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ORIGINAL PAPER

Predicting the performance of cosmopolitan species: dynamic energy budget model skill drops across large spatial scales

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Abstract

Individual-based models are increasingly used by marine ecologists to predict species responses to environmental change on a mechanistic basis. Dynamic Energy Budget (DEB) models allow the simulation of physiological processes (maintenance, growth, reproduction) in response to variability in environmental drivers. High levels of computational capacity and remote-sensing technologies provide an opportunity to apply existing DEB models across global spatial scales. To do so, however, we must first test the assumption of stationarity, i.e., that parameter values estimated for populations in one location/time are valid for populations elsewhere. Using a validated DEB model parameterized for the cosmopolitan intertidal mussel *Mytilus galloprovincialis*, we ran growth simulations for native, Mediterranean Sea, populations and non-native, South African populations. The model performed well for native populations, but overestimated growth for non-native ones. Overestimations suggest that: (1) unaccounted variables may keep the physiological performance of non-native *M. galloprovincialis* in check, and/or (2) phenotypic plasticity or local adaptation could modulate responses under different environmental conditions. The study shows that stationary mechanistic models that aim to describe dynamics in complex physiological processes should be treated carefully when implemented across large spatial scales. Instead, we suggest placing the necessary effort into identifying the nuances that result in non-stationarity and explicitly accounting for them in geographic-scale mechanistic models.

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Introduction

Understanding and predicting species' responses to environmental variability requires careful consideration of individual-level physiological processes (Kearney 2006; Denny and Helmuth 2009; Monaco and Helmuth 2011). Individual-based energy budget models offer an opportunity to make mechanistic links between environmental drivers and the ecological success of species in both natural and altered systems (Hochachka and Somero 2002). The main strength of such mechanistic models, as opposed to the more widely applied statistical models (e.g., species distribution correlative models), is an explicit focus on the organism's fundamental niche. The more process-based nature of this approach implies no assumptions about the influence of locally contingent factors (e.g., biotic interactions) on species baseline responses, and therefore holds greater potential for reliably anticipating dynamics in a species' performance and distribution (Kearney 2006).

Different types of energy budget models exist, varying in degree of generality, sophistication, or theoretical justification (Karasov and Martínez del Rio 2007). Depending

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on the investigator's research goals, these models can be as complex as desired. For example, energy budget models have been constructed to account for gradients in single or multiple stressors that can be either biotic or abiotic (Branch 1981; Widdows and Johnson 1988; Hölker and Mehner 2005; Kitazawa et al. 2008; Sokolova 2013), and can incorporate behavior (e.g., microhabitat use for regulating body temperature, Grant and Porter 1992). Indeed, thorough descriptions of the ecological and physiological context are increasingly favoured in mechanistic studies (Denny and Helmuth 2009; Pincebourde and Woods 2012; Potter et al. 2013). Simultaneously, given the global scale of some of the challenges facing species today (e.g., climate change) and the growing number of species exhibiting shifting or expanding distribution limits, notably, invasive species (Walther et al. 2002; Seebens et al. 2017), there is a pressing need for accurate models that can be implemented at both local and global scales. Ideally, models should, therefore strive to balance the context dependence of physiological performance, without compromising the power to describe the larger-scale processes that may ultimately define the ecological performance of the species.

While technological bottlenecks prevented the application of individual-based models across large spatial scales in the past, advances in remote-sensing technology and computational power provide today's marine biologists with access to large-scale environmental data, and allow the rapid performance of the necessary calculations (Kerr and Ostrovsky 2003; Hofmann and Gaines 2008). It is now possible for energy budget models to describe and project the physiological condition of species across their entire distributional range.

Importantly, however, for many existing mathematical models to be applicable across space, we must assume 'spatial stationarity', i.e., that parameter values estimated for populations in one location/time are valid for populations elsewhere (Stenseth et al. 2003; Woodin et al. 2013; Montalto et al. 2015). The assumption of model stationarity has been challenged extensively in the literature on species distribution models (i.e., correlative modeling), and innovative solutions have been proposed. For instance, instead of assuming fixed regression coefficients for the whole distribution of their species, Kupfer and Farris (2007) relied on geographically weighted regression models that are flexible/adaptive across space. Such flexibility was also embraced by Hothorn et al. (2011) using a method that decomposes the variability of local and global effects of environmental drivers to produce statistical models that can deal with not only non-stationarity, but also spatiotemporal autocorrelation. While such implementations can incorporate non-stationarity, these solutions still suffer from the drawbacks of species distribution models: they are grounded on statistical approximations that describe relationships, often neglecting cause–effect mechanisms. Unfortunately, however, predictive mechanistic models put forward by physiological ecologists rarely test the stationarity assumption, and few attempts have been made to account for non-stationarity in parameter values (for exceptions, see Buckley 2008; Alunno-Bruscia et al. 2011). For energy budget models, this implies that parameter values defining flow of energy through an individual are constant. Because phenotypic plasticity and local adaptation are pervasive in nature (Sanford and Kelly 2011; Valladares et al. 2014), regarding species as uniform entities is probably incorrect. Thus, for energy budget models to be useful at all spatial scales, we must first test the assumption of stationarity.

Here, we examine stationarity in a Dynamic Energy Budget (DEB) model (Kooijman 2010) developed for the Mediterranean mussel *Mytilus galloprovincialis*. We choose to use DEB modeling due to its growing popularity among ecologists owing to its ability to model underlying physiological processes (growth, reproduction, and maintenance) based on first principles that are applicable across different taxa and ontogenetic stages (Sousa et al. 2010; Monaco et al. 2014). DEB models also have the advantage of being able to accommodate temporal/spatial variability in environmental drivers such as temperature, food availability (Saraiva et al. 2011), and pH (Klok et al. 2014), all of which are predicted to vary at a global scale with climate change. We worked with *M. galloprovincialis* because, as a cosmopolitan species present on all continents except Antarctica, this mussel offers the chance to compare the model's performance across very large (inter-hemispheric) geographical scales. Additionally, because *M. galloprovincialis* is such a successful invasive species, evaluating its physiological performance at non-native sites could improve our understanding of its spread and impact on natural systems.

Although DEB theory has existed for over 35 years and its utility has been widely confirmed by virtue of the many species already parameterized (van der Meer et al. 2014), its application to model species, including *M. galloprovincialis*, is mostly constrained to very local spatial scales (but see Tagliarolo et al. 2016). DEB models are generally parameterized based on real data collected from few populations, and plasticity in traits is often ignored, i.e., stationarity is assumed. Given the rapid progress in DEB theory and the prospect of applying it to large spatial scales in applied and exploratory research (Alunno-Bruscia et al. 2011; Montalto et al. 2015), testing the assumption of stationarity, thus, becomes an imperative.

This study tests the stationarity assumption by comparing the ability of a DEB model to predict size at age for individuals collected from Mediterranean Sea native sites, for which we develop the model (control region), and South African non-native sites. Anticipating possible non-stationarity, we explored variability in the two main driving

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variables, temperature and food availability, in relation to the model's skill. Finally, in light of these environmental data, we examine and discuss possible ways to incorporate non-stationarity in key DEB model parameters to obtain better predictions for non-native regions.

Materials and methods

Study regions and sites

Mytilus galloprovincialis is a cosmopolitan species spread across temperate rocky shores in both hemispheres. Here, we focused on two regions, the European coast of the Mediterranean Sea (Italy), and the southern tip of Africa (South Africa) (Fig. 1a). *M. galloprovincialis* is a European native, and the original DEB model used here was parameterized based on populations from that region, specifically located

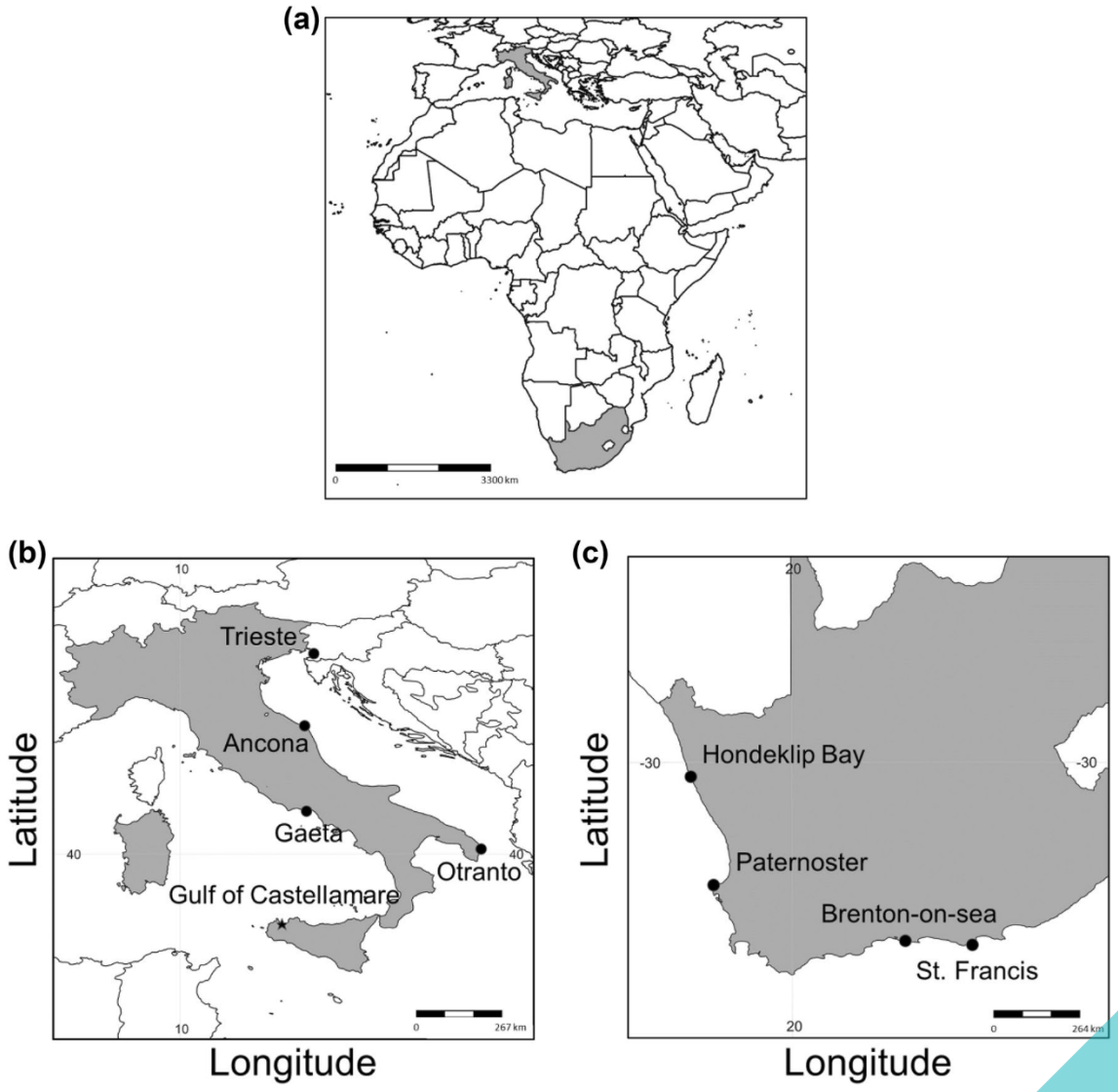


Fig. 1 Maps illustrating the geographical extent covered by this study and that which resulted on the original parameterization of the dynamic energy budget model used here (Sarà et al. 2012). **a** Global scale showing a portion of Europe and Africa. The countries sampled, Italy and South Africa, are indicated in grey. The main bodies of water influencing our sampled mussels are also provided. The sampled populations in the Mediterranean Sea region are shown in **b**, and those from the South African region in **c**. Our study sites are represented by circles, while that used by Sarà et al. (2012) is indicated by a star. Maps produced using SimpleMappr (http://www.simplemappr.net)

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in the Gulf of Castellammare (38°02′26.9″ N, 12°55′18.5″ E) (Sarà et al. 2012). Here, we sampled four intertidal Italian populations that were different from those used by Sarà et al. (2012) to develop the original model: Gaeta (41°13′00.7″ N, 13°32′02.9″ E), Otranto (40°08′ 38.0″ N, 18°30′08.3 E), Ancona (43°33′32.7″ N, 13°36′24.1″ E), and Trieste (45°38′58.3″ N, 13°46′36.5″ E) (Fig. 1b), which were used for quality control of the performance of the existing DEB model. To test the current model under conditions experienced by mussels in a non-native region, we used four intertidal South African populations: Hondeklip Bay (20°18′19.2″ S, 17°16′18.5″ E), Paternoster (32°48′44.3″ S, 17°52′48.8″ E), Brenton-on-sea (34°04′31.1″ S, 23°01′26.1″ E), and St. Francis (34°12′30.5″ S, 24°50′00.6″ E) (Fig. 1c). Important differences in wave height and tidal range exist between the regions and can presumably influence the degree of mussel submergence and body temperatures. On average, the Mediterranean experiences negligible tidal fluctuations, while the tidal range in South Africa is c. 2 m. Food availability in the form of primary production also differs significantly between the studied sites. The Mediterranean Sea is characteristically oligotrophic (Colella et al. 2016), and the west coast of South Africa, where two of our four sites occur, exhibits higher productivity due to more frequent upwelling than on the south coast, where the other two sites occur (Brown 1992; Bustamante et al. 1995).

Mussel size-at-age determination

At each of our sites (Fig. 1) we collected animals to determine size at age. Italian and South African sites were sampled on July 2013 and August 2014, respectively. The earlier study that employed DEB to model subtidal *M. galloprovincialis* from Gulf of Castellammare covered the period 2006–2009 (Sarà et al. 2012). We sampled the lower section of mussel beds by collecting all individuals within each of three randomly placed quadrats of 20 × 20 cm. Mussels were fixed in 70% ethanol and transported to the laboratory where shell length, soft tissue dry weight (gonads and soma separated), and age 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. 2013). The age–length relationship obtained with this method was compared with previous studies done in the same area using several different methods and the results were comparable (Kaehler and McQuaid 1999; McQuaid and Lindsay 2000). Shell length was measured using callipers (± 1 mm).

In this study, we used all mussels from the quadrats that were estimated to be 1 or 2 years old. Because mussels were collected from random quadrats, the number of individuals reaching 1 and 2 years was unbalanced among sites and between regions.

DEB model and original parameter values

Using the DEB model, we simulated mussel growth, in terms of soma dry weight, from birth to age 1 and 2 years at all our sites. Predictions were then compared with the observed size (see *Mussel size-at-age determination*).

Here, we briefly refer to the fundamentals of the DEB model and the main components that allowed testing of the stationarity assumption. More detailed descriptions are given in Kooijman (2010), Sarà et al. (2013), and Monaco and McQuaid (2018). We used a 'standard DEB model' (i.e., one reserve compartment, one structure compartment, isomorphic growth). Food, measured as chlorophyll-*a* concentration (a proxy for phytoplankton concentration in the water), enters the organism's body following a Type II functional response model dependent on a half-saturation coefficient (X_κ) (Holling 1959). Assimilated energy is stored in a reserve pool, from which it is allocated according to the κ-rule; a fixed proportion (κ) goes to maintenance of somatic tissues and growth of structure, while the rest ($1 - \kappa$) is used for maintenance of maturity level and maturation (or gamete production in adults). The rates of all energy flows are modulated by a thermal sensitivity model that describes a typical negatively skewed curve, with zero values marking the temperature tolerance range, and highest values at the temperature at which rates are at maximum values. The chief parameter here, controlling thermal sensitivity within the thermal-tolerance range, is the Arrhenius temperature (T_A). These and other parameters (Appendix S1 in Supporting Information) directly or indirectly influence growth (Kooijman 2010; Sarà et al. 2013; Monaco et al. 2014).

Driving variables: temperature, food availability, and tidal height

For intertidal mussels, both body temperature and food ingestion vary with the tidal cycle. To account for this in our model simulations, we included tidal height as a modulating variable. When the tidal height was below the shore level of the mussel bed, feeding was suspended and all temperature-dependent physiological processes were stalled on the basis of metabolic depression (Anestis et al. 2007; Tagliarolo and McQuaid 2015; Monaco and McQuaid 2018). To identify emersion/immersion periods in South Africa, we used tidal height values estimated for each site by the prediction software Marées dans le monde 4.00 (StrassGrauerMarina Softwares), and body temperature data logged by three biomimetic sensors or "robomussels" deployed between June 2014 and January 2015 at each site (Helmuth et al. 2016). The height on the shore was identified by a sharp drop in temperature of ≥ 3 °C in 30 min during summer following Harley and Helmuth (2003) and comparison with tide tables. The effective shore level (m above MLLW) for each site was

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determined by averaging the height on the shore estimated over 20 days (Hondeklip Bay = 0.77 m; Paternoster = 0.72 m; Brenton-on-sea = 0.72 m; St. Francis = 0.72 m). Because waves are important at South African sites, a buffer zone of +0.3 m was added to this estimated tidal height to ensure temperature readings represented periods when loggers were completely submerged at high tide. For Italian sites, periods of emersion/immersion were identified based on empirical observations of water level and the same tidal prediction software (Gaeta = 0.1 m; Otranto = 0.15 m; Ancona = 0.25; Trieste = 0.3 m).

The DEB model was run for each site using estimated body temperature (derived from Sea Surface Temperature [SST] and air temperature) and chlorophyll-*a* data as driving variables. Time series of daily SST and concentration of chlorophyll-*a*, both at processing Level 4 (i.e. spatially gridded and continuous over the time period analysed), were extracted for the years 2011–2014 for all of our sites (Fig. 1) via the R packages raster (Hijmans 2016) and ncdf4 (Pierce 2015) (R Core Team 2016). Air temperature data were extracted from Weather Underground's API, accessed via the R package rwunderground (https://github.com/ALShum/rwunderground).

Time series of daily SST were obtained from the "Group for High Resolution Sea Surface Temperature" (GHRSST—NASA; JPL MUR MEaSUREs Project, 2010) produced using wavelets as basic functions through an optimal interpolation, with a spatial resolution of 0.011° grid (≈1 km). Data were obtained from numerous instruments, such as the NASA Advanced Microwave Scanning Radiometer-EOS (AMSRE), the Moderate Resolution Imaging Spectroradiometer (MODIS) on the NASA Aqua and Terra platforms, the US Navy microwave WindSat radiometer and in situ SST observations from the NOAA iQuam project.

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; Smit et al. 2013). For this reason, the satellite-derived SST dataset was ground-truthed using in situ data obtained either from the Italian Oceanographic Buoy Network (Mediterranean Sea sites) or from "robomussels" (South African sites) (Helmuth et al. 2016). In situ SST data were correlated with satellite data to establish site-specific linear relationships (Tagliarolo et al. 2016). The estimated submerged body temperature fed into the DEB models was computed based on these relationships (see Appendix S2 in Supporting Information for linear regression parameters, and S5 for underlying data). Similarly, estimated aerial body temperature was obtained from a relationship between robomussel data and air temperature data computed aggregately for all sites (Appendix S3 and S6).

Daily chlorophyll-*a* data (μg L^{-1}), with a spatial resolution of 4 km, were provided by the European MyOcean project (Copernicus Marine Environment Monitoring Service–CMEMS–Ocean monitoring and forecasting service; http://www.myocean.eu/) produced by the merging of MERIS, MODIS/AQUA, VIIRS and SeaWiFS data using Optimal-Interpolation, based on the kriging method with regional settings of the estimated covariance between the chlorophyll-*a* anomalies observations (Saulquin et al. 2011). We used these data directly in the DEB model, as previous accounts have revealed that satellite data do not differ significantly from in situ intertidal measurements, at least in the Mediterranean Sea (Sarà et al. 2011).

The DEB model R script used to run the mussel growth simulations is available in Appendix S4 and all the environmental data compiled in Appendix S7.

Model skill comparisons

Model predictions of soma dry weight at the end of the simulated periods (1- and 2-year-old mussels grouped together) were compared against observed size at age. First, to assess the magnitude of differences between observations and simulations for each site, we calculated the error statistics Mean Absolute Error (MAE) and Root-Mean Square Error (RMSE). Second, we compared the model skill between regions and sites using absolute errors. Because the number of samples was unbalanced (see *Mussel size-at-age determination*), we conducted bootstrapped ANOVA (Wilcox 2012; Mancuso et al. 2015). The bootstrap involved resampling the data from each region 1000 times and calculating 95% confidence intervals, which were then contrasted against the critical *F* value to evaluate statistical differences (Wilcox 2012). Statistical significance was additionally assessed based on the *p* value ($\alpha = 0.05$). The bootstrap ANOVA to test for site effects was followed by a post hoc pairwise comparison with Bonferroni correction.

Results

Size-at-age observations

Random sampling of mussels provided the necessary 1- and 2-year-old individuals for testing the DEB model. Unfortunately, however, the numbers were unbalanced between ages, sites, and regions (Table 1).

Mean observed size at age was homogenous amongst sites and regions, ranging between 0.297 (0.093 SD) g for 2-year-old mussels in Brenton-on-sea and 0.024 (0.007 SD) g for 1-year-old mussels in Gaeta. The difference in mean soma dry weight between 1- and 2-year-old mussels was consistently greater for Mediterranean than South African sites (Fig. 2).

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Table 1 Error statistics (*RMSE* root mean square error, *MAE* mean absolute error) to compare dynamic energy budget model mussel shell length (g) predictions against observations of size at age

Region/site	*N* age 1	*N* age 2	Total *N*	RMSE (g)	MAE (g)
Mediterranean Sea					
Gaeta	93	4	97	0.014	0.012
Otranto	153	21	174	0.039	0.035
Ancona	44	47	91	0.188	0.140
Trieste	88	12	100	0.197	0.152
Total *N*	378	84	462		
South Africa					
Hondeklip Bay	2	25	27	0.958	0.930
Paternoster	31	78	109	0.698	0.608
Brenton-on-sea	4	9	13	0.286	0.234
St. Francis	40	68	108	0.923	0.780
Total *N*	77	180	257		

The number (*N*) of individuals aged as 1 or 2 years old is provided

DEB model growth simulations and skill comparisons

Using DEB model parameters validated for Mediterranean Sea *Mytilus galloprovincialis* (Appendix S1), we successfully simulated increases in size (soma dry weight) from birth to 1- and 2-years-old (Fig. 2). Simulated growth dynamics varied among sites and between regions in response to differences in the driving environmental variables temperature and food availability. For example, growth in the Mediterranean Sea was greater in Ancona and Trieste than Gaeta and Otranto, and generally more pronounced for South African than Mediterranean Sea sites. Growth was similar amongst South African sites despite generally warmer SST on the south (Brenton-on-sea and St. Francis) than the west (Hondeklip Bay and Paternoster) coast. This probably reflects compensation for low temperatures by the much higher chlorophyll levels in the west coast Benguela system, where values can be three times higher than on the south coast (Demarcq et al. 2003; see Model non-stationarity: influence of environmental drivers).

Our assessment yielded no support for model stationarity across the studied regions. Both error statistics, root mean square error and mean absolute error revealed consistently better agreement between observed and predicted soma dry weight for Mediterranean Sea than South African mussel populations (Table 1; Figs. 2, 3). This was confirmed by a bootstrapped 1-way ANOVA (Table 2). An effect of site on the model mean absolute error was also detected, and post hoc analysis revealed differences among all sites, expect Brenton-on-sea (South Africa), Ancona, and Trieste (Mediterranean Sea) (Fig. 3).

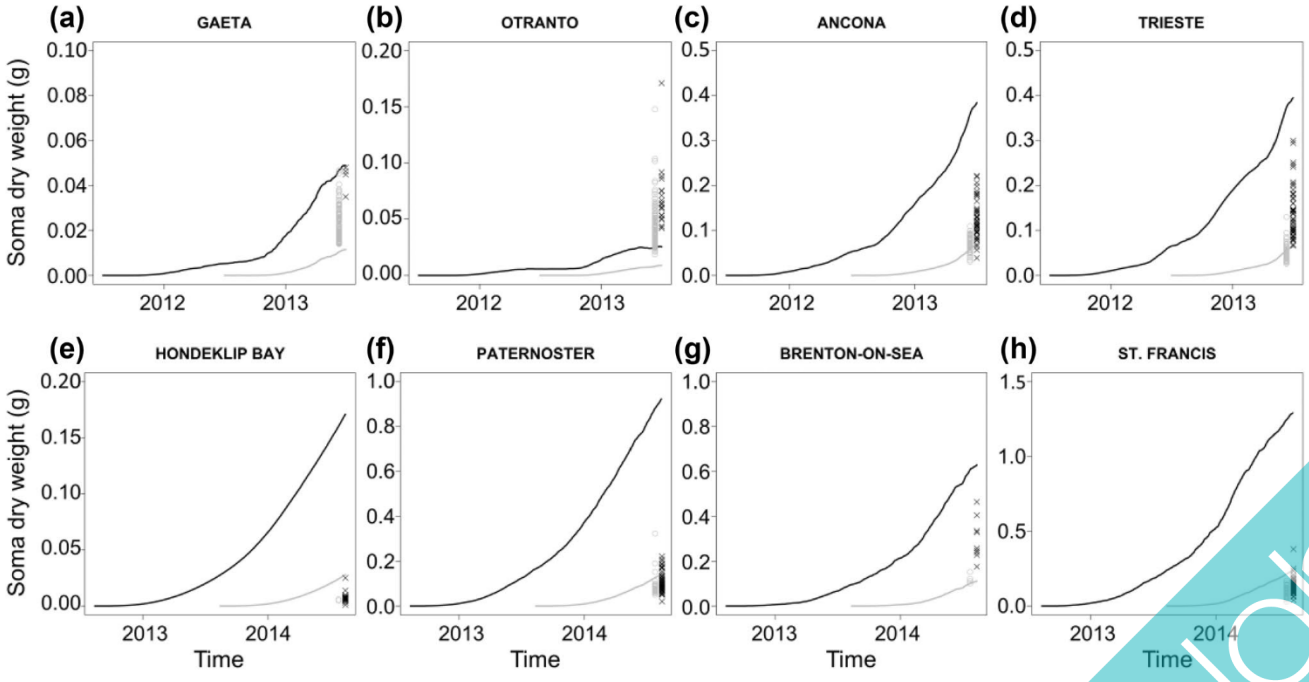


Fig. 2 Dynamic Energy Budget model soma dry weight (g) growth simulations for 1 (gray) and 2 (black) year old *Mytilus galloprovincialis* (using original parameter values and local environmental conditions). Observations of size-at-age are illustrated by circles and crosses for 1- and 2-year-old mussels, respectively. The symbols are slightly offset to prevent cluttering. The scale differs among panels. Panels **a**–**d** correspond to Mediterranean Sea populations, and **e**–**h** South African populations

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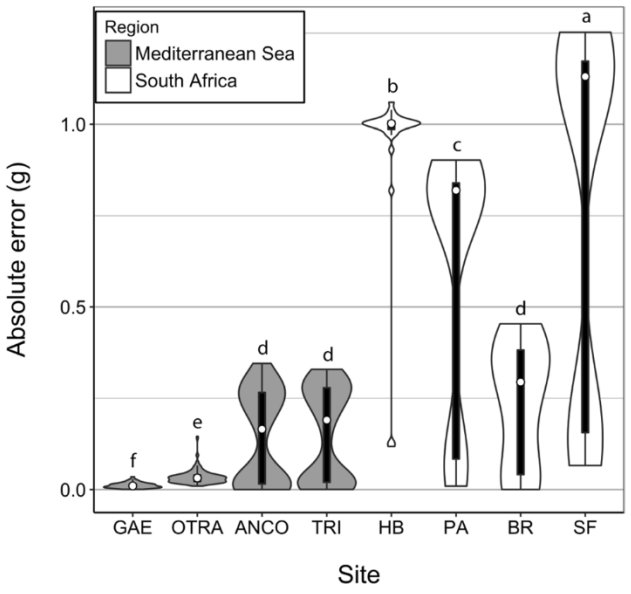


Fig. 3 Absolute errors calculated from Dynamic Energy Budget model simulations vs. observed growth for each site (see Fig. 2). Data are separated by region: native populations from the Mediterranean Sea in grey (*GA* Gaeta, *OTRA* Otranto, *ANCO* Ancona, *TRI* Trieste) and non-native South African populations (*HB* Hondeklip Bay, *PA* Paternoster, *BR* Brenton-on-sea, *SF* St. Francis) in white. The violin shapes represent distribution densities. The white circles are the medians. The boxes are the 25th and 75th percentiles of the distribution. The lines extending vertically are maximally 1.5 times the interquartile range. Different letters above the violins reflect significant differences among sites (bootstrapped ANOVA, post hoc pairwise comparison with Bonferroni correction)

Table 2 Bootstrapped one-way ANOVA results testing the effect of region (Mediterranean Sea *vs.* South African coast) on *Mytilus galloprovincialis* DEB model skill (absolute error)

Source	SS	*df*	*F*	95% CI	*p*
Region	64.69	1	987.35	782.16–1236.35	< 0.001
Residuals	53.53	817			

Model non-stationarity: influence of environmental drivers

We found marked differences between regions in the data for the environmental drivers chlorophyll-*a* and estimated submerged temperature (Fig. 4a, b), but not estimated aerial body temperature (Fig. 4c). Variability in mean chlorophyll-*a* across sites was positively correlated with the model's skill (Fig. 4d), while submerged temperature affected model skill negatively (Fig. 4e). Importantly, while the overall relationships were strong for data pooled for both regions, the regions differed in where they lay along the spectrum of values for both chlorophyll-*a* and submerged temperature (Fig. 4d, e). The similar mean aerial temperatures experienced by mussels across regions did not correlate with the model's skill (Fig. 4f).

Model non-stationarity: parameter re-estimation

Since the original DEB model failed to provide good fits for non-native populations, we re-estimated some parameters searching for better matches in that region. To narrow the search for candidate parameters, we focused on two physiological processes that are critical for growth, energy intake and thermal sensitivity, which respond to variability in chlorophyll-*a* and temperature, respectively. The former is primarily controlled in the model by the half-saturation coefficient (X_κ), and the latter by the Arrhenius temperature (T_A), which is homologous to the more widely utilized Q_{10} (for reference, $T_A = 6000$ equates to a Q_{10} of ~ 2). A comprehensive grid search allowed us to vary these parameters simultaneously and test the model predictions using 10,000 combinations ($X_\kappa = 0.05$–5 µg L^{-1}; $T_A = 2080$–$10{,}000$ °K). Predictions improved from a mean absolute error of 0.995 g, when using original parameters, to 0.049 g when using the parameters that provided the best fit. Despite the improvements, however, the parameter values that minimized the error were extreme ($X_\kappa = 5$ µg L^{-1}; $T_A = 10000$ K) and unrealistic, in comparison to other temperate filter feeder species listed in the DEB add_my_pet collection (http://www.bio.vu.nl/thb/deb/deblab/). Note that this grid search also considered values that matched empirical derivations available in the literature. For example, a value of $T_A = 7090$ K was reported by Tagliarolo and McQuaid (2015) for South African populations of *M. galloprovincialis*.

Discussion

Climate change is driving dramatic alterations to natural ecosystems through changes in species distributions and by exacerbating the trend of increasing frequency of biological invasions (Walther et al. 2002; Seebens et al. 2017). Anticipating the consequences of these two effects on ecosystem services can be accomplished using mechanistic models that can quantify the physiological condition of native and non-native individuals. A wealth of individual-based models, which can account for aspects of physiology and behaviour, is becoming available (Kearney 2006; Buckley 2013). Because these models capture life-history traits that are susceptible to evolution, their parameter values can presumably vary as a function of genetic differentiation (Valladares et al. 2014). Thus, to apply these models across global scales, we must test the assumption of 'stationarity'.

We provide evidence that a standard Dynamic Energy Budget model developed for native, Mediterranean Sea populations of *Mytilus galloprovincialis* (Sarà et al. 2012) is

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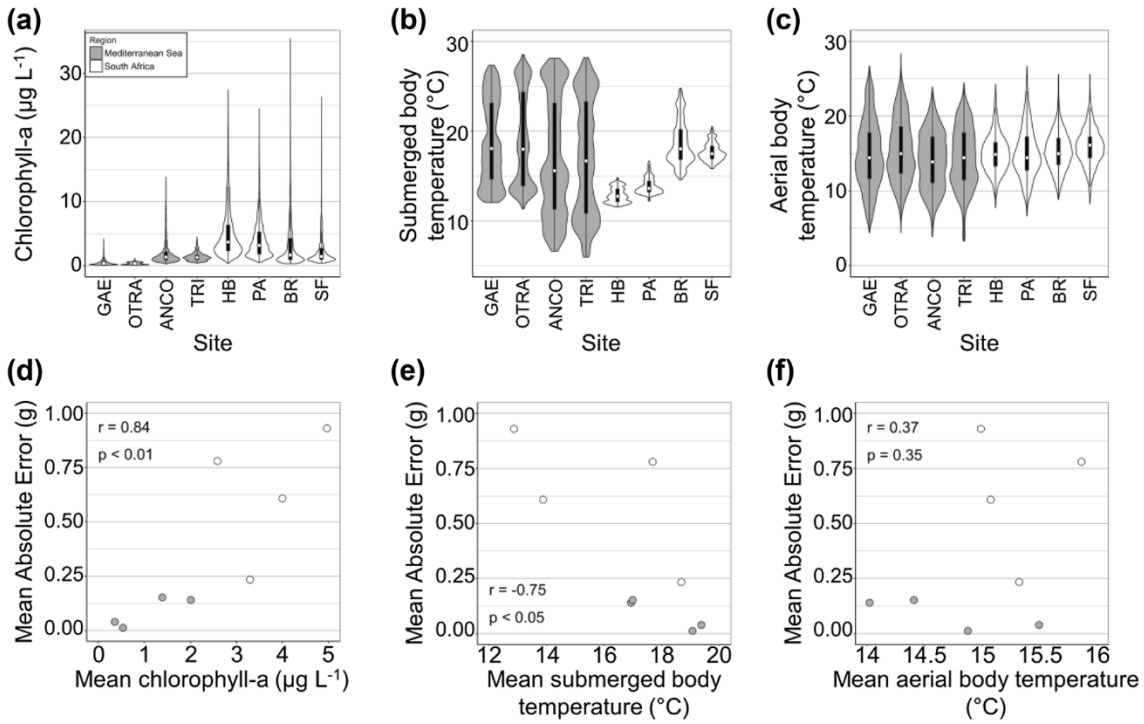


Fig. 4 Environmental conditions, **a** chlorophyll-*a*, **b** submerged body temperature, and **c** aerial body temperature experienced by mussel populations at each site over a period of 2 years. Data are given in violin plots and separated by region as in Fig. 3. Correlations between mean absolute error (MAE) and mean environmental variables **d** chlorophyll-*a* concentration, **e** submerged body temperature, and **f** aerial body temperature

unable to perform well for non-native, South African populations. We now discuss possible causes of poor performance in DEB models, and then propose ways of moving forward. In general, a model's ability to describe real-world processes depends on the estimated parameter values, which in turn are inherently constrained by the number and magnitude of external forces (e.g., environmental drivers) considered during the parameterization stage, as well as physiological constraints imposed by genetics.

Models and parameter values are a reflection of the environmental and biological data used to train and validate them. The model used here explicitly considered the effect of variability in the two main environmental drivers of mussel physiological performance: temperature (during periods of both aquatic submergence and aerial exposure) and food as expressed by chlorophyll-*a*. Taking these variables into account, the model predictably provided good fits for the growth of native populations, but overestimated growth for non-native populations. In both regions, we strove to describe realistic conditions actually experienced by intertidal mussels by validating SSTs and aerial body temperatures experienced in the field and determining periods of submergence/emergence (Appendices S1–S7). It is important to note, however, that these calculations can only yield rough estimates of the conditions experienced by populations. During aerial exposure, the body temperature of individual ectotherms responds to several weather variables that operate in concert, including not only air temperature but also solar radiation and wind speed (Helmuth 1998). In the absence of direct measurements of body temperatures, our estimates nevertheless captured the expected differences between sites, and thus should serve for large-scale analyses like the one conducted here.

Another *caveat* is that the DEB model used here does not explicitly account for possible anaerobic metabolism or oxidative stress incurred by intertidal mussels during prolonged aerial exposure, which can further affect the energy balance of organisms (Anestis et al. 2007; Jimenez et al. 2016; Lesser 2016). Based on recent evidence from Tagliarolo and McQuaid (2015), our model simply assumed metabolic depression during emersion, thus buffering the influence of variable body temperatures in air on energetics and growth. While real mussels probably exhibit initial metabolic depression followed by increased energetic expenditure through the costs of heat shock responses during low tide periods, their exact responses depend on the magnitude, frequency, and duration of thermal/desiccation stress events. Consequently, further empirical work is needed before we can integrate these costs into dynamic models like DEB (Gilman 2017). Note, however, that, although we cannot assess how much of

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submerged time is spent being splashed vs. fully submerged, the estimated duration of high tide periods was comparable between regions (Mediterranean Sea = 74.9%; South Africa = 78.3%). Thus, based on duration alone, failing to consider the extra costs of anaerobiosis would contribute to the model error equally across regions. We also found that similar mean aerial temperatures were experienced by mussels in both regions, suggesting that the effect of temperature on physiological rates during periods of low tide should not differ greatly either. The data presented here suggest that the differences in model skill between regions are more tightly linked to those conditions experienced during high tide periods than low tide events. Indeed, while chlorophyll-*a* and submerged temperatures were correlated with the model error, aerial temperatures differed little between sites and had no discernible effect on model skill.

Therefore, the poor predictions of the model for populations in South Africa suggest that other factors that limit energy allocation towards growth were overlooked. First, intertidal mussels in South Africa are often parasitized by endolithic cyanobacteria that cause considerable shell damage, prompting shell repair and increasing the energetic costs of maintenance. These parasites are known to occur in Europe, on the Atlantic coast of Portugal, but both prevalence and intensity of infestation are dramatically lower there (Marquet et al. 2013). Second, wave exposure also increases maintenance costs in mussels, as more energy is directed towards byssal thread production (Carrington 2002; Zardi et al. 2007; Nicastro et al. 2010). Because wave action is much lower in the Mediterranean Sea (Izaguirre et al. 2011), mussels in South Africa sites are again likely to be more energetically constrained (e.g., Zardi et al. 2007). Both of these external factors limit the scope for growth in mussels. That they were not considered in the original DEB model parameterization can help to explain the model overestimates at non-native sites. Upon entering new systems, non-native species can both benefit (e.g., increased food, predator/disease release) and suffer (e.g., new enemies, physical stressors) from the new conditions encountered. Our overestimations of growth in non-native sites suggest that the potentially higher physiological performance of *M. galloprovincialis* in South Africa linked to food availability is kept in check by unaccounted variables such as parasitism and wave action (Nicastro et al. 2010; Marquet et al. 2013) that may nullify the advantages of higher chlorophyll concentrations.

The role of genetic variability may also help to explain our results. For models seeking to describe physiological processes subject to plasticity and local adaptation, like individual-based energy budget models, model skill is additionally determined by the capacity of the parameters to capture variability in traits across time and space (Woodin et al. 2013; Valladares et al. 2014; Montalto et al. 2015). By comparing populations from vastly different coastlines, our study captured a range of environmental conditions, which *M. galloprovincialis* is necessarily adapted to cope with. The fact that our model can simulate growth for one region but not the other suggests that traits can be flexible. To perform well at a global scale, this DEB model needs to incorporate such flexibility in its parameters. The notion that species exhibit phenotypic plasticity and local adaptation has, of course, existed for a long time. Different populations coping with disparate environmental conditions can have different sensitivities to these drivers (Sinervo and Adolph 1994). Little work has, however, been done on the incorporation of genetic variability into predictive models applied across distant populations (but see Buckley 2008).

Previous DEB modeling efforts to capture differences in physiological performance between distant sites have taken one of two approaches: (1) maintaining parameter values by assuming stationarity (Montalto et al. 2015), or (2) modifying key parameters based on specific conditions (Alunno-Bruscia et al. 2011), i.e., non-stationarity. As a third approach (not discussed here), we could consider independent DEB parameterizations done by separate studies/researchers; however, because these efforts are uncoordinated, their parameter values and predictions are not easily comparable. Our results revealed that the first alternative was not viable for this inter-hemispheric model application. Therefore, we explored the possibility that simple adjustments of parameter values controlling food ingestion (X_κ) and temperature sensitivity (T_A) could improve our predictions, offering a 'quick-fix' solution. Alunno-Bruscia et al. (2011) successfully used this approach to model growth and reproduction in the invasive pacific oyster (*Crassostrea gigas*) collected from different sites with contrasting food quality/quantity conditions along the French coastline. By allowing X_κ to vary freely, they significantly improved model fits at each site. This 'quick fix', however, did not yield better predictions for our data.

The most parsimonious explanation for our poor predictions in South Africa is that the greater distance between populations in our study than in that of Alunno-Bruscia et al. (2011) prevents connectivity, allowing genetic divergence through drift and adaptation to local conditions. This explanation is partly supported at a local scale in Italy by the fact that the model performed better at sites closer to the location where it was first parameterized (Otranto and Gaeta) than those farther away (Ancona and Trieste). However, food availability and SST were similar at Ancona and Trieste in Italy and at Brenton-on-sea and St. Francis in South Africa, but, while the model error for Brenton-on-sea was on a par with that for Ancona and Trieste, it was worse at St Francis, suggesting that environmental similarity alone does not explain model skill.

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The assumption that evolutionary relatedness among species is reflected in similarity in parameter values is a fundamental tenet in DEB theory. While DEB models are commonly built for a 'species', the theory maintains that the continuum in parameter values could be followed down to population and individual levels (Nisbet et al. 2000; Kooijman 2010; Sousa et al. 2010). Theoretically then, one could envision different sets of parameter values for different individuals and populations. In practice however, this is not feasible for realistic ecological application, and parameterizations are typically conducted to the species level.

The underlying mechanisms that orchestrate phenotypic plasticity and local adaptation at the genome level are complex and still poorly understood in many model species. While flexibility in traits or parameter values due to existing genetic variance can be exposed experimentally (Lesser et al. 2010; Pespeni et al. 2013), plastic responses may not be obvious unless properly tested. Context dependence can complicate the issue to the point that it is impossible to recommend general solutions. Instead, we suggest that a better approach is to expend the necessary effort in identifying the traits that drive poor performance of the model. For instance, because feeding in bivalves depends on several behavioural and physiological responses (filtration efficiency, particle selection, assimilation efficiency) that vary with the environment (Bayne et al. 1993), some DEB models have suggested explicitly incorporating them in models to widen their spatial application (Alunno-Bruscia et al. 2011; Saraiva et al. 2011; Lavaud et al. 2014). Fine-tuning of model parameters appears to be the only way to maintain the mechanistic nature of this approach. Alternatively, one may re-parameterize the model using locally collected data, but this implies ignoring the processes driving differences between regions, therefore incurring similar drawbacks to those of correlative models (Buckley 2008).

Conclusions and future directions

Mechanistic models hold great potential for anticipating species' physiological and ecological performance across increasingly large spatial scales (Kearney and Porter 2004). However, when working with cosmopolitan species at global scales, notably invasive generalists, ecologists must test the assumption of model stationarity. This study reveals that spatial stationarity cannot be assumed in a Dynamic Energy Budget model built for *Mytilus galloprovincialis*, and non-stationarity should, thus, be embraced. The reasons behind a model's failure can be categorized as either 'unaccounted environmental or biological drivers' or as 'genetics'. Unfortunately, the two cannot be separated with our data. Optimal use of DEB models across global scales should address this question by conducting tailored experiments. Furthermore, explicit consideration of the relevant factors that vary amongst populations requires moving beyond the standard DEB model used here to more specialized formulations (Kooijman 2010).

Physiological ecologists have warned about the dangers of predicting species distributions in the future based on habitat conditions experienced by populations today (i.e., a 'climate envelope' approach). Although climate envelope models may accurately predict responses under conditions within the realized niche of a species, they perform poorly in scenarios that lie outside of the envelope (Kearney 2006). Therefore, unless corrected, these models inherently assume stationarity in parameter values (Kupfer and Farris 2007; Hothorn et al. 2011). Because mechanistic models aim at describing a species' fundamental niche, they could be considered safe from this problem. However, as we have shown, when used across large geographical scales, mechanistic models can also provide flawed predictions. Progress in the critical endeavour of predicting species' responses to climate change requires addressing the issues responsible for poor predictive power rather than ignoring them.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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