Vol. 558: 51–63, 2016
doi: 10.3354/meps11876

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published October 25

Low temperature trumps high food availability to determine the distribution of intertidal mussels *Perna perna* in South Africa

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ABSTRACT: Explanations of species distributions often assume that the absence of a species is due to its inability to tolerate an environmental variable. Recent modelling techniques based on the dynamic energy budget (DEB) theory offer an effective way of identifying how interacting environmental parameters influence distributions through non-lethal effects on growth and development. The mussel *Perna perna* is an abundant ecosystem engineer around the coasts of Africa, South America and the Arabian peninsula, with an unexplained 1500 km lacuna in its distribution on the west coast of South Africa. We used a DEB approach to explain its distribution in southern Africa and test the hypothesis that this lacuna is caused by sublethal effects of low temperatures on its metabolism. We parameterized a standard DEB model for *P. perna* using eco-physiological parameters measured in the laboratory, validated by comparison with the body size and reproductive effort of animals from the field throughout South Africa. The model highlighted the importance of reproductive failure under the cold water conditions of the west coast, despite particularly high food availability there, and the surprisingly good performance of *P. perna* under the warm, highly oligotrophic conditions of the east coast. The results suggest that *P. perna* is well adapted to low food conditions, but is reproductively vulnerable to low temperatures. DEB models accurately described and explained the anomalous biogeography of this intertidal mussel, allowing us to disentangle the interaction of antagonistic stressors and reveal the critical importance of sublethal temperature effects on reproduction to the species' distribution.

KEY WORDS: Thermal limits · Mussel · Physiology · Metabolism · Dynamic energy budget model

INTRODUCTION

Predicting the response of species distributions to a changing environment requires modelling approaches that can ideally separate the direct effects of environmental drivers on present distributions from those of biotic interactions. A large number of predictive models describing species distributions are now available, allowing the exploration of a wide variety of questions related to the biogeography, ecology and conservation of species (Jiménez-Valverde et al. 2008, Elith & Leathwick 2009). Some models based on presence-only or presence/absence data can provide accurate predictions for species with narrow niches, but are generally not suitable for describing species with wider niches (Tsoar et al. 2007). Recently, new techniques coupling species physiological traits to abiotic environmental gradients have been successfully applied to a variety of species (Thomas et al. 2011, Kearney 2012, Sarà et al. 2013a). Among these, the dy-

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namic energy budget (DEB) (Kooijman 2010) models are more data-intensive than traditional correlative approaches and can be a powerful tool for explaining the spatial and temporal distributions of species (Kearney et al. 2012).

Recent studies indicate that marked changes in the structure and distribution of intertidal and shallow coastal communities are occurring along South African coasts (Teske et al. 2011, Bolton et al. 2012, Reimers et al. 2014). Many of these changes are related to anthropogenic effects and the arrival and spread of introduced species, but changes in environmental conditions around the coast may also have influenced these communities (De Greef et al. 2013, Mead et al. 2013, Blamey et al. 2015). In attempting to predict the response of species distributions to changing environmental conditions, there has been a strong focus on the use of models that define the bioclimate envelope of species. Broadly, these are based either on correlations between distribution and climatic conditions, or on the study of physiological responses to environmental variables (Pearson & Dawson 2003). Both approaches have limitations, including their failure to accommodate local adaptation (Kuo & Sanford 2009), and a hierarchical approach that also incorporates the effects of biotic interactions and limitations on dispersal is increasingly advocated (Guisan & Thuiller 2005). Given a context of changing climatic and oceanographic conditions, we asked whether modelling approaches that incorporate non-lethal environmental effects could explain how, or if, physical conditions establish the geographic distribution of a key ecological engineer; the intertidal mussel *Perna perna*.

The ecological value of coastal mussels beds is widely recognized (Seitz et al. 2014). Mussels are ecosystem engineers, creating biogenic reefs that support rich communities (Wright & Jones 2006, Commito et al. 2008) contributing to both the deposition and the resuspension of particles (Graf & Rosenberg 1997), and they are the main shellfish consumed around the world (Seitz et al. 2014). *P. perna* is widespread in the Atlantic and western Indian Oceans (Cunha et al. 2014), and is one of the most abundant mussel species on South African rocky shores, constituting an important component of the diet of coastal indigenous communities through a subsistence-level fishery (Hockey & Bosman 1986, van Erkom Schurink & Griffiths 1990, Kyle et al. 1997). *Mytilus galloprovincialis* is a widespread invasive mussel in South Africa, and how abiotic conditions and competitive interactions with the indigenous *P. perna* influence the within- and along-shore distributions of the 2 species has been extensively studied (Rius et al. 2006, Bownes & McQuaid 2006, Rius & McQuaid 2006, Nicastro et al. 2010, McQuaid et al. 2015). Both are characterized by limited (<100 km) dispersal of the majority of their larvae (McQuaid & Phillips 2000) and have similar thermal limits (Tagliarolo & McQuaid 2015). Resistance to sand stress and wave action can explain local patterns of within-shore partial habitat segregation (Zardi et al. 2008, Carrington et al. 2015) but cannot explain their distributions across large scales. *P. perna* is abundant along the entire east and south coasts of South Africa, but has a 1500 km gap in distribution on the west coast before reappearing further north in Namibia and Angola (Hockey & van Erkom Schurink 1992). The absence of *P. perna* in this area is anomalous, as this is a globally important upwelling system with extremely high levels of primary production, and *P. perna* shows excellent survival and metabolic performance at the cool-temperate surface temperatures (of around 13 to 15°C) that prevail there (Demarcq et al. 2003).

As the DEB approach has been used successfully to explain the distributions of bivalves in other parts of the world (e.g. Sarà et al. 2011, 2013b), we built a DEB model fed with local body temperature and food availability data to provide a mechanistic explanation for the 1500 km gap in *P. perna* distribution along the west coast of South Africa. Our objective was to parameterize a standard DEB (Kooijman 2010) model to describe the growth, reproduction and physiology of constantly immersed *P. perna* individuals. This allowed us (1) to identify the mechanisms by which the influence of the environment on the physiology limits its distribution and (2) to establish whether the geographical distribution of *P. perna* along South African coasts is determined by its physiological traits. To do this, the distribution of *P. perna* was studied at 11 sites along the South African coast.

MATERIALS AND METHODS

Eco-physiological experiments

Mussels of similar size (3–4 cm shell length) were sampled in March 2014 at Morgan Bay, South Africa (34° 10′ 15″ S, 24° 50′ 05″ E; Fig. 1) and transported to the laboratory at Rhodes University, South Africa, where they were temporarily housed in natural seawater tanks for 2 d, enabling them to recover from sampling stress. Animals were then transported to the Experimental Ecology Lab at the University of Palermo (Italy) by plane in less than 48 h, while kept

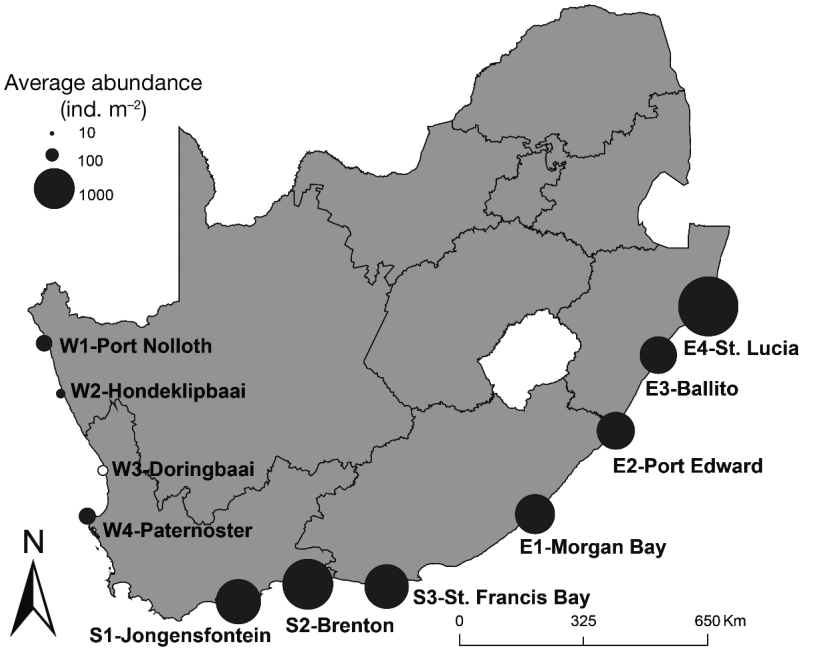

Fig. 1. Distribution of sampling sites along the South African coast. Sites are coded accordingly to their position on the West (W 1–4), South (S 1–3) or East (E 1–4) coasts. Average *Perna perna* abundance (ind. m^{-2}) is shown for each site. Note no *P. perna* were found at Doringbaai

in damp air. Mussels were subsequently acclimated to laboratory conditions for 2 wk in 100 l seawater tanks at the original temperature and salinity conditions measured in the field (20°C temperature and 35 ppt salinity) and fed ad libitum with a mono-algal culture of *Isochrysis galbana*. Seawater in the aquaria was continuously aerated using aquarium air pumps. During the transport and acclimation period, 10% of the individuals died and all others recovered as indicated by the production of byssal threads and pseudo-faeces.

Clearance rate (CR, l h^{-1}), food absorption efficiency (AE, a dimensionless ratio) and respiration rate were measured according to Widdows & Staff (2006) and Sarà et al. (2013a). Animals were starved for 24 h before the start of the experiment. CR and AE were measured at 5 different concentrations of algal cells (*I. galbana*) by placing 14 mussels in individual beakers containing 1 l of filtered, temperature-controlled seawater continuously mixed by a stirrer. Mussels were allowed to recover from handling for 20 min before algal cells were added to each beaker. Changes in algal cell concentrations were measured with a Coulter counter (Beckman Coulter Model© Z2) every 30 min over a 2 h period by sampling 20 ml aliquots. Algal cell concentrations were also measured in 2 control beakers lacking mussels and demonstrated that algal concentrations did not decline in the absence of filter-feeders. CR was calculated using the following equation:

$$CR = V\frac{\log_e C1 - \log_e C2}{\Delta t} \quad (1)$$

where V is volume (l) of water, and $C1$ and $C2$ are the cell concentration at the beginning and end of each time increment (Δt, h) respectively. The ingestion rate (IR, mg h^{-1}) is derived by multiplying CR by the content of suspended particulate organic matter in the natural habitat (Widdows & Staff 2006).

At the end of the 2h incubation period, mussels were separately transferred into 1 l beakers of filtered seawater and left undisturbed overnight to produce faeces; then both faeces and 3 replicates of food solutions used to perform experiments were filtered onto combusted and pre-weighed GFC filters. Filters were washed by rinsing alternatively with deionised water and ammonium formate to eliminate salt and were then dried at 90°C before ashing in a furnace at 450°C for 4 h. Since some of the material can be easily lost during this process, faeces and algal food were carefully handled at all stages and a calibrated balance with a precision of ±0.02 mg was used to avoid significant errors (Widdows & Staff 2006). After determining the difference between ash-free dry weight (AFDW, mg) and dry weight, we calculated AE using the following equation:

$$AE = (F - E)/[(1 - E) \times F] \quad (2)$$

where F and E are the ratio between AFDW and dry weight of the food and the faeces, respectively.

Respiration rate was measured by placing single individual mussels in sealed glass jars (500 ml) containing filtered seawater saturated with air. Magnetic stirrer bars ensured water mixing in the jars and the decline in oxygen was measured using a FIRE STING O_2 oxygen meter (Pyro-Science). Oxygen consumption was measured at 11 different temperatures from 9° to 39°C. Water temperature in the experimental jars was increased or decreased from the acclimation temperature of 20°C at 3°C per hour.

At the end of the physiological experiments, the dry weight of each specimen was determined by drying the flesh at 80° and then burning it at 450°C to determine AFDW.

DEB data

A standard DEB model (Kooijman 2010) adapted to bivalve traits (Sarà et al. 2013a) was used to describe energy allocation dynamics in permanently immersed *P. perna*. The covariation method implemented in the MATLAB 2010 software package DEBtool (www.bio.vu.nl/thb/deb/deblab/debtool/) was used to estimate the DEB parameter values for *P. perna*. This method employs the simultaneous minimization of weighted sum of squared deviations between a number of data sets and model predictions in a single-step procedure (Rinaldi et al. 2014). When no empirical data were available, the covariate method was applied using parameters estimated from closely related species (Saraiva et al. 2014). Data used to model species-functioning were collected from the literature or directly estimated from laboratory experiments (life-history parameters in Table 1). Laboratory experiments on the CR and AE were used to estimate the DEB ingestion rate coefficient J_X, and the assimilation rate J_{EA} following Sarà et al. (2013a). The oxygen consumption rates measured in the laboratory at 11 temperatures were used to estimate the Arrhenius temperature T_A. The lower and upper boundaries of the thermal tolerance range (T_{AL} and T_{AH}) were estimated from previous results on *P. perna* heart rate variability under increasing and decreasing temperature ramping protocols (Tagliarolo and McQuaid 2015). To optimize the estimates obtained for parameters, the shape coefficient was determined empirically from the length–weight relationship obtained for the individuals collected in Morgan Bay.

Field validation

During August 2014 animals were collected from the low intertidal zone at 11 sites along the South African coast (Fig. 1). Mussel beds were sampled by collecting all individuals within each of 3 randomly placed quadrats of 20 × 20 cm. Mussels were fixed in formalin and transported back to the laboratory where shell length, age, gonad and body dry weight were recorded for each individual. Age was estimated by cutting the shell with a rotary disk and counting the number of annual rings under a stereomicroscope (Peharda et al. 2011; Sarà et al. 2013a). The age–length relationship obtained with this method was compared with previous studies done in the same area with different methods and the results were comparable (Kaehler & McQuaid 1999, McQuaid & Lindsay 2000). Total shell length was measured using callipers (±1 mm) and gonad and somatic weights (without shell) were determined after drying at 60°C for 24 h. Population parameters such as density, mean and maximum shell length and biomass were calculated for each site using the data from the 3 random quadrats at each site.

Environmental parameters

Bivalve physiology and growth are mainly influenced by body temperature and food density (Sarà et al. 2013a). Chlorophyll *a* (chl *a*) concentration is recognized as a good proxy for the availability of phytoplankton, which provides intertidal mussels with the majority of their energy requirements (Pouvreau et al. 2006). Consequently, satellite images of chlophyll concentrations are an effective proxy for food avail-

Table 1. Life-history parameter data used to implement the covariation method for *Perna perna*

Parameters	Symbol	Units	Observed	Predicted	Reference
Age at birth	ab	days	2	1.293	Aarab et al. (2013)
Age at metamorphosis	aj	days	12	13.27	www.issg.org/database/species/ecology.asp?si=742&&lang=TC
Age at first spawning	ap	days	255	292.9	Phillips (1995)
Life span	am	years	9	9.5	Lindsay (1998)
Length at birth	Lb	µm	88.22	31.86	Aarab et al. (2013)
Length at metamorphosis	Lj	µm	259.52	224.7	Porri et al. (2006), Aarab et al. (2013)
Length at first spawning	Lp	cm	2.9	2.74	Phillips (1995), Bownes & McQuaid (2006), Narváez et al. (2008)
Maximum observed length	Li	cm	10.5	10.77	This study
Dry weight at first spawning	Wp	g	0.045	0.028	Lindsay (1998)
Maximum observed weight	Wi	g	1.75	1.73	This study
Maximum reproductive rate	Ri	#/d	1.59e5	1.578e5	McFarland et al. (2015)

ability when modelling mussel growth (Thomas et al. 2011). Mean monthly chl *a* concentration and sea surface temperature (SST, °C) with a spatial resolution of 4 km were obtained for the 5 yr period 2010–2014 from the Ocean Colour website (http://oceancolor.gsfc.nasa.gov/cms/) using the Aqua MODIS (Moderate Resolution Imaging Spectoradiometer) algorithm. The SeaWiFS Data Analysis System (SeaDAS) version 7.2 was used to process the data. We considered data located about 15 km offshore from each of our sampling sites in order to exclude shallow water and minimize the effect of bottom reflectance (Ohde & Siegel 2001). The means of arrays of 3 × 3 pixels were processed to take into account geographical variability (Bailey & Werdell 2006). A time period of 5 yr was chosen to encompass the average life span of *P. perna* (McQuaid & Lindsay 2000).

Previous studies comparing SST and *in situ* loggers revealed that satellite data are often ineffective at capturing extremes in intertidal water variability (Lathlean et al. 2011). For this reason, the SST dataset was corrected using *in situ* data from biomimetic temperature logger devices or 'robomussels' (n = 2 per site) (Helmuth & Hofmann 2001, Lima & Wethey 2009, Tagliarolo & McQuaid 2016). Robomussels were deployed next to natural mussel beds at 9 of our 11 sites (excluding St. Lucia and Port Nolloth) in June 2014 and temperatures were recorded for a total of 8 mo. Temperature data, with a resolution of 0.06°C, were collected continuously with a sampling interval of 30 min. Changes in tidal height every 30 min were calculated for each site using free tidal prediction software (Marées dans le monde 4.00, StrassGrauer-Marina Softwares). Air and seawater temperature data were determined by identification of the immersion/emersion periods using the tidal height values. The height on the shore was identified by a sharp drop in temperature of ≥3°C in 30 min during summer following Harley & Helmuth (2003) and comparison with tide tables. Once the tidal height of the loggers was calculated, an additional 30 cm was added to provide a 'buffer zone' as previously suggested by Lathlean et al. (2011). Mean monthly seawater temperatures calculated from robomussels for each site were correlated with monthly data from the satellite images, and SST data were corrected according to the regression.

DEB simulation

Once we had parametrized the DEB model developed for bivalves using the covariate method (Sarà et al. 2013a), simulations were performed by implementing the model with the climatic data for each site. This allowed us to investigate differences among the 11 sites in the way that *P. perna* utilised the energy obtained from food and differences in the effect of seawater temperature on its metabolism rates. The DEB end-points were estimated values for life history traits at each site (Sarà et al. 2014). These traits were maximum body size, age at maturity, reproductive output and number of spawning events during the entire life span. The model was run using the Excel spreadsheet provided by Kearney (2012), which allows one to depict the metabolism of organisms exposed to different body temperatures and food availability for each time step (monthly averages).

Statistical analysis

The effects of site on each morphological variable (shell length, age, body biomass and gonad biomass) derived from field samples were tested using 1-way ANOVA. A linear regression and Pearson's correlation were used to compare satellite SST values and temperature data obtained in the field from robomussels. Comparison of the outcome of the model for shell length (cm) and body biomass (g dry weight) against our field results were computed following the overall error equation (Saraiva et al. 2011, Rinaldi et al. 2014, Montalto et al. 2015):

$$E = e^{\mathrm{Var}(\varepsilon)} - 1 \quad (3)$$

$$\varepsilon = \sqrt{\log\left(\hat{Y}_{\mathrm{pred}} / Y_{\mathrm{obs}}\right)^2} \quad (4)$$

where E is the overall error, $\mathrm{Var}^{(\varepsilon)}$ is the variance of ε, $\hat{Y}_{\mathrm{pred}}$ are the data predicted by the model and Y_{obs} are the data obtained in the field. The overall error computed for each comparison aims to quantify the difference between model estimation and real data. A null value of E is assumed to be a perfect match between the model and the observed data and increasing values represent increasing errors (Saraiva et al. 2011).

RESULTS

Laboratory physiological experiments

CR, ingestion rate (IR, mg h^{-1}) and AE were calculated at 5 chl *a* concentrations from 0.4 to 2.52 µg l^{-1} (Table 2). All 3 parameters showed a marked re-

Table 2. Mean, standard deviation (SD) and standard error (SE) of clearance rate (CR), ingestion rate (IR) and absorption efficiency (AE) at 5 chl *a* concentrations for *Perna perna* in the laboratory

Chl *a*	CR (l h^{-1})			IR (mg h^{-1})			AE		
(µg l^{-1})	Mean	SD	SE	Mean	SD	SE	Mean	SD	SE
0.40	1.42	0.43	0.11	6.24	1.88	0.50	0.45	0.19	0.05
0.88	1.15	0.32	0.09	5.92	1.64	0.44	0.98	0.01	0.00
1.14	1.36	0.37	0.10	8.72	2.36	0.63	0.76	0.15	0.04
1.49	1.23	0.45	0.12	9.95	3.62	0.97	0.92	0.09	0.02
2.52	0.27	0.38	0.10	3.33	4.69	1.25	0.36	0.15	0.04

duction at the highest food concentration of 2.52 µg Chl *a* l^{-1}. Maximum CR and IR for *Perna perna* acclimated to a temperature of 20°C were 1.36 ± 0.10 l h^{-1} and 9.95 ± 0.97 mg h^{-1}, respectively. The average food absorption efficiency was 0.69 ± 0.03.

Individual oxygen consumption ranged from 0.08 µmol O_2 h^{-1} g^{-1} at 9°C to 2.24 µmol O_2 h^{-1} g^{-1} at 33°C (Fig. 2), while the resulting Arrhenius temperature, calculated as the slope of respiration rates against the inverse of the temperature (i.e. the Arrhenius plot) was equal to 4872 K.

Field validation

During the sampling in August 2014, a total of 1115 *P. perna* individuals were collected and measured. *P. perna* was found at 10 of the 11 studied sites (Fig. 1). Abundances were lowest on the west coast and greatest in St. Lucia, the most easterly site.

The individuals of the studied populations reached a maximum size of 10.5 cm at 7 yr of age in Jongensfontein and 9.6 cm at 5 yr of age in Ballito. The average shell length per site was smaller at the west coast sites (3.3–4.2 cm) than on the south (3.3–6.1 cm) and east coasts (5.1–7.4 cm). Average and maximum dry weight were greatest at Ballito, on the east coast, where individuals also showed higher gonad dry weights (Fig. 3, Table S1 in the Supplement at www.int-res.com/articles/suppl/m558p051_supp.xlsx). One-way ANOVA comparing the sites showed that site had a significant effect for each of the studied parameters ($p < 0.05$ in all cases). The Tukey post-hoc test showed strong similarity between the sites on the west coast and St. Francis bay, while the Jongensfontein population was similar to the one in Port Edward, and Ballito was significantly different from all the others ($p < 0.05$).

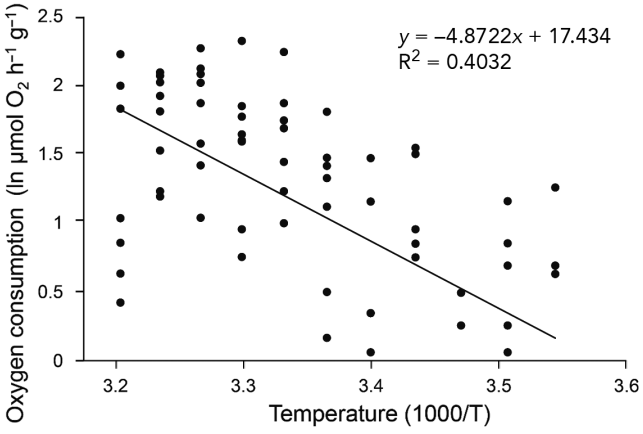

Fig. 2. Arrhenius plot for oxygen consumption rates of *Perna perna* against temperature (mean ± SD, n = 8), measured in laboratory experiments

Environmental parameters

Comparison of satellite SST and *in situ* water temperatures recorded by robomussels revealed that the 2 data sets were significantly correlated (Pearson's correlation, r = 0.93; Fig. 4). The correlation was stronger when data from all 9 sites were combined due to the greater coverage across the temperature spectrum. Satellite temperatures were generally higher than those measured by the robomussels, with maximum and mean differences of 4.9°C and 1.3°C, respectively.

Satellite SST values used in the DEB model were subsequently corrected using the regression between satellite and robomussel data (Fig. 4). Mean monthly SST exhibited a clear seasonal pattern ranging between 11.5°C in winter in the western regions and 25.5°C in summer in the east (Fig. 5).

Chl *a* concentration did not show any clear seasonal pattern across any of the sites. The average monthly concentration ranged between 0.1 µg l^{-1} in St Lucia and a maximum of 23.8 µg l^{-1} in Port Nolloth. Chl *a* concentration differed among sites, with clear differences among the 3 biogeographical regions. Note that the ranking of biogeographic regions from high to low values of chlorophyll is the inverse of the temperature ranking (Fig. 5).

DEB model

Since all the physiological data in this study were measured from individuals collected in Morgan Bay,

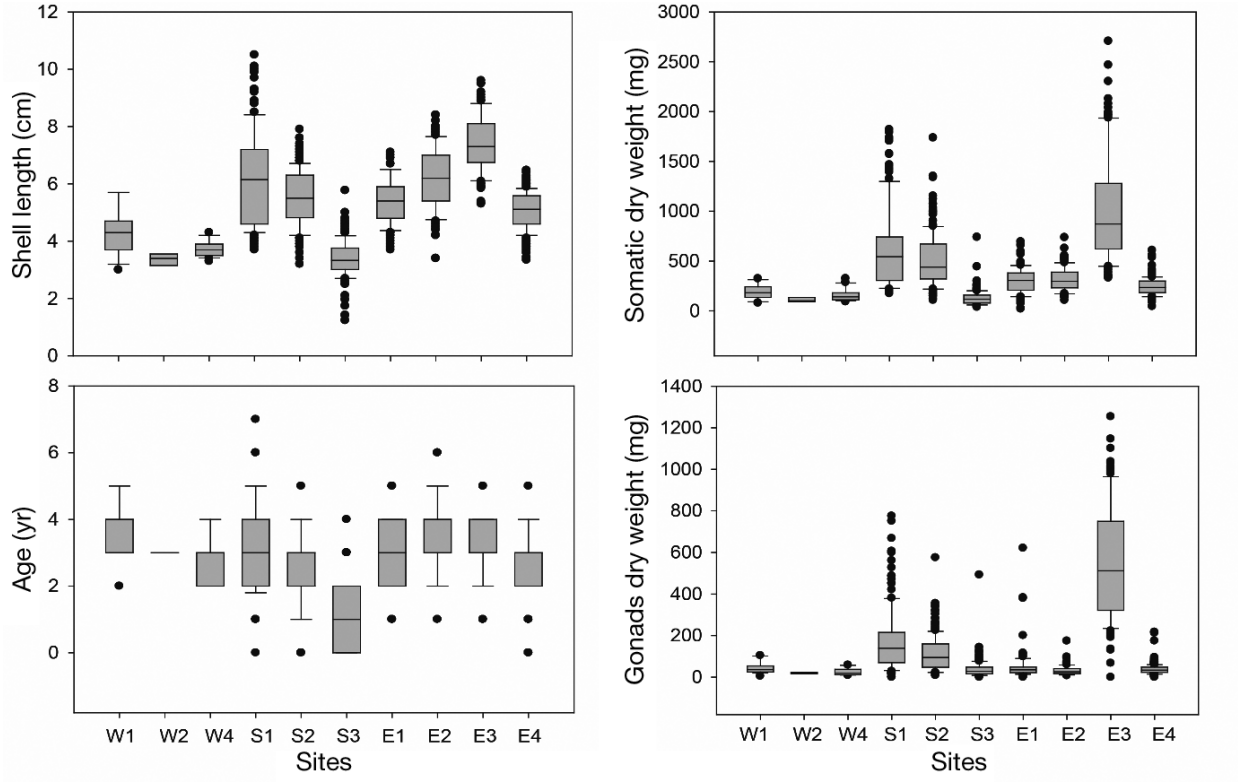

Fig. 3. Box plot for the different parameters measured in natural populations of *Perna perna*. See Fig. 1 for site abbreviations and location. The box plots depict the median and interquartile range, with circles representing outliers

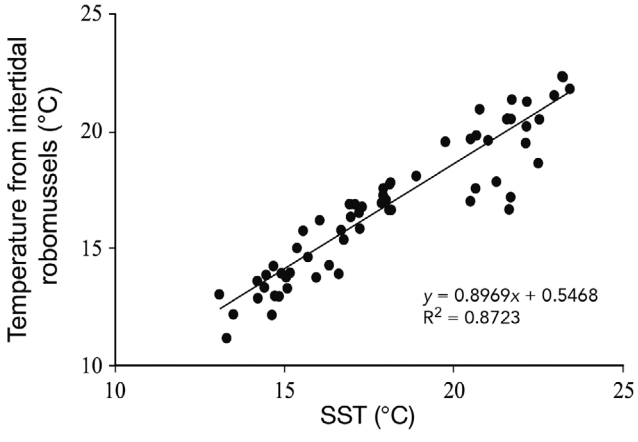

Fig. 4. Linear regression between the monthly average sea surface temperature (SST) calculated from satellite data and the *in situ* water temperature measured using the robomussel technique

the model was calibrated using the size/age/biomass dataset from Morgan Bay. Due to the difficulty in measuring all the parameters, well-studied species generally have a completeness level of around 3 or 4 (Lika et al. 2011). Completeness is defined by the mean of the type and quantity of data employed in the DEB parametrisation, and, as a main consequence, we assigned a completeness mark of 2.6 to our data. Similarly, the goodness-of-fit for our model, (defined as 10 × 1 – (mean relative error)) (MRE, 0.18 for our model) among all data types expressed as a fraction, was 8.2 on a scale from 0 (poor) to 10 (good). Indeed, following Lika et al. (2011), the estimation procedure was developed so that for each entry (excluding pseudodata) a MRE was first calculated as the sum of the absolute differences between observed and expected values, divided by the observed values, and then computed to help judge the goodness-of-fit.

The observed and predicted life-history parameters for *P. perna* are presented in Table 1. The primary DEB parameters obtained from *P. perna* fell in the same range as values for other mussel species reported in the literature at a reference temperature of 20°C as presented by Matzelle et al. (2015). The estimated specific maximum assimilation rate (p_{Am} = 6.5) was lower than the one calculated for almost all other species, including the congeneric *P. viridis* (p_{Am} = 26.79). The fraction of mobilized reserve allocated to soma was also lower than for the other species, indicating equal energy partition between reproductive and somatic maintenance compartments.

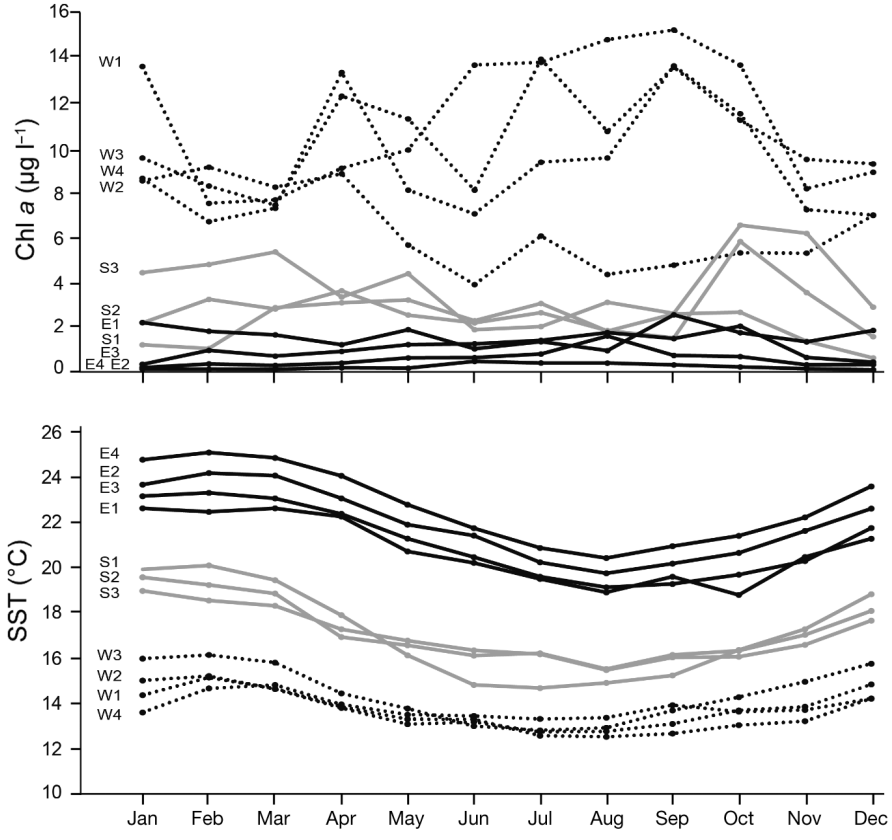

Fig. 5. Average monthly sea surface temperature (SST) and chl *a* (µg l^{-1}) for the period 2010–2014. Solid black lines represent the 4 sites on the east coast, the continuous grey lines represent the 3 sites on the south coast and the dotted lines represent the 4 sites on the west coast. See Fig. 1 for site abbreviations and location

Shell length and tissue dry weight predicted by the model for the first 5 yr were compared with the corresponding average shell length and dry biomass measured in the field for each site (Figs. 6 & 7). The site at Hondeklipbaai was excluded from the analysis since only one age class was present there. The overall error computed for shell length at each site was slightly higher for Brenton and Jongensfontein (E = 0.016 and 0.012, respectively), but the overall error calculated on the entire data set (E = 0.008) indicates good agreement between the model and the field observations (Fig. 6). The relationship between observed and predicted somatic tissue dry weight had a higher overall error than the shell length (E = 0.185) (Fig. 7). The error was greatest for Brenton and St. Francis Bay (E = 0.277 and 0.229, respectively).

The outcome of the model simulations underline important differences in reproductive effort among sites. The model was able to predict complete reproductive failure on the west coast where *P. perna* has historically been absent (van Erkom Schurink & Griffiths 1990). The time to reach maturity

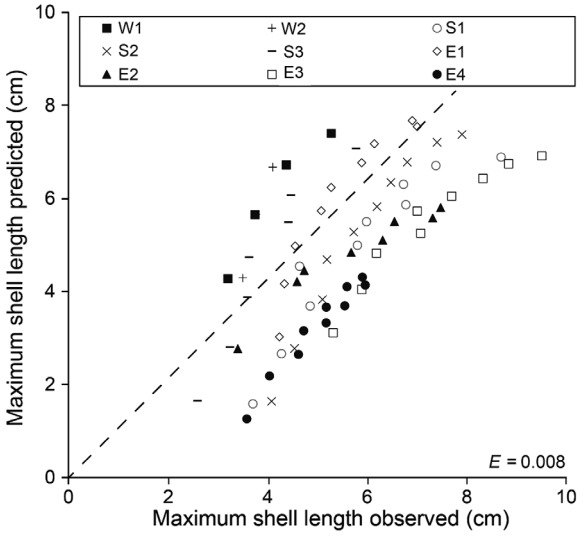

Fig. 6. Relationship between observed and predicted maximum shell length for *Perna perna* from 0.5 to 5 yr old at the different sampling sites. The E-value reflects the overall variance of error obtained from all data points, assuming zero for a perfect match (dashed line) and increasing values for increasing errors (Saraiva et al. 2011). See Fig. 1 for site abbreviations and location

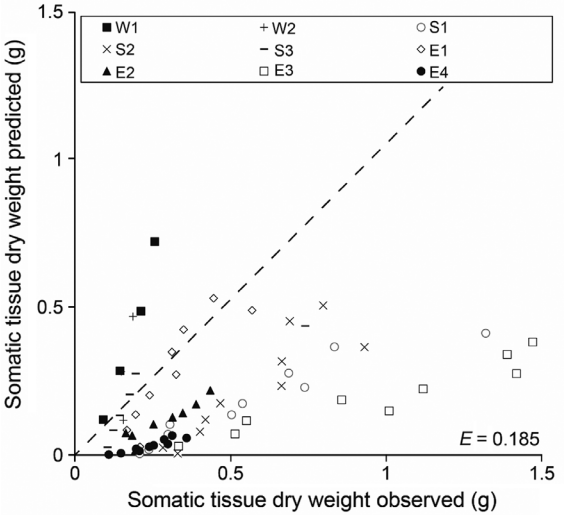

Fig. 7. Relationship between observed and predicted somatic tissue dry weights for mussels from 0.5 to 5 yr old at the different sampling sites. The E-value indicates the overall variance of error obtained from all data points; assuming zero for a perfect match (dashed line) and increasing values for increasing errors (Saraiva et al. 2011). See Fig. 1 for site abbreviations and location

Table 3. Principal outcome from the DEB model for *Perna perna* obtained using environmental data (chl *a* concentration and corrected SST) for the different sites along the South African coast (see Fig. 1)

Site	Shell length after 5 yr (cm)	Total no. of eggs produced by a single individual per life span	No. of reproductive events in 5 yr	Maturity time (d)
Port Nolloth	7.59	0	0	452
Hondeklipbaai	7.61	0	0	447
Doringbaai	7.77	194150	1	423
Paternoster	7.48	0	0	451
Jongensfontein	7.07	4892575	8	420
Brenton on Sea	7.54	8432399	9	400
St. Francis Bay	7.80	7589243	8	396
Morgan Bay	7.80	11250108	21	359
Port Edward	6.03	2668926	23	428
Ballito	7.09	6216756	22	344
St. Lucia	4.48	684262	19	637

was shortest in Ballito and Morgan Bay and longest in St. Lucia, where food availability was lowest. Morgan Bay, Port Edward and Ballito showed maximum values for spawning events combined with high numbers of eggs (Table 3).

DISCUSSION

Apart from history, species distributions are constrained by a multitude of contemporary biotic and abiotic factors and their interactions, which can exert different degrees of influence in different portions of a species' distribution (Jiménez-Valverde et al. 2008, Fly et al. 2015). Disentangling the effects of interacting and sometimes antagonistic stressors can be extremely challenging, but is something that DEB is uniquely equipped to achieve by integrating the effects of multiple factors on a species' metabolism. In this case, the approach allowed us to come to a non-intuitive understanding of how sub-lethal temperature effects on reproduction override the benefits of high food availability to determine the distribution of our study organism. The South African coast is characterized by several biogeographical regions because of its location between the Atlantic and the Indian Ocean biomes (Emanuel et al. 1992). Despite the potential for wide dispersal through its planktonic larval stage and its wide physiological thermal range, *Perna perna* has a complex genetic history and spatial phylogeograpic structure (Zardi et al. 2007, Cunha et al. 2014) and has historically been absent from the west coast (von der Meden et al. 2010, Tagliarolo & McQuaid 2015). Understanding the absence of this species from 1500 km of coastline that offers suitable habitat requires taking into account the roles of biotic interactions and the limitations of dispersal (Guisan & Thuiller 2005). Predation is a relatively minor source of mortality for adult mussels along this coast (Griffiths & Hockey 1987), and, although lethal effects of infestation by shell-eroding cyanobacteria can lead to high rates of mortality (Marquet et al. 2013), the most critical biotic interaction is competition for space (Bownes & McQuaid 2010). In this case, *P. perna* was absent from the west coast at times when its principal competitors were different mussel species (i.e. before and after the invasion by *Mytilus galloprovincialis*, Hockey & van Erkom Schurink 1992). While biotic exclusion by different competitors is possible, it seems unlikely. Similarly, we discount dispersal limitation as a critical factor, as models based on Lagrangian particle simulations show good connectivity among populations of *M. galloprovincialis* occupying the part of the coast where *P. perna* is absent (Assis et al. 2015). Instead, previous studies have hypothesized that the distribution of *P. perna* can be explained by inshore thermal conditions (Zardi et al. 2011, 2015). For this reason, we applied DEB theory and a functional trait-based mechanistic approach to describe the fundamental niche and potential distribution of *P. perna* using its physiological characteristics (Rinaldi et al. 2014). The DEB model parametrized here allowed a convincing simulation of growth, reproduction and energetic expenditure of *P. perna* populations from sites located around the South African coast. The model was effective in predicting adult age–size and age–biomass relationships and was able to mimic spatial diversity among sites that accorded with field data.

Earlier studies using simpler static energy models with a single balance equation (scope for growth models) successfully modelled the mechanisms limiting the distributions of *Mytilus* spp. towards the warm ends of their distributions, but the models did not offer an explanation for the colder distributional limits (Fly & Hilbish 2013, Fly et al. 2015). Both our field results and model predictions support a hypothesis of reproductive failure for *P. perna* on the cold-water west coast. Our DEB model predicted zero to very low egg production and no spawning events up

to the age of 5 yr on the west coast. Results from the field survey confirmed these findings, revealing the presence of extremely few individuals with minimal gonad dry weight at west coast sites. Low seawater temperature is the only parameter that can explain this physiological limitation since satellite chl *a* data indicate food availability to be highest in this region; up to an order of magnitude higher than on the east and south coasts. Different thermal vulnerability of adult and larval stages is common in bivalves and spawning can be seriously limited by cold waters (McMahon 1996, Verween et al. 2007). The presence of limited numbers of individuals belonging to few age classes on the west coast where the species is normally assumed to be absent suggests that these are sink populations (Pulliam 2000). Presumably, temporarily favourable temperature and current conditions allowed the arrival of autochthonous larvae originating from neighbouring areas such as Namibia, where *P. perna* is common (Zardi et al. 2007), resulting in sparse, recently established populations with dramatically curtailed size structure.

The model was able to establish appropriate links between the physiological traits of individuals and the geographic distribution of the species and offer an explanation for distribution based on simple and easily accessible environmental parameters (SST and chl *a*). The differences between satellite and *in situ* robomussel data are in line with previous comparisons for rocky shores (Lathlean et al. 2011) and confirm the reliability of satellite SST data when appropriately calibrated against *in situ* data (Smit et al. 2013).

The model was parametrized using physiological traits measured for mussels collected in Morgan Bay; therefore, the predictions for this site and the neighbouring ones were the most accurate. Generally, both somatic weight and shell length were slightly overestimated on the west coast and underestimated on the east coast. This can be due to the site-specific influence of environmental factors other than temperature and food availability, such as substratum, hydrodynamics or the presence of upwelling, which are known to have important effects on the establishment and persistence of mussel beds (Widdows & Brinsley 2002, Zardi et al. 2008). The lack of long-term high-frequency data for these parameters along the South African coast prevents us from discriminating among those factors and further studies are necessary to better understand local variability.

Importantly, this type of modelling cannot take into consideration the influence of anthropogenic pressures. Active harvesting and urban pollution can both have important effects on these mussels (Rius et al. 2006) and may explain why the model showed better performance at some sites than others. For example, both size and dry weight were generally underestimated by the model for Brenton. This site is very close to a marine protected area which is likely to have a positive influence on surrounding areas through the maintenance of reproductive stocks and the production of good-quality food (Branch & Odendaal 2003), although there is evidence that, on the east coast of South Africa, marine protected areas are not effective at exporting mussel larvae to adjacent areas (Cole et al. 2011). Nor did our model account for the effects of aerial exposure during low tide. The physiological responses of intertidal animals differ dramatically between emersion and immersion (Tagliarolo et al. 2012, Tagliarolo & McQuaid 2015, Fusi et al. 2016), and the implementation of a DEB/BE (biophysical–ecological) approach could improve predictions of intertidal distribution (Sarà et al. 2011).

Although satellite chl *a* data have been widely used in the literature as a proxy for food availability to mussels, this may still be a simplification of real mussel diets (Thomas et al. 2011, Sarà et al. 2013b). Fatty acid analysis indicates that the diets of intertidal bivalves can be highly variable and change according to the microhabitat and local food sources (Puccinelli et al. 2016). This too could contribute to differences between the simulated and observed values.

Both model outputs and field results underline the existence of important differences among populations along the coast as a whole. The results were particularly interesting for the most easterly sites, St. Lucia and Ballito, where *P. perna* populations reached maximum abundance and higher somatic biomasses despite the fact that food availability is lowest there. In this study, the model was implemented using laboratory data of oxygen consumption, feeding and digestion for animals kept under standard conditions. Observations made under conditions of starvation or variable food quality and quantity would be a useful implementation of the model to understand the growth and reproduction dynamics of *P. perna* in oligotrophic areas, such as these 2 sites.

The model can also contribute to describing species distribution patterns in more complex simulations involving biotic interactions. The implementation of a mechanistic trait-based approach comparing *P. perna* and *M. galloprovincialis* could provide important insights into their fundamental and realised niches and how the interactions and distributions of the 2 species are likely to change under a regime of altering climate.

The DEB model adopted in this study was able to realistically capture the distribution pattern of *P. perna* along the South African coast, providing insight into the mechanisms shaping this distribution. The model highlighted the importance of reproduction as a factor limiting the establishment of *P. perna* populations in cold-water areas, despite the high availability of food. In contrast, and surprisingly, areas with low food availability but higher seawater temperature proved to be the most favourable for *P. perna* development, suggesting that the species is well adapted to poor food conditions, but that low temperatures have a strongly limiting effect on reproduction. Providing insight into exactly how environmental conditions affect where species can or cannot exist makes DEB models a particularly useful tool for predicting distributions under changing physical conditions.

Acknowledgements. This work is based upon research supported by the South African Research Chairs Initiative of the Department of Science and Technology and the National Research Foundation and was supported by a Rhodes University post-doctoral fellowship and by PRIN TETRIS 2010 grant no. 2010PBMAXP_003. G.S. was supported in his research by the Italian Minister of Research and University (MIUR). We thank Marco Martinez for help with shell aging, Alessandro Rinaldi for help with Matlab and Marco Ruisi for help with the satellite software. Many thanks also to Jacqueline Trassierra, Carlota Fernandez Muniz and Cristian Monaco for assistance in the field and in the laboratory. Ethical approval: all applicable institutional and/or national guidelines for the care and use of animals were followed. Permits were released by the Department of Agriculture, Forestry and Fisheries of the Republic of South Africa (1) for collection, possessiom and transportation of marine species for research (permit reference RES2014/12), and (2) to export fish or part or product thereof for scientific research purpose only (Permit number 1404055).

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Editorial responsibility: Lisandro Benedetti-Cecchi, Pisa, Italy

Submitted: February 25, 2016; Accepted: August 17, 2016
Proofs received from author(s): September 25, 2016