence of *U. pinnatifida*. However, other factors such as density (Black et al. 1982; Garrido, 2003), feeding habit or preference, and reproductive cycle may be also important to evaluate. The results found in this study along with the differences found in reproductive traits (Epherra et al., 2014) support the idea that *A. dufresnii* presents high phenotypic plasticity that allows the species to have a wide distribution in different environments.

## ACKNOWLEDGMENTS

We gratefully acknowledge Damian Gil from the Universidad Nacional de la Patagonia San Juan Bosco, Sede Comodoro Rivadavia for providing Aristotle's lantern of La Tranquera, San Jorge Gulf. This study is part of the Doctoral Thesis of L. Epherra at the Universidad Nacional de Mar del Plata. The present study received financial supported from the Universidad Nacional del Comahue (Project M0-19), the Universidad Nacional de Mar del Plata (EXA586/12) and by PIP 0798 CONICET.

## RESUMEN

**Plasticidad morfológica en la linterna de Aristoteles en *Arbacia dufresnii* (Phykosomatoida: Arbaciidae) en la costa Patagónica.** El tamaño relativo de la linterna de Aristóteles en la mayoría de las especies de erizos de mar varía en relación con la disponibilidad de alimentos y se utiliza a menudo para inferir la disponibilidad de alimentos en el medio ambiente en que los erizos de mar habitan. El objetivo de este estudio fue evaluar la plasticidad morfológica de la linterna de Aristóteles de *Arbacia dufresnii* en poblaciones con diferentes características ambientales, ya sean con bancos de mejillones o áreas modificadas por el alga invasora *Undaria pinnatifida*, a largo de la costa patagónica atlántica. Se midió el diámetro del caparazón, el peso y el alto de las linternas, la longitud de la semipirámide y la longitud de la rótula. Los datos se analizaron utilizando técnicas de morfometría clásica y geométrica con el objetivo de probar diferencias entre las poblaciones. La longitud de la semipirámide fue el mejor indicador para describir los cambios relativos en el tamaño de la linterna. La mayor longitud de la semipirámide se observó en las poblaciones que habitan áreas dominadas por el alga invasora *U. pinnatifida*. La forma de la semipirámide no varía

entre las poblaciones ni con el tamaño de los erizos de mar, mientras que la forma de la rótula cambia en relación al tamaño de los erizos, siendo más alargada cuando el tamaño de los individuos es mayor.

**Palabras clave:** Echinoidea, *Arbacia dufresnii*, Patagonia, mandíbula, morfometría geométrica, disponibilidad de alimento.

## REFERENCES

- Adams, D. C., Rohlf, F. J., & Slice, D. (2004). Geometric morphometrics: ten years of progress following the 'revolution'. *Italian Journal of Zoology*, *71*, 5-6.
- Agnetta, D., Bonaviri, C., Badalamenti, F., Scianna, C., Vizzini, S., & Gianguzza, P. (2013). Functional traits of two co-occurring sea urchins across a barren/forest patch system. *Journal of Sea Research*, *76*, 170-177.
- Akselman, R. (1996). *Estudios ecológicos en el Golfo San Jorge y adyacencias (Atlántico sudoccidental). Distribución, abundancia y variación del fitoplancton en relación a factores físicos-químicos y a la dinámica hidrográfica* (Tesis de doctorado). Universidad de Buenos Aires, Argentina.
- Amoroso, R. O., & Gagliardini, D. A. (2010). Inferring complex hydrographic processes using Remote-Sensed Images: Turbulent fluxes in the Patagonian Gulfs and implications for scallop metapopulation dynamics. *Journal of Coastal Research*, *26*, 320-332.
- Arnedo, M. & Ibañez, M. (1985). Estudio comparativo de la Linterna de Aristóteles en dos poblaciones del erizo de mar *Paracentrotus lividus* (Lamarck) (Echinodermata, Echinoidea). *Lurralde: Investigación y espacio*, *8*, 13-19.
- Black, R., Johnson, M. S., & Trendall, J. T. (1982). Relative size of Aristotle's lantern in *Echinometra mathaei* occurring at different densities. *Marine Biology*, *71*, 101-106.
- Black, R., Codd, C., Hebbert, D., Vink, S., & Burt, J. (1984). The functional significance of the relative size of Aristotle's lantern in the sea urchin *Echinometra mathaei* (de Blainville). *Journal of Experimental Marine Biology and Ecology*, *77*, 81-97.
- Bolker, B., & R Development Core Team. (2013). *bbmle: Tools for general maximum likelihood estimation*. Retrieved from <http://CRAN.R-project.org/package=bbmle>.
- Bonaviri, C., Vega Fernández, T., Fanelli, G., Badalamenti, F., & Gianguzza, P. (2011). Leading role of the sea urchin *Arbacia lixula* in maintaining the barren state in southwestern Mediterranean. *Marine Biology*, *158*, 2505-2513.
- Bookstein, F. L. (1998). A hundred years of morphometrics. *Acta Zoologica Academiae Scientiarum Hungaricae*, *44*, 7-59.
- Bookstein, F. L., Chernoff, B., Elder, R. L., Humphries, J. M., Smith, G. R., & Strauss, R. E. (1985). Morphometrics in evolutionary biology: the geometry of size and shape change, with examples from fishes. *The Academy of Natural Sciences of Philadelphia*, *15*, 1-277.
- Boraso de Zaixso, A. L., Zaixso, H. E., & Casas, G. (1999). Asociaciones de algas bentónicas submareales en el golfo San José (Chubut, Argentina). *Physis*, *57*, 17-27.
- Brey, T., Pearse, J. S., Basch, L., Mc Clintock, J. B., & Slattery, M. (1995). Growth and production of *Stechinus neumayeri* (Echinoidea: Echinodermata) in McMurdo Sound, Antarctica. *Marine Biology*, *124*, 279-292.
- Burnham, K. E., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, *65*, 23-35.
- Casas, G. N., & Piriz, M. L. (1996). Surveys of *Undaria pinnatifida* (Laminariales, Phaeophyta) in Golfo Nuevo, Argentina. *Hidrobiología*, *326/327*, 213-215.
- Casas, G. N., Piriz, M. L., & Parodi, E. R. (2008). Population features of the invasive kelp *Undaria pinnatifida* (Phaeophyceae: Laminariales) in Nuevo Gulf (Patagonia, Argentina). *Journal of the Marine Biological Association of the United Kingdom*, *88*, 21-28.
- Casas, G. N., Piriz, M. L., & Scrosati, R. (2004). The invasive kelp *Undaria pinnatifida* (Phaeophyceae, Laminariales) reduces native seaweed diversity in Nuevo Gulf (Patagonia, Argentina). *Biological Invasions*, *6*, 411-416.
- Castro, K. L. (2014). *Dieta del erizo verde de mar Arbacia dufresnii y su relación con el alga invasora Undaria pinnatifida en costas del Golfo San José, Patagonia* (Tesis). Universidad Nacional del Comahue, Bariloche, Argentina.
- Cobb, J., & Lawrence, J. M. (2005). Diets and coexistence of the sea urchin *Lytechinus variegatus* and *Arbacia punctulata* (Echinodermata) along the central Florida gulf coast. *Marine Ecology Progress Series*, *205*, 171-182.
- Contreras, S., & Castilla, J. C. (1987). Feeding behavior and morphological adaptations in two sympatric sea urchin species in central Chile. *Marine Ecology Progress Series*, *38*, 217-224.
- Díaz de Vivar, M. E., Pastor, C. T., Rubilar, T., Gil, D. G., Tolosano, J. A., Epherra, L., ... Pérez-Gallo, S. (2012). *Arbacia dufresnii* (Blainville, 1825) (Echinodermata, Echinoidea): Dieta, Estado Nutricional

- y Ciclo Reproductivo en dos poblaciones de la Patagonia Central (Reporte técnico). Chubut, Argentina: Universidad Nacional de la Patagonia San Juan Bosco.
- Doldan, M. S. (2013). *Patrones y procesos de la dinámica poblacional de la ostra puelche, Ostrea puelchana, (D'Orbigny, 1842)* (Tesis de doctorado). Instituto de Biología Marina y Pesquera "Almirante Storni", Universidad de Buenos Aires. Argentina.
- Ebert, T. A. (1980). Relative growth of sea urchin jaws: an example of plastic resource allocation. *Bulletin of Marine Science*, 30, 467-474.
- Ebert, T. A. (1982). Longevity, life history, and relative body wall size in sea urchins. *Ecological Monograph*, 52, 353-394.
- Ebert, T. A., & Russell, M. P. (1992). Growth and mortality estimates for red sea urchin *Strongylocentrotus franciscanus* from San Nicolas Island, California. *Marine Ecology Progress Series*, 81, 31-41.
- Ebert, T. A., Hernández, J. C., & Clemente, S. (2014). Annual reversible plasticity of feeding structures: cyclical changes of jaw allometry in a sea urchin. *Proceedings of the Royal Society B*, 281, 20132284.
- Edwards, P. B., & Ebert, T. A. (1991). Plastic responses to limited food availability and spine damage in the sea urchin *Strongylocentrotus purpuratus* (Stimpson). *Journal of Experimental Marine Biology and Ecology*, 145, 205-220.
- Epherra, L., Gil, D. G., Rubilar, T., Pérez Gallo, S., Reartes, B., & Tolosano, J. A. (2014). Temporal and spatial differences in the reproductive biology of the sea urchin *Arbacia dufresnii*. *Marine and Freshwater Research*, 66(4), 329-342.
- Escofet, A., Orensanz, J. M., Olivier, S. R., & Scarabino, F. (1977). Biocenología bentónica del Golfo San Matías (Río Negro, Argentina): metodología, experiencias y resultados del estudio ecológico de un gran espacio geográfico en América latina. *Anales Centro Ciencias del Mar y Limnología Universidad Autónoma de México*, 5, 59-82.
- Fernández, C., & Boudouresque, C. F. (1997). Phenotypic plasticity of *Paracentrotus lividus* (Echinodermata: Echinoidea) in a lagoonal environment. *Marine Ecology Progress Series*, 152, 145-154.
- Galván, D. E., Botto, F., Parma, A. M., Bandieri, L., Mohamed, N., & Iribarne, O. (2009). Food partitioning and spatial subsidy in shelter-limited fishes inhabiting patchy reefs of Patagonia. *Journal of Fish Biology*, 75, 2585-2605.
- Garrido, M. J. (2003). *Contribución al conocimiento de Diadema antillarum Philippi 1845, en Canarias* (Tesis de doctorado). Departamento de Biología, Universidad de las Palmas de Gran Canaria, España.
- Gianguzza, P., & Bonaviri, C. (2013). *Arbacia*. In J. M. Lawrence (Ed.), *Sea Urchins: Biology and Ecology* (pp. 275-283). Oxford: Academic Press.
- Hagen, N. T. (2008). Enlarged lantern size in similar-sized, sympatric, sibling species of Strongylocentrotid sea urchins: from phenotypic accommodation to functional adaptation for durophagy. *Marine Biology*, 153, 907-924.
- Hernández, J. C., & Russell, M. P. (2010). Substratum cavities affect growth-plasticity, allometry, movement and feeding rates in the sea urchin *Strongylocentrotus purpuratus*. *The Journal of Experimental Biology*, 213, 520-525.
- Hill, S. K., & Lawrence, J. M. (2006). Interactive effects of temperature and nutritional condition on the energy budgets of the sea urchins *Arbacia punctulata* and *Lytechinus variegatus* (Echinodermata: Echinoidea). *Journal of Marine Biological Association of the United Kingdom*, 86, 783-790.
- Irigoyen, A. J. (2009). *Undaria pinnatifida en el Golfo Nuevo, Argentina*. (Reporte Técnico). Chubut, Argentina: Dirección de pesca de la Provincia del Chubut y Ministerio de Ambiente y Control del Desarrollo Sustentable.
- Irigoyen, A. J., Trobbiani, G., Sgarlatta, M. P., & Raffo, M. P. (2011). Effects of the alien algae *Undaria pinnatifida* (Phaeophyceae, Laminariales) on the diversity and abundance of benthic macrofauna in Golfo Nuevo (Patagonia, Argentina): potential implications for local food webs. *Biological Invasions*, 13, 1521-1532.
- Isla, F. I., Iantanos, N., & Estrada, E. (2002). Playas reflectivas y disipativas macromareales del Golfo San Jorge, Chubut. *Revista de la Asociación Argentina de Sedimentología*, 9, 155-164.
- Lawrence, J. M. (1990). The effect of stress and disturbance on echinoderms. *Zoological Science*, 7, 17-28.
- Lawrence, J. M., Vásquez, J., Robbins, B. D., & Vega, A. (1996). Lack of plasticity of the body form, Aristotle's lantern and spines of *Tetrapygus niger* (Echinodermata: Echinoidea). *Gayana Oceanology*, 4, 93-97.
- Lessios, H. A., Lockhart, S., Collin, R., Sotil, G., Sánchez-Jerez, P., Zigler, K., ... Bernardi, G. (2012). Phylogeography and bindin evolution in *Arbacia*, a sea urchin genus with an unusual distribution. *Molecular Ecology*, 21, 130-144.
- Levitan, D. R. (1991). Skeletal changes in the test and jaws of the sea urchin *Diadema antillarum* in response to food limitation. *Marine Biology*, 111, 431-435.
- Levitan, D. R. (1992). Community structure in time past: Influence of human fishing pressure on algal-urchin interactions. *Ecology*, 73, 1597-1605.

- Mazio, C. & Vara, C. (1983). Las mareas del Golfo San Matías, Argentina. *Technical Report Servicio de Hidrografía Naval*, 13.
- McShane, P. E., & Anderson, O. F. (1997). Resource allocation and growth rates in the sea urchin *Evechinus chloroticus* (Echinoidea: Echinometridae). *Marine Biology*, 128, 657-663.
- Morsan, E. M. (2008). Impact on biodiversity of scallop dredging in San Matías Gulf, northern Patagonia (Argentina). *Hidrobiología*, 619, 167-180.
- Mouzo, F., Garza, M., Izquierdo, J., & Zibecchi, R. (1978). Rasgos de la geología submarina del Golfo Nuevo (Chubut). *Acta Oceanographica Argentina*, 2, 69-91.
- Pederson, H. G., & Johnson, C. R. (2008). Growth and age structure of sea urchins (*Heliocidaris erythrogramma*) in complex barrens and native macroalgal beds in eastern Tasmania. *ICES Journal of Marine Science*, 65, 1-11.
- Penchaszadeh, P., & Lawrence, J. M. (1999). *Arbacia dufresnei* (Echinodermata: Echinoidea): A carnivore in Argentinian waters. In M. D. Candia-Carnevali, & F. Bonasoro (Eds.), *Echinoderm Research* (pp. 525-530). Rotterdam: Balkema.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Development Core Team (2013). nlme: Linear and Nonlinear Mixed Effects Models. *R package version*, 3, 1-111.
- Piriz, M. L., Eyra, M. C., & Rostagno, C. M. (2003). Changes in biomass and botanical composition of beach-cast seaweeds in a disturbed coastal area from Argentine Patagonia. *Journal of Applied Phycology*, 15, 67-74.
- R Development Core Team (2013). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from <http://www.R-project.org/>
- Richtsmeier, J. T., Burke de Leon, V., & Lele, S. R. (2002). The promise of geometric morphometrics. *Yearbook of Physiology and Anthropology*, 45, 63-91.
- Rivas, A. L., & Beier, E. J. (1990). Temperature and salinity fields in the Northpatagonic Gulfs. *Oceanologica Acta*, 13, 15-20.
- Rohlf, F. J. (1998). On applications of geometric morphometrics to studies of ontogeny and phylogeny. *Systematic Biology*, 47, 147-158.
- Rohlf, F. J. (1999). Shape statistics: Procrustes superimpositions and tangent spaces. *Journal of Classification*, 16, 197-223.
- Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, 65, 13-21.
- Teso, S. V., Bigatti, G., Casas, G. N., Piriz, M. L., & Penchaszadeh, P. E. (2009). Do native grazers from Patagonia, Argentina consume the invasive kelp *Undaria pinnatifida*? *Revista Museo Argentino de Ciencias Naturales*, 11, 7-14.
- Vásquez, J., Castilla, J. C., & Santelices, B. (1984). Distributional patterns and diets of four species of sea urchins in giants kelp forest (*Macrocystis pyrifera*) of Puerto Toro, Navarino Islands, Chile. *Marine Ecology Progress Series*, 19, 55-63.
- Wangensteen, O. S. (2013). *Biology and phylogeography of the black sea urchin Arbacia lixula (Echinoidea: Arbacioida)* (Doctoral thesis). Departament de Biologia Animal, Universitat de Barcelona, España.
- Wangensteen, O. S., Turon, X., García-Cisneros, A., Recasens, M., Romero, J., & Palacín, C. (2011). A wolf in sheep's clothing: carnivory in dominant sea urchins in the Mediterranean. *Marine Ecology Progress Series*, 128, 117-128.
- Wing, S. R., Gibbs, M. T., & Lamare, J. (2003). Reproductive sources and sinks within a sea urchin, *Evechinus chloroticus*, population of a New Zealand fjord. *Marine Ecology Progress Series*, 248, 109-123.
- Zaixso, H. E., Boraso de Zaixso, A. L., Pastor de Ward, C. T., Lizarralde, Z., Dadón, J., & Galván, D. E. (2006). El bentos costero patagónico. In H. E. Zaixso (Ed.), *La zona costera patagónica Argentina*. Comodoro Rivadavia: Editorial Universitaria Patagónica.
- Zaixso, H. E., Lizarralde, Z. I., Pastor, C. T., Gomes-Simes, E., Romanello, E., & Pagnoni, G. (1998). Distribución espacial del macrozoobentos submareal del Golfo San José (Chubut, Argentina). *Revista de Biología Marina y Oceanografía*, 33, 43-72.
- Zelditch, M. L., Swiderski, D. L., Sheets, H. D., & Fink, W. (2004). *Geometric Morphometrics for Biologists*. New York: Elsevier Academic Press.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer.

