



## ORIGINAL ARTICLE

# Growth pattern and changes in abundance of the endangered bat star *Asterina stellifera*

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## Keywords

Asteroidea; growth modeling; population dynamics; subtidal habitat; threatened species.

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## Abstract

The sea star *Asterina stellifera* has declined during the last decade and is currently abundant only in the southern limit of its former range. We surveyed this population over 5 years to model individual growth and explore the relationship of changes in local abundance with variation in environmental factors and the reproductive status of individuals. Our results show that *A. stellifera* is a species with slow growth and a relatively long lifespan. Contrary to expectations for temperate species, growth rates were fairly constant through the year and therefore models including seasonal oscillations were inappropriate. The abundance of this species increased significantly from early spring to early summer, likely due to augmented activity and small-scale aggregation during the reproductive season that affected our estimates of abundance. No significant recruitment occurred during the 5 years studied. The lack of recruitment during long periods and the slow individual growth rates make *A. stellifera* particularly vulnerable to local extinction. This study was performed prior to the arrival in the study area of the invasive kelp *Undaria pinnatifida* and side-gilled sea slug *Pleurobranchaea maculata*, species that threaten the community structure where *A. stellifera* lives. Therefore, the information reported here will be essential to assessing the impacts of these exotic species on this sea star population.

## Introduction

The bat star *Asterina stellifera* (Valvatida: Asterinidae) is an important omnivorous predator in rocky bottoms of shallow-water areas (Farias *et al.* 2012). The species is endemic to the Southwestern Atlantic Ocean, ranging from Cabo Frio, Brazil (23° S, 42° W) to Mar del Plata, Argentina (35° S, 56° W) (Clark & Downey 1992). During the last decade the abundance of *A. stellifera* in northern and central areas has declined to the point of being included in the Brazilian list of endangered species (Ministério do meio ambiente 2004; Calil *et al.* 2009). Recent surveys of northern populations indicated that this trend is not reverting (Meretta 2014). Given the role of *A. stellifera* at a community level (Farias *et al.* 2012),

the potential consequences of such declines are of concern beyond the sole loss of diversity.

Currently, the only location where *A. stellifera* is still commonly seen (Farias *et al.* 2012) is the city of Mar del Plata, Argentina, which, interestingly, is the southern limit of its latitudinal distribution (Fig. 1). The accelerating development of Mar del Plata's shoreline for industry, agriculture and tourism during the last decade (Boschi 2004; Isla 2004) is degrading coastal ecosystems by habitat disturbance and pollution (Orensanz *et al.* 2002; Albano *et al.* 2013). Moreover, the recent arrival in the area of two invasive species, the kelp *Undaria pinnatifida* (Meretta *et al.* 2012) and the sea slug *Pleurobranchaea maculata* (Farias *et al.* 2015) add potential threats to this *A. stellifera* population. The algae *U. pinnatifida*

competes for space and often displaces many benthic species (Casas *et al.* 2004; Farias *et al.* 2012; Meretta 2014) that are important prey items of *A. stellifera* while *P. maculata* is a voracious predator whose diet widely overlaps that of this sea star (Meretta 2014). This scenario of declining populations in the context of accelerating habitat degradation (Nuñez *et al.* 2012; Albano *et al.* 2013) highlights the need to assess the current status of *A. stellifera* along its entire distribution and gather the basic biologic data essential for conservation purposes. Changes in abundance are commonly used as indicators of population health and well-being. However, predicting responses to environmental changes at a population level requires knowledge of quantitative values of life-history traits such as physiologic condition and individual growth rates. Changes in these parameters may affect demographic model predictions and the reliability of analyses that are often used to assist in management and conservation of species (*e.g.* elasticity analysis, Spencer & Janzen 2010).

The aim of this study was to survey the growth rates of *A. stellifera* individuals in the only place where it is still abundant and to assess the relationship among changes in local abundance and variations in selected intrinsic (gonadal stage) and extrinsic (water temperature and salinity, rainfall) factors. To this end, we used a monthly data set covering 5 years prior to the arrival of the invasive kelp *U. pinnatifida* (Meretta *et al.* 2012) and grey sea slug *P. maculata* (Farias *et al.* 2015). Thus, this work provides crucial baseline information for further assessments of the effect of these invasive species on *A. stellifera*.

## Material and Methods

### Study site, sampling and collection of environmental data

Monthly population censuses were conducted by SCUBA diving within the Mar del Plata port, Argentina ( $38^{\circ}02' S$ ,

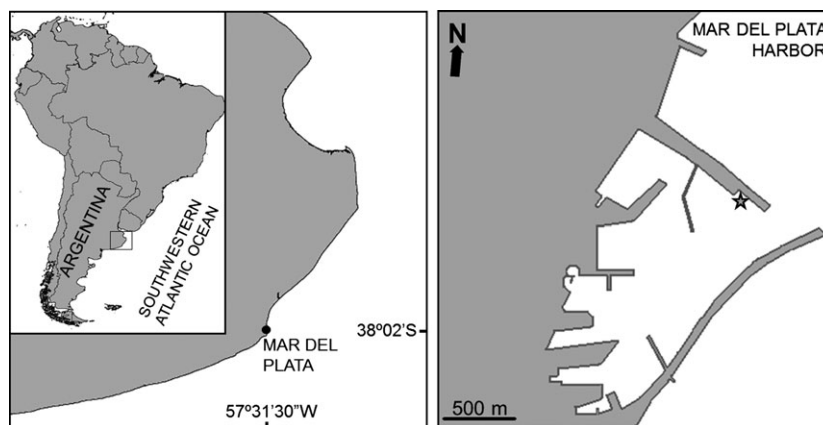
$57^{\circ}31' W$ , Fig. 1), between September 2006 and May 2012. The port is an artificial harbor delimited by two large breakwaters surrounded by a sandy bottom. Within the harbor the bottom is muddy and fine grained. The breakwaters and internal docks are made of orthoquartzite blocks and boulders at 6–8 m depth, with numerous nooks and crevices that provide shelter for many organisms.

Except for 2006 and 2007 when only the body size of *Asterina stellifera* was recorded, censuses consisted of collecting all individuals found in a 15-min dive along a 2-m-wide transect placed parallel to the breakwater of sampling collection (Fig. 1). *Asterina stellifera* specimens were counted and the radius (distance from center of disc to arm tip opposite to madreporite) measured to the nearest 0.1 mm, and then returned to the same place where they were collected.

Seawater temperature and salinity averages were obtained monthly from 2008 to 2012 from the National Institute of Fisheries Research and Development (INIDEP). Monthly cumulative mean precipitation records were obtained from the Mar del Plata Aerodrome database.

### Size structure and growth modeling

To model individual growth we first solved the multimodal size frequency distributions for each month using Bhattacharya's method as included in the program FISAT II (Gayanilo *et al.* 2001). This technique has been used successfully to study individual growth in other sea star species (Guillou & Guillaumin 1984; Freeman *et al.* 2001; Bos *et al.* 2011). From this, we obtained a modal progression over time to which we fitted nine different growth models by maximum likelihood. The performance of the nine candidate models was assessed by information-theoretic (IT) procedures. For all models we calculated the Akaike information criterion for small samples (AICc) and differences in AICc ( $\Delta_i$ ) and AICc weights ( $w_i$ ) (Burnham *et al.* 2011; Symonds & Moussalli 2011).



**Fig. 1.** Study area and location of sampling collection and SCUBA surveys (star).

Under this criterion, the model with the lowest AICc and highest  $w_i$  is the one that best describes the data. The 95% confidence intervals (CI) of the parameters values were calculated in each case.

The nine candidate models can be grouped as follows: (i) four models assuming asymptotic growth and constant growth rates (von Bertalanffy,  $m_1$ ; Gompertz,  $m_2$ ; Richards,  $m_3$ ; logistic,  $m_4$ ), these are the most commonly used in growth analyses; (ii) one with asymptotic growth but accounting for seasonal variations in growth rates (von Bertalanffy with seasonal oscillations,  $m_5$ ); and (iii) following Ebert & Russell (1993), four models specially developed for long-lived echinoderms with apparent continuous growth that have a non-asymptotic growth (Schnute,  $m_6$ ; Tanaka,  $m_7$ ; Power,  $m_8$ ; Linear,  $m_9$ ). The corresponding equations and parameterizations are summarized in Table 1.

**Local abundance and its relationship with intrinsic and extrinsic variables**

We estimated sea star abundance as records per unit effort (RPUE), calculated as the number of sea stars col-

lected during the 15-min dives. RPUE is systematically used to assess abundance in many contexts, typically in fisheries, but also in other studies which aimed to analyse echinoderm populations traits where collecting individuals requires diving (e.g. Palleiro-Nayar et al. 2011). In order to analyse the proportionality between RPUE and sea star density, two methods were simultaneously performed during dives lasting 15 min each (n = 11): RPUE and density counts using 0.25 m<sup>2</sup> quadrats (Farias et al. 2012). According to Harley et al. (2001), the simplest non-linear model explaining this relationship is the power function:  $U = qN^\beta$ ; where N is the density, U the RPUE, q the catchability co-efficient and  $\beta$  the shape parameter. As our interest was in the relationship between RPUE and density, only the shape parameter ( $\beta$ ) is relevant here. Thus, a non-linear power model was fitted using maximum likelihood in order to analyse the relationship between the two measures of abundance.

Additionally, a generalized least square (GLS) model was fitted to assess whether RPUE (dependent variable) varied with time (sampled month) and changes in extrinsic (seawater temperature, salinity, monthly cumulative precipitation) and intrinsic (reproductive status) factors.

**Table 1.** *Asterina stellifera* alternative growth models fitted to monthly modal radius data. Letters represent model parameters.

model	equation	model/source	description of parameters
asymptotic growth models			
$m_1$	$R_t = a \times (1 - e^{-b \times (t - c)})$	von Bertalanffy (vB)	a is the size reached after an infinite time of growth, b is the growth constant, c is the age at which size would be zero
$m_2$	$R_t = a \times e^{-e^{-[b \times (t - c)]}}$	Gompertz	d determines the shape of the curve
$m_3$	$R_t = a \times \left(1 + \frac{1}{d \times e^{-b \times (t - c)}}\right)^{-d}$	Richards	
$m_4$	$R_t = \frac{a}{1 + e^{-b \times (t - c)}}$ $R_t = a \times \left(1 - e^{-b \times [(t - c) + T_1 - T_2]}\right)$	logistic	
$m_5$	$T_1 = C \times \sin(2 \times \pi \times (t - ts)) \div (2 \times \pi)$ $T_2 = C \times \sin(2 \times \pi \times (c - ts)) \div (2 \times \pi)$	seasonal von Bertalanffy	has the same parameters as the vB model but adds other two, T1 and T2, that control the oscillation: C, account for the amplitude and ts, the starting point of the seasonal oscillation (ts, given as a fraction of the year)
non-asymptotic growth models			
$m_6$	$R_t = \left(\frac{a^c + (b^c + a^c) \times 1 - e^{-d \times (t - \tau_1)}}{1 - e^{-d \times (\tau_2 - \tau_1)}}\right)^{\frac{1}{c}}$	Schnute	$\tau_1$ and $\tau_2$ correspond to a minimum and maximum age, respectively, specified in the model in advance. a and b are sizes expected at ages $\tau_1$ and $\tau_2$ , respectively; and d and c are related to growth rate. If $d > 0$ , and $c = 1$ the model reduces to the vB growth model in which case d is the growth constant
$m_7$	$R_t = \left(\frac{1}{\sqrt{a}}\right) \times \ln\left(2a \times (t - b) + 2\sqrt{a^2 \times (t - b)^2 + a \times c}\right) + d$	Tanaka	a is a measure of rate of change of growth rate, b is the age at which growth rate is maximum, c is related to maximum growth rate and d is body size at which growth is maximum
$m_8$	$R_t = a \times b^t$	power	a is the age at which size would be zero and b determines the shape of the curve
$m_9$	$R_t = a + b \times t$	linear	a is the age at which size would be zero and b determines the slope of the line

Rt = radius; t = time.

Abundance values were temporally auto-correlated and therefore the assumption of independence was not met. In order to deal with this violation and to account for the auto-correlation effect, a temporal correlation structure (auto-regressive model of order 1: AR-1) was included in the GLS analyses. This correlation structure considers that the further away two data points are separated in time, the lower their correlation is (for more details see Zuur *et al.* 2009). During the comparison procedure, we first constructed a global model (*i.e.* with all independent variables) without auto-correlation structure so that we had a reference point. Then, a model without any of the independent variables (*i.e.* null model), a global model (with the AR-1 structure) and finally models with different numbers and combinations of the explanatory variables (with the AR-1 structure) were constructed (Zuur *et al.* 2009). Again, the best model was selected comparing the respective AICc,  $\Delta_i$  and  $w_i$  of each model (Burnham *et al.* 2011; Symonds & Moussalli 2011). For the parameters of the best model we calculated the CI.

All analyses were performed using R software version 3.0.2 (R Development Core Team 2013). Non-linear models, growth and power functions were fitted using maximum likelihood with the 'bbmle' library (Bolker & R Development Core Team 2013). Fitting of the GLS models was performed using the function 'glms' from the 'nlme' package (Pinheiro *et al.* 2013). Both libraries allow model selection to be performed using an IT-AIC approach and model parameter values that maximize the likelihood to be found. The 'bbmle' library was also used to generate CI for each estimated parameter for all constructed models.

## Results

### Size structure and growth modeling

During the sampling period (September 2006 to May 2012) a total of 2337 sea stars was measured. The radius (R) ranged from 26.51 to 80.00 mm (mean 51.64 mm, SE = 4.63).

The originally bimodal size frequency (September–November 2006) changed to unimodal in July 2007. This unimodal distribution remained unchanged after July 2007 (Fig. 2). The smallest cohort (~30 mm, September 2006) increased by about 130% during the 5 years sampled (reaching 65 mm arm length in May 2012). From 2006 to 2007, size within the smallest cohort increased by 18 mm (16% increment), from 30 mm in September 2006 to 48 mm in October 2007. In the following years, larger sea stars grew more slowly, approximately 3 mm per year. They were 54 mm by October 2009. Lastly, growth was around 4 mm in the last 2 years, from 54 mm in October 2009 to 58 mm in October 2011, giv-

ing 2 mm per year. Thus, there was a clear decrease in growth rate as size increased (Fig. 2).

Individuals from the largest 2006 cohort (radius of 55–75 mm) gradually disappeared from the population by September 2008. Throughout 2011 and 2012, larger size classes were well represented, growing slowly to the maximum sizes registered in March and May of 2012. As growth decreased with size, a size class overlap was evident among large individuals (Fig. 2).

Sea stars with a radius smaller than 26 mm in length were not found despite extensive searches in extra dives. Some new small individuals of *c.* 30 mm (not recorded in the previous months) appeared in April 2009 and with less frequency in November 2009 and September 2011 (Fig. 2). It therefore seems there was some successful recruitment during the sampling period. No further recruitment was detected in 2012.

Based on the size frequencies, we adjusted the nine alternative growth models (Table 1). The results from model selection and the parameter estimates are presented in Table 2. Models with values of  $\Delta_1 < 3$  are considered to be essentially as good as the best model (Burnham *et al.* 2011; Symonds & Moussalli 2011). Two growth models, an asymptotic and a non-asymptotic one, were equally good based on the IT approach: the von Bertalanffy ( $m_1$ ) and Schnute ( $m_6$ ), respectively (Table 2, Fig. 3). However, given that the value of parameter  $c$  did not differ from 1 (CI: 0.76–2.16), when in  $m_6$  (Schnute) the value of the parameter  $c$  is 1, it becomes into vB model ( $m_1$ ). Furthermore, parameter  $d$  of  $m_6$  is the growth constant, the same growth constant represented for the parameter  $b$  in  $m_1$ . That's why both growth constants (from  $m_1$  and  $m_6$ ) presented similar values and CI. The mathematical demonstration of these is explained in Harley *et al.* (2001). Both models,  $m_1$  and  $m_6$ , yield the same annual growth constant (Table 2, Fig. 3). According to the IT approach, when two or more models are good candidates, the simplest one is chosen to describe the data,  $m_1$  is the simplest one, thus vB is the best to describe the growth of *Asterina stellifera*.

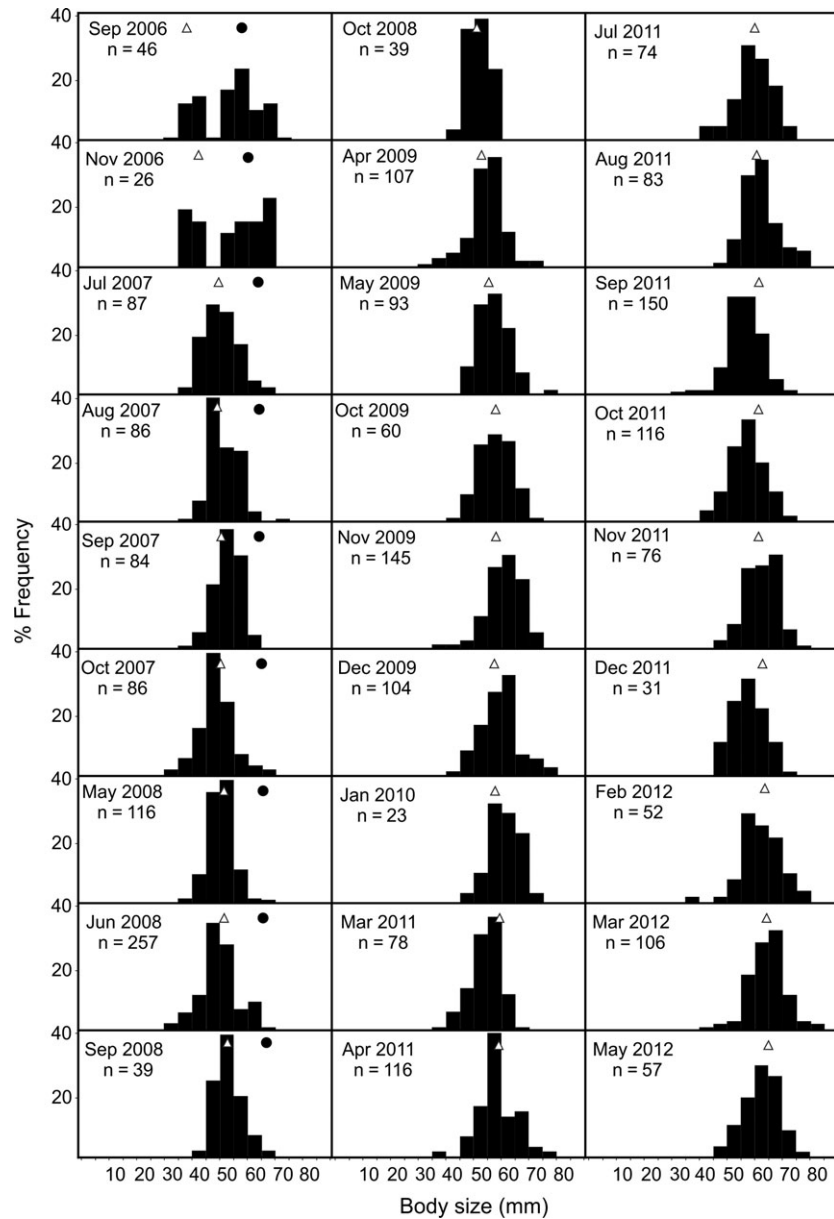
From the von Bertalanffy model we estimated *A. stellifera* growth parameters: the asymptotic size  $a = 65.97$  mm, the annual growth constant  $b = 0.022$  and the age at size zero  $c = 40.76$ . Therefore, the growth of *A. stellifera* in Mar del Plata is properly described as:

$$R_t = 65.97 \times (1 - e^{-0.022 \times (t-40.76)}) \quad (1)$$

where  $R_t$  is radius and  $t$  is time.

From these data, we estimated that the individual lifespan was longer than 5.5 years.

Given that small individuals (radius of less than 26 mm) were absent from routine samplings, we performed ancillary dives in different seasons within the



**Fig. 2.** Size frequency distribution and modal size (black dots and white triangles) of *Asterina stellifera* cohorts at Mar del Plata port from September 2006 to May 2012. Size classes = 5 mm.

port, searching for sea stars that might be hidden in small crevices and nooks among boulders. Other complex structures that could hold small sea stars, such as leafy algae and small tubeworm reefs, were collected and examined thoroughly, but we were unable to find any specimens during these inspections.

#### Local abundance and its relationship with intrinsic and extrinsic variables

During the sampled period, the sea surface temperature ranged from 23 °C (in February 2010) to 9 °C (in August 2010). Cumulative monthly precipitation was highly vari-

able and presented no clear annual pattern, ranging from 13 to 191 mm. Salinity was not affected by rainfall, which was relatively constant throughout the studied period (Fig. 4).

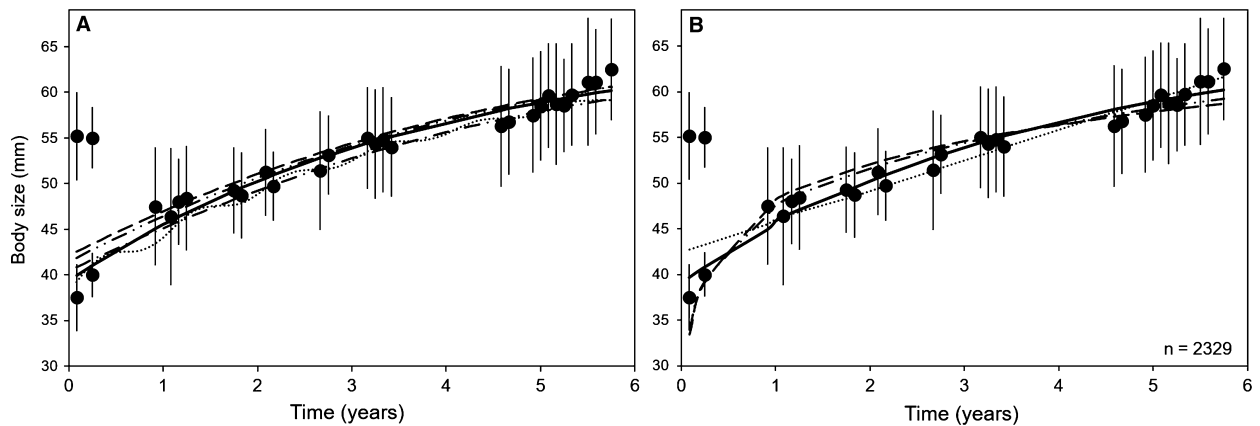
The parameter  $\beta$  of the power function explaining the proportionality between RPUE and density was close to 1 (Fig. 5). This suggests that sea star abundance, estimated as RPUE, is a good estimator of population density.

Abundance, expressed as RPUE, was highly variable within each year, varying from 11.6 ind. $\cdot$ min $^{-1}$  (in October 2009 and September 2011) to 0.92 ind. $\cdot$ min $^{-1}$  (in January 2010) (Fig. 4), but overall abundance remained relatively constant over the years of study. In the GLS

**Table 2.** *Asterina stellifera* growth model selection and model parameter estimates. The lower and upper 95% confidence intervals (CI) are given in parentheses. The best models are highlighted in bold.

model	AICc	$\Delta_i$	$w_i$	parameter estimates			
				a	b	c	d
<b><math>m_1</math></b>	<b>22.72</b>	<b>0.00</b>	<b>0.516</b>	65.97 (61.31–70.63)	0.022 (0.018–0.026)	40.76 (38.28–43.13)	–
$m_2$	30.53	7.81	0.010	64.56 (57.58–87.97)	0.028 (0.01–0.06)	–25.44 (–60.97 to –10.74)	–
$m_3$	32.45	9.73	0.004	64.78 (59.09–70.46)	0.027 (0.019–0.035)	–25.87 (–27.16 to –31.08)	6474 (5847–7100)
$m_4$	33.68	10.96	0.002	63.68 (54.52–88.49)	0.033 (0.01–0.07)	–15.16 (–39.25 to –3.83)	–
$m_5$	34.24	11.52	0.002	65.89 (56.50–75.28)	0.022 (–0.076 to 0.12)	–40.78 (–34.55 to –47.01)	–
<b><math>m_6</math></b>	<b>22.95</b>	<b>0.23</b>	<b>0.460</b>	39.66 (34.01–46.73)	60.30 (56.85–63.85)	1.20 (0.76–2.16)	0.022 (–0.018 to 0.050)
$m_7$	32.06	9.34	0.004	0.025 (0.019–0.031)	0.001 (0.0004–0.002)	0.029 (–0.069 to 0.127)	46.45 (40.02–52.88)
$m_8$	38.27	15.55	0.000	33.49 (27.44–39.51)	0.134 (0.09–0.191)	–	–
$m_9$	46.03	23.31	0.000	43.55 (38.55–47.55)	0.261 (0.180–0.342)	–	–

AICc = Akaike's information criterion for small samples;  $\Delta_i$  = AICc differences;  $w_i$  = normalized weights of AICc.



**Fig. 3.** Seasonal increments in *Asterina stellifera* mean body size ( $\pm$ SE) at Mar del Plata port from September 2006 to May 2012 (dots). Superimposed lines correspond to the fitted growth models. (A) von Bertalanffy (solid line); seasonal von Bertalanffy (dotted line); logistic (dot dashed line); Gompertz (double dot dashed line); and Richards (dashed line). (B) Schnute (solid line); Tanaka (dashed line); power (dot dashed line); and linear (dotted line).

analysis, the AICc indicated that the temporal correlation structure AR-1 improved the model compared with the linear regression model. The correlation parameter  $\rho$  estimate was 0.36. The minimal adequate GLS model (with AR-1) based on both AICc and normalized weights of AICc incorporated the reproductive season as the only explanatory variable (Table 3). Thus, this intrinsic variable explained RPUE variation within a year: the Mar del Plata population of *A. stellifera* had its highest abundance values during the reproductive season.

## Discussion

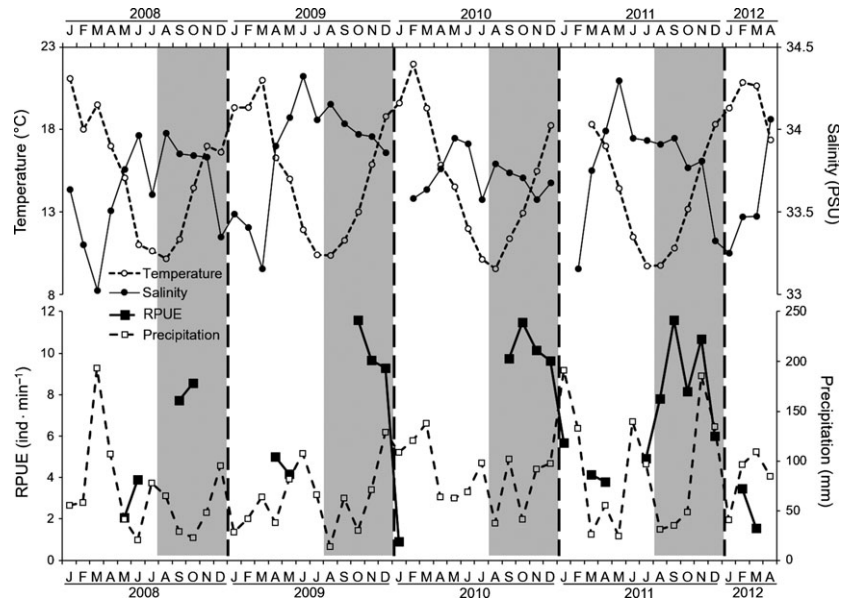
### Size structure and growth modeling

Most studies dealing with sea stars calculate growth as the ratio between two consecutive size modes (*e.g.* Guillou & Guillaumin 1984; Zann *et al.* 1987; Freeman *et al.*

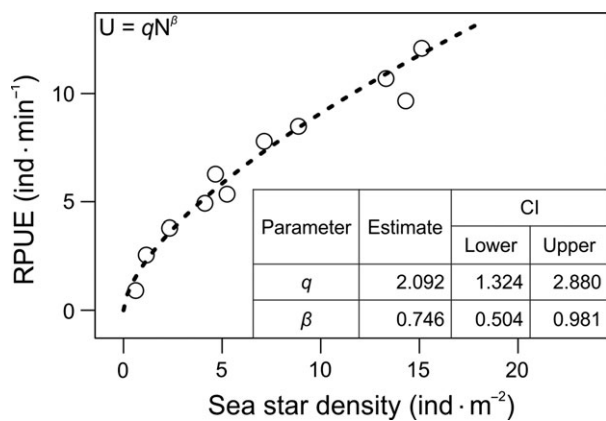
2001; Bos *et al.* 2008). Thus, there are few data available for comparison with our results in the literature. Among the few studies that have applied theoretical models to growth, most used von Bertalanffy and logistic models in a straightforward manner (Lucas 1984; Rumrill 1989; Ebert 1999), without testing alternative models that might fit equally well or even better to growth data (see table 5 in Flores *et al.* 2010). With very few exceptions (*e.g.* Ventura 1999), more sophisticated models, such as those incorporating seasonal growth, have been almost ignored, even when populations came from temperate waters.

Here we tested nine alternative models. Contrary to expectations for temperate sea stars (Nojima 1982; Ventura 1999; Freeman *et al.* 2001), the simple von Bertalanffy model performed better than the model with seasonal oscillations. Thus, growth of *Asterina stellifera* in Mar del Plata is not seasonal but slow and constant through the year. This may be explained by two concurrent facts: (i) a





**Fig. 4.** Mean records per unit effort (RPUE) of *Asterina stellifera* individuals from Mar del Plata and monthly sea surface temperature, salinity and cumulative monthly precipitation at Mar del Plata port during the sampling period. Gray zones represent the reproductive season according to Meretta et al. (2014). RPUE was estimated by counting all sea stars caught during each 15-min dive.



**Fig. 5.** Relationship between *Asterina stellifera* records per unit effort (RPUE, ind. min<sup>-1</sup>) and sea star density (ind. m<sup>-2</sup>). Superimposed line corresponds to the fitted power model of proportionality, where N is the abundance, U the RPUE, q the catchability coefficient and β the shape parameter. In the inset are shown model parameter estimates and 95% confidence intervals (CI).

rather constant food supply throughout the year, as suggested by the absence of seasonal variation in the reserves stored in the pyloric caeca of *A. stellifera* (Meretta et al. 2014); and (ii) the high population densities registered here, which are often associated with lower individual growth rates in echinoderms (e.g. *Archaster typicus*, Feder & Christensen 1966).

The growth parameters reported here differ from those available for species supposed to be similar to *A. stellifera*, either from an ecologic or phylogenetic perspective. The closely related *Patiria* (formerly *Asterina*) *miniata* reaches similar maximum sizes, plays a comparable ecologic role

and lives in almost identical temperature ranges and hydrographic conditions to *A. stellifera* (Rumrill 1989; Farias et al. 2012). However, *P. miniata* growth parameters are quite different to those reported here (Rumrill 1989). Interestingly, the growth rate of *A. stellifera* is rather comparable to some unrelated species described as slow growers, such as *Oreaster reticulatus* and *Protoreaster nodosus* (Scheibling 1980b; Bos et al. 2008). Both of these oreasterids inhabit shallow waters, and grow less than 1 cm per year as *A. stellifera* does, but reach larger sizes (up to 50 and 30 cm, respectively) and inhabit tropical waters.

It has been described for some asteroids that after a recruitment episode, cohorts can be followed for several years as they grow and join adult size (Ebert 1983; Rumrill 1989). The population that we followed seems to have had a significant recruitment event prior to our first sampling (marked by the smaller peak in 2006) but we did not detect further recruitments after that. However, there should have been some input of small individuals to keep the abundance stable over the years as observed, despite the expected losses by natural death. High degrees of spatial and temporal variability in settlement and recruitment at very different scales, from meters to hundreds of kilometers, are common features of echinoderm populations (Ebert 1983; Balch & Scheibling 2001; Uthicke et al. 2009) and *A. stellifera* does not seem to be an exception.

The lack of individuals less than 30 mm in our samples is puzzling. We performed thorough and extensive searches for newly settled individuals but failed to find any. However, it is still possible that smaller sea stars were hidden deep inside the spaces among the boulders

**Table 3.** Generalized least squares analyses explaining variation in *Asterina stellifera* records per unit effort (RPUE, ind. min<sup>-1</sup>) due to environmental variables and reproductive state. The null model, global model and models with a support of  $w_i > 0$  are provided. Models are listed in decreasing order of importance. The best model is highlighted in bold.

response variable	k	explanatory variables	correlation structure	AICc	$\Delta_i$	$w_i$
RPUE	1	rep	AR-1	<b>62.00</b>	<b>0.00</b>	<b>0.783</b>
	2	rep + T	AR-1	64.80	2.80	0.193
	2	rep + P	AR-1	70.80	8.80	0.001
	3	rep + T + S	AR-1	72.00	10.00	0.005
	2	rep + M	AR-1	72.20	10.20	0.005
	global	rep + T + S + P + M	AR-1	73.50	11.50	0.002
	global	rep + T + S + P + M	–	75.10	13.10	0.001
	null	–	AR-1	96.10	34.10	0.000
	parameters		estimate (SE)		CI	
	intercept		3.37 (0.53)		lower	upper
	rep		5.74 (0.75)		2.33	4.41
	$\rho$		0.36		4.26	7.22
				–	–	

k = number of parameters; AICc = Akaike's information criterion for small samples;  $\Delta_i$  = AICc differences,  $w_i$  = normalized weights of AICc; rep = reproductive state; T = temperature; P = precipitation; S = salinity; M = month; AR-1 = temporal correlation structure;  $\rho$  = correlation structure parameter; CI = 95% confidence intervals.

The parameter for reproductive state is given as relative to non-reproductive specimens.

of the breakwaters such that we did not find them. As *A. stellifera* has an annual synchronous reproductive cycle and gametes are released every year (Meretta *et al.* 2014), the number of potential settlers might be expected to be high. There were anecdotal findings of small individuals (<10 mm) inside aggregates of a tubicolous polychaete within the sampling period but at negligible density and frequency (Albano & Obenat 2009). Therefore, settlement appears to have occurred at a low rate, at least to some extent, within the port during the study period. Asexual reproduction by fission of the disc has never been documented for *A. stellifera*, and therefore, cannot be considered as an alternative hypothesis to explain the input of small individuals.

The sampled area is a semi-enclosed system, hydrodynamically retentive (Speroni *et al.* 2007), surrounded by sandy bottoms, which this species is reluctant to; and the nearest rocky bottoms are more than 5 km apart. Thus, it is unlikely that significant numbers of individuals migrate from the adjacent rocky bottoms to the sampling site or vice versa, particularly small individuals. In brief, the weak level of recruitment registered might be due to deficient larval supply, failure in the settlement process, high post-settlement mortality, or any combination of these, but we cannot discern among these options with the current data. Specific experimental studies must be performed to answer these questions. Given the high densities found, density-dependent regulatory processes, such as cannibalism as suggested in Farias *et al.* (2012), also deserve further consideration.

#### Local abundance and its relationship with intrinsic and extrinsic variables

Seasonal changes in distribution and abundance of sea stars are well documented, but studies considering correlations with environmental variables and physiologic condition are rare (Scheibling 1980b; Lawrence & Lane 1982; Freeman *et al.* 2001; Metaxas *et al.* 2002). We found that variations in abundance of *Asterina stellifera* were not related with variations in seawater temperature, salinity or rainfall, as has been found in other sea star species (Lawrence & Lane 1982; Freeman *et al.* 2001). Instead the abundance was clearly related to the overall reproductive condition, with an increase in RPUE during the reproductive season. Sea stars that reproduce as broadcast-spawners are known to perform reproductive aggregations with synchronized gamete release, thus maximizing fertilization success (*e.g.* *Astropecten latespinosus*, Nojima 1983; *Leptasterias polaris* and *Acanthaster planci*, Beach *et al.* 1975; Hamel & Mercier 1995). As *A. stellifera* has annual reproduction and synchronized spawning (Meretta *et al.* 2014), temporal reproductive aggregation is expected to occur to some degree.

Although RPUE is a widely used technique, its validity as a measure of abundance has long been questioned as it can lead to overestimation of abundance (*e.g.* Gillis & Peterman 1998; Harley *et al.* 2001). In this study, the power function that explained the relationship between RPUE and true density showed that the occurrence of *A. stellifera* increased as its population density increased (Fig. 5), as indicated by the resulting  $\beta < 1$  (Harley



et al. 2001). This shows that in this case RPUE is a reliable measure of abundance. Thus, the temporal aggregations here recorded would affect our estimates of abundance in the same way that immigration does. If the reproductive groups encompass an area larger than that of sampling, RPUE-based estimates of abundance may result in an apparent increase in the total number of individuals within the port, particularly in this case, in which estimations come from repeated measures at one point. As it is unlikely that significant migration of *A. stellifera* occurs in the study area (see above), we believe that behavioral changes related to reproductive activity are the cause of the seasonal changes in RPUE found here.

Given the bionomic features described here (i.e. slow growth and low population renewal), *A. stellifera* appears to be particularly vulnerable to local extinction in those areas in which adult stocks are already low. Many factors are degrading the habitat in the only area that still holds dense populations of this species (Orensanz et al. 2002; Boschi 2004; Isla 2004; Albano et al. 2013). Furthermore, invasive species have recently been introduced that may compete directly and/or indirectly for prey with *A. stellifera* (Meretta et al. 2012; Farias et al. 2015). These facts together set a concerning scenario for its conservation, with possible impacts at the community level considering the importance that *A. stellifera* has as a predator of a wide variety of benthic organisms (Farias et al. 2012; Meretta 2014).

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