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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51 Introduction

52 Understanding and predicting species' responses to environmental variability requires careful consideration of individual-level physiological processes (Kearney 2006; Denny and 53 Helmuth 2009; Monaco and Helmuth 2011). Individual-based energy budget models offer 54 55 an opportunity to make mechanistic links between environmental drivers and the ecological 56 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 57 58 models (e.g. species distribution correlative models), is an explicit focus on the organism's 59 fundamental niche. The more process-based nature of this approach implies no assumptions 60 about the influence of locally contingent factors (e.g. biotic interactions) on species baseline 61 responses, and therefore holds greater potential for reliably anticipating dynamics in a

62 species' performance and distribution (Kearney 2006).

63 Different types of energy budget models exist, varying in degree of generality, 64 sophistication, or theoretical justification (Karasov and Martínez del Rio 2007). Depending 65 on the investigator's research goals, these models can be as complex as desired. For 66 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 67 68 1988; Hölker and Mehner 2005; Kitazawa et al. 2008; Sokolova 2013), and can incorporate 69 behaviour (e.g. microhabitat use for regulating body temperature, Grant and Porter 1992). 70 Indeed, thorough descriptions of the ecological and physiological context are increasingly 71 favoured in mechanistic studies (Denny and Helmuth 2009; Pincebourde and Woods 2012;

72 Potter et al. 2013). Simultaneously, given the global scale of some of the challenges facing 73 species today (e.g. climate change) and the growing number of species exhibiting shifting or 74 expanding distribution limits, notably, invasive species (Walther et al. 2002; Seebens et al. 75 2017), there is a pressing need for accurate models that can be implemented at both local 76 and global scales. Ideally, models should therefore strive to balance the context-77 dependence of physiological performance, without compromising the power to describe the larger scale processes that may ultimately define the ecological performance of the species. 78 79 While technological bottlenecks prevented the application of individual-based 80 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 81 82 environmental data, and allow the rapid performance of the necessary calculations (Kerr 83 and Ostrovsky 2003; Hofmann and Gaines 2008). It is now possible for energy budget 84 models to describe and project the physiological condition of species across their entire 85 distributional range.

Importantly, however, for many existing mathematical models to be applicable 86 across space, we must assume 'spatial stationarity', i.e. that parameter values estimated for 87 88 populations in one location/time are valid for populations elsewhere (Stenseth et al. 2003; 89 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 90 modelling), and innovative solutions have been proposed. For instance, instead of assuming 91 92 fixed regression coefficients for the whole distribution of their species, Kupfer and Farris 93 (2007) relied on geographically weighted regression models that are flexible/adaptive across 94 space. Such flexibility was also embraced by Hothorn et al. (2011), using a method that 95 decomposes the variability of local and global effects of environmental drivers to produce

96 statistical models that can deal with not only non-stationarity, but also spatiotemporal 97 autocorrelation. While such implementations can incorporate non-stationarity, these 98 solutions still suffer from the drawbacks of species distribution models: they are grounded 99 on statistical approximations that describe relationships, often neglecting cause-effect 100 mechanisms. Unfortunately, however, predictive mechanistic models put forward by 101 physiological ecologists rarely test the stationarity assumption, and few attempts have been 102 made to account for non-stationarity in parameter values (for exceptions see Buckley 2008; 103 Alunno-Bruscia et al. 2011). For energy budget models, this implies that parameter values 104 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), 105 106 regarding species as uniform entities is probably incorrect. Thus, for energy budget models 107 to be useful at all spatial scales, we must first test the assumption of stationarity. 108 Here we examine stationarity in a Dynamic Energy Budget (DEB) model (Kooijman

109 2010) developed for the Mediterranean mussel Mytilus galloprovincialis. We choose to use DEB modelling due to its growing popularity among ecologists owing to its ability to model 110 111 underlying physiological processes (growth, reproduction, and maintenance) based on first 112 principles that are applicable across different taxa and ontogenetic stages (Sousa et al. 113 2010; Monaco et al. 2014). DEB models also have the advantage of being able to 114 accommodate temporal/spatial variability in environmental drivers such as temperature, 115 food availability (Saraiva et al. 2011), and pH (Klok et al. 2014), all of which are predicted to 116 vary at a global scale with climate change. We worked with *M. galloprovincialis* because, as 117 a cosmopolitan species present on all continents except Antarctica, this mussel offers the 118 chance to compare the model's performance across very large (inter-hemispheric) 119 geographical scales. Additionally, because *M. galloprovincialis* is such a successful invasive

species, evaluating its physiological performance at non-native sites could improve ourunderstanding of its spread and impact on natural systems.

122 Although DEB theory has existed for over 35 years and its utility has been widely 123 confirmed by virtue of the many species already parameterized (van der Meer et al. 2014), 124 its application to model species, including *M. galloprovincialis*, is mostly constrained to very 125 local spatial scales (but see Tagliarolo et al. 2016). DEB models are generally parameterized 126 based on real data collected from few populations, and plasticity in traits is often ignored, 127 i.e. stationarity is assumed. Given the rapid progress in DEB theory and the prospect of 128 applying it to large spatial scales in applied and exploratory research (Alunno-Bruscia et al. 129 2011; Montalto et al. 2015), testing the assumption of stationarity thus becomes an

130 imperative.

131 This study tests the stationarity assumption by comparing the ability of a DEB model

132 to predict size-at-age for individuals collected from Mediterranean Sea native sites, for

133 which we develop the model (control region), and South African non-native sites.

134 Anticipating possible non-stationarity, we explored variability in the two main driving

variables, temperature and food availability, in relation to the model's skill. Finally, in light

136 of these environmental data, we examine and discuss possible ways to incorporate non-

137 stationarity in key DEB model parameters to obtain better predictions for non-native

138 regions.

139

140 Materials and methods

141 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

144	Mediterranean Sea (Italy), and the southern tip of Africa (South Africa) (Fig. 1A). M.
145	galloprovincialis is a European native, and the original DEB model used here was
146	parameterized based on populations from that region, specifically located in the Gulf of
147	Castellammare (38°02'26.9'' N, 12°55'18.5'' E) (Sarà et al. 2012). Here we sampled four
148	intertidal Italian populations that were different from those used by Sarà et al. (2012) to
149	develop the original model: Gaeta (41°13′00.7″ N, 13°32′02.9″ E), Otranto (40°08′ 38.0″ N,
150	18°30'08.3 E), Ancona (43°33'32.7" N, 13°36'24.1" E), and Trieste (45°38'58.3" N,
151	13°46'36.5" E) (Fig. 1B), which were used for quality control of the performance of the
152	existing DEB model. To test the current model under conditions experienced by mussels in a
153	non-native region, we used four intertidal South African populations: Hondeklip Bay
154	(20°18'19.2" S, 17°16'18.5" E), Paternoster (32°48'44.3" S, 17°52'48.8" E), Brenton-on-sea
155	(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).
156	Important differences in wave height and tidal range exist between the regions and can
157	presumably influence the degree of mussel submergence and body temperatures. On
158	average, the Mediterranean experiences negligible tidal fluctuations, while the tidal range in
159	South Africa is c. 2m. Food availability in the form of primary production also differs
160	significantly between the studied sites. The Mediterranean Sea is characteristically
161	oligotrophic (Colella et al. 2016), and the west coast of South Africa, where two of our four
162	sites occur, exhibits higher productivity due to frequent upwelling than the south coast,
163	where the other two sites occur (Brown 1992; Bustamante et al. 1995).
164	
165	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

168 that employed DEB to model subtidal *M. galloprovincialis* from Gulf of Castellammare 169 covered the period 2006-2009 (Sarà et al. 2012). We sampled the lower section of mussel 170 beds by collecting all individuals within each of three randomly placed quadrats of 20 x 20 171 cm. Mussels were fixed in 70% ethanol and transported to the laboratory where shell 172 length, soft tissue dry weight (gonads and soma separated), and age were recorded for each 173 individual. Age was estimated by cutting the shell with a rotary disk and counting the 174 number of annual rings under a stereomicroscope (Peharda et al. 2011; Sarà et al. 2013). 175 The age-length relationship obtained with this method was compared with previous studies 176 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 177 178 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 y was unbalanced among sites and between regions.

182

183 **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 y at all our sites. Predictions were then compared with the observed size (see *Mussel size-at-age determination*).

- 187 Here, we briefly refer to the fundamentals of the DEB model and the main
- 188 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
- 190 a 'standard DEB model' (i.e. one reserve compartment, one structure compartment,
- 191 isomorphic growth). Food, measured as *chlorophyll-a* concentration (a proxy for

192 phytoplankton concentration in the water), enters the organism's body following a Type II 193 functional response model dependent on a half-saturation coefficient (X_{κ}) (Holling 1959). 194 Assimilated energy is stored in a reserve pool, from which it is allocated according to the κ -195 rule; a fixed proportion (κ) goes to maintenance of somatic tissues and growth of structure, 196 while the rest $(1 - \kappa)$ is used for maintenance of maturity level and maturation (or gamete 197 production in adults). The rates of all energy flows are modulated by a thermal sensitivity 198 model that describes a typical negatively skewed curve, with zero values marking the 199 temperature tolerance range, and highest values at the temperature at which rates are at 200 maximum values. The chief parameter here, controlling thermal sensitivity within the 201 thermal-tolerance range, is the Arrhenius temperature (T_A). These and other parameters 202 (Appendix S1 in Supporting Information) directly or indirectly influence growth (Kooijman 203 2010; Sarà et al. 2013; Monaco et al. 2014).

204

205 Driving variables: temperature, food availability, and tidal height

206 For intertidal mussels, both body temperature and food ingestion vary with the tidal cycle. 207 To account for this in our model simulations, we included tidal height as a modulating 208 variable. When the tidal height was below the shore level of the mussel bed, feeding was 209 suspended and all temperature-dependent physiological processes were stalled on the basis 210 of metabolic depression (Anestis et al. 2007; Tagliarolo and McQuaid 2015; Monaco and 211 McQuaid 2018). To identify emersion/immersion periods in South Africa, we used tidal 212 height values estimated for each site by the prediction software Marées dans le monde 4.00 213 (StrassGrauerMarina Softwares), and body temperature data logged by 3 biomimetic 214 sensors or "robomussels" deployed between June 2014 and January 2015 at each site 215 (Helmuth et al. 2016). The height on the shore was identified by a sharp drop in

216 temperature of \geq 3°C in 30 min during summer following Harley and Helmuth (2003) and 217 comparison with tide tables. The effective shore level (m above MLLW) for each site was 218 determined by averaging the height on the shore estimated over 20 days (Hondeklip Bay = 219 0.77 m; Paternoster = 0.72 m; Brenton-on-sea = 0.72 m; Saint Francis = 0.72 m). Because 220 waves are important at South African sites, a buffer zone of +0.3 m was added to this 221 estimated tidal height to ensure temperature readings represented periods when loggers 222 were completely submerged at high tide. For Italian sites, periods of emersion/immersion 223 were identified based on empirical observations of water level and the same tidal prediction 224 software (Gaeta = 0.1 m; Otranto = 0.15 m; Ancona = 0.25; Trieste = 0.3 m).

225 The DEB model was run for each site using estimated body temperature (derived 226 from Sea Surface Temperature [SST] and air temperature) and *chlorophyll-a* data as driving 227 variables. Time series of daily SST and concentration of chlorophyll-a, both at processing 228 Level 4 (i.e. spatially gridded and continuous over the time period analysed), were extracted 229 for the years 2011-2014 for all of our sites (Fig. 1) via the R packages raster (Hijmans 2016) 230 and ncdf4 (Pierce 2015) (R Core Team 2016). Air temperature data were extracted from 231 Weather Underground's API, accessed via the R package rwunderground 232 (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 basis 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.

240 Previous studies comparing SST and *in situ* loggers revealed that satellite data are 241 often ineffective at capturing extremes in intertidal water variability (Lathlean et al. 2011; 242 Smit et al. 2013). For this reason, the satellite-derived SST dataset was ground-truthed 243 using *in situ* data obtained either from the Italian Oceanographic Buoy Network 244 (Mediterranean Sea sites) or from "robomussels" (South African sites) (Helmuth et al. 2016). 245 In situ SST data were correlated to satellite data to establish site-specific linear relationships (Tagliarolo et al. 2016). The estimated submerged body temperature fed into the DEB 246 247 models was computed based on these relationships (see Appendix S2 in Supporting 248 Information for linear regression parameters, and S5 for underlying data). Similarly, estimated aerial body temperature was obtained from a relationship between robomussel 249 250 data and air temperature data computed aggregately for all sites (Appendix S3 and S6). 251 Daily *chlorophyll-a* data (μ g L⁻¹), with a spatial resolution of 4km, were provided by 252 the European MyOcean project (Copernicus Marine Environment Monitoring Service -253 CMEMS – Ocean monitoring and forecasting service; http://www.myocean.eu/) produced 254 by the merging of MERIS, MODIS/AQUA, VIIRS and SeaWiFS data using Optimal-255 Interpolation, based on the kriging method with regional settings of the estimated 256 covariance between the *chlorophyll-a* anomalies observations (Saulquin et al. 2011). We 257 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 258 Mediterranean Sea (Sarà et al. 2011). 259 260 The DEB model R script used to run the mussel growth simulations is available in 261 Appendix S4 and all the environmental data compiled in Appendix S7. 262

263 Model skill comparisons

264 Model predictions of soma dry weight at the end of the simulated periods (1 and 2-y old 265 mussels grouped together) were compared against observed size-at-age. First, to assess the 266 magnitude of differences between observations and simulations for each site, we calculated 267 the error statistics Mean Absolute Error (MAE) and Root-Mean Square Error (RMSE). 268 Second, we compared the model skill between regions and sites using absolute errors. 269 Because the number of samples was unbalanced (see *Mussel size-at-age determination*), we 270 conducted bootstrapped ANOVA (Wilcox 2012; Mancuso et al. 2015). The bootstrap 271 involved resampling the data from each region 1000 times and calculating 95% confidence 272 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-273 value (α = 0.05). The bootstrap ANOVA to test for site effects was followed by a post hoc 274 275 pairwise comparison with Bonferroni correction.

- 276
- 277 Results

278 Size-at-age observations

279 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,

281 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-y old mussels in Brenton-on-sea and 0.024 (0.007 SD) g for 1-y old mussels in Gaeta. The difference in mean soma dry weight between 1 and 2-y old mussels was consistently greater for Mediterranean than South African sites (Fig. 2).

286

287 DEB model growth simulations and skill comparisons

288 Using DEB model parameters validated for Mediterranean Sea Mytilus galloprovincialis 289 (Appendix S1), we successfully simulated increases in size (soma dry weight) from birth to 1 290 and 2-y old (Fig. 2). Simulated growth dynamics varied among sites and between regions in 291 response to differences in the driving environmental variables temperature and food 292 availability. For example, growth in the Mediterranean Sea was greater in Ancona and 293 Trieste than Gaeta and Otranto, and generally more pronounced for South African than 294 Mediterranean Sea sites. Growth was similar amongst South African sites despite generally 295 warmer SST on the south (Brenton-on-sea and St. Francis) than the west (Hondeklip Bay and 296 Paternoster) coast. This probably reflects compensation for low temperatures by the much 297 higher chlorophyll levels in the west coast Benguela system, where values can be three 298 times higher than on the south coast (Demarcq et al. 2003; see Model non-stationarity: 299 influence of environmental drivers).

300 Our assessment yielded no support for model stationarity across the studied regions. 301 Both error statistics, root mean square error and mean absolute error, revealed a 302 consistently better agreement between observed and predicted soma dry weight for 303 Mediterranean Sea than South African mussel populations (Table 1, Fig. 2-3). This was 304 confirmed by a bootstrapped 1-way ANOVA (Table 2). An effect of site on the model mean 305 absolute error was also detected, and post hoc analysis revealed differences between all 306 sites, expect Brenton-on-sea (South Africa), Ancona, and Trieste (Mediterranean Sea) (Fig. 307 3).

308

309 Model non-stationarity: influence of environmental drivers

310 We found marked differences between regions in the data for the environmental drivers

311 *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 to 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).

319

320 Model non-stationarity: parameter re-estimation

321 Since the original DEB model failed to provide good fits for non-native populations, we re-322 estimated some parameters searching for better matches in that region. To narrow the 323 search for candidate parameters, we focused on two physiological processes that are critical 324 for growth, energy intake and thermal sensitivity, which respond to variability in chlorophyll-325 a and temperature respectively. The former is primarily controlled in the model by the half-326 saturation coefficient (X_{κ}), and the latter by the Arrhenius temperature (T_A), which is 327 homologous to the more widely utilized Q_{10} (for reference, $T_A = 6000$ equates to a Q_{10} of 328 ~2). A comprehensive grid search allowed us to vary these parameters simultaneously and 329 test the model predictions using 10000 combinations ($X_{\kappa} = 0.05-5 \ \mu g \ L^{-1}$; $T_A = 2080-10000$ [°]K). Predictions improved from a mean absolute error of 0.995 g, when using original 330 331 parameters, to 0.049 g when using the parameters that provided the best fit. Despite the 332 improvements, however, the parameter values that minimized the error were extreme (X_{κ} = 5 μ g L⁻¹; T_A = 10000 K) and unrealistic, in comparison to other temperate filter feeder 333 334 species listed in the DEB add_my_pet collection (http://www.bio.vu.nl/thb/deb/deblab/). 335 Note that this grid search also considered values that matched empirical derivations

336	available in the literature. For example, a value of T_A = 7090 K was reported by Tagliarolo
337	and McQuaid (2015) for South African populations of <i>M. galloprovincialis</i> .

339 Discussion

340 Climate change is driving dramatic alterations to natural ecosystems through changes in 341 species distributions and by exacerbating the trend of increasing frequency of biological 342 invasions (Walther et al. 2002; Seebens et al. 2017). Anticipating the consequences of these 343 two effects on ecosystem services can be accomplished using mechanistic models that can 344 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 345 346 becoming available (Kearney 2006; Buckley 2013). Because these models capture life-347 history traits that are susceptible to evolution, their parameter values can presumably vary 348 as a function of genetic differentiation (Valladares et al. 2014). Thus, to apply these models 349 across global scales, we must test the assumption of 'stationarity'. 350 We provide evidence that a standard Dynamic Energy Budget model developed for 351 native, Mediterranean Sea populations of Mytilus galloprovincialis (Sarà et al. 2012) is 352 unable to perform well for non-native, South African populations. We now discuss possible 353 causes of poor performance in DEB models, and then propose ways of moving forward. In 354 general, a model's ability to describe real world processes depends on the estimated 355 parameter values, which in turn are inherently constrained by the number and magnitude of

356 external forces (e.g. environmental drivers) considered during the parameterization stage,

as well as physiological constraints imposed by genetics.

358 Models and parameter values are a reflection of the environmental and biological 359 data used to train and validate them. The model used here explicitly considered the effect

360 of variability in the two main environmental drivers of mussel physiological performance: 361 temperature (during periods of both aquatic submergence and aerial exposure) and food as 362 expressed by *chlorophyll-a*. Taking these variables into account, the model predictably 363 provided good fits for the growth of native populations, but overestimated growth for non-364 native populations. In both regions we strove to describe realistic conditions actually experienced by intertidal mussels by validating SSTs and aerial body temperatures 365 366 experienced in the field and determining periods of submergence/emergence (Appendices 367 S1-S7). It is important to note, however, that these calculations can only yield rough 368 estimates of the conditions experienced by populations. During aerial exposure, the body temperature of individual ectotherms responds to several weather variables that operate in 369 370 concert, including not only air temperature but also solar radiation and wind speed 371 (Helmuth 1998). In the absence of direct measurements of body temperatures, our 372 estimates nevertheless captured the expected differences between sites, and thus should 373 serve for large-scale analyses like the one conducted here.

374 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 375 376 prolonged aerial exposure, which can further affect the energy balance of organisms 377 (Anestis et al. 2007; Jimenez et al. 2016; Lesser 2016). Based on recent evidence from 378 Tagliarolo and McQuaid (2015), our model simply assumed metabolic depression during emersion, thus buffering the influence of variable body temperatures in air on energetics 379 380 and growth. While real mussels probably exhibit initial metabolic depression followed by 381 increased energetic expenditure through the costs of heat shock responses during low tide 382 periods, their exact responses depend on the magnitude, frequency, and duration of 383 thermal/desiccation stress events. Consequently, further empirical work is needed before

384 we can integrate these costs into dynamic models like DEB (Gilman 2017). Note, however, 385 that, although we cannot assess how much of that time is spent being splashed vs. fully 386 submerged, the estimated duration of high tide periods was comparable between regions 387 (Mediterranean Sea = 74.9%; South Africa = 78.3%). Thus, based on duration alone, failing 388 to consider the extra costs of anaerobiosis would contribute to the model error equally 389 across regions. We also found that similar mean aerial temperatures were experienced by 390 mussels in both regions, suggesting that the effect of temperature on physiological rates 391 during periods of low tide should not differ greatly either. The data presented here suggest 392 that the differences in model skill between regions are more tightly linked to those 393 conditions experienced during high tide periods than low tide events. Indeed, while 394 chlorophyll-a and submerged temperatures were correlated with the model error, aerial 395 temperatures differed little between sites and had no discernible effect on model skill. 396 Therefore, the poor predictions of the model for populations in South Africa suggest 397 that other factors that limit energy allocation towards growth were overlooked. First, 398 intertidal mussels in South Africa are often parasitized by endolithic cyanobacteria that 399 cause considerable shell damage, prompting shell repair and increasing the energetic costs 400 of maintenance. These parasites are known to occur in Europe, on the Atlantic coast of 401 Portugal, but both prevalence and intensity of infestation are dramatically lower there 402 (Marquet et al. 2013). Second, wave exposure also increases maintenance costs in mussels, 403 as more energy is directed towards byssal thread production (Carrington 2002; Zardi et al. 404 2007; Nicastro et al. 2010). Because wave action is much lower in the Mediterranean Sea 405 (Izaguirre et al. 2011), mussels in South Africa sites are again likely to be more energetically 406 constrained (e.g. Zardi et al. 2007). Both of these external factors limit the scope for growth 407 in mussels. That they were not considered in the original DEB model parameterization can

408 help explain the model overestimates at non-native sites. Upon entering new systems, non-409 native species can both benefit (e.g. increased food, predator/disease release) and suffer 410 (e.g. new enemies, physical stressors) from the new conditions encountered. Our 411 overestimations of growth in non-native sites suggest that the potentially higher 412 physiological performance of *M. galloprovincialis* in South Africa linked to food availability is 413 kept in check by unaccounted variables such as parasitism and wave action (Nicastro et al. 414 2010; Marquet et al. 2013) that may nullify the advantages of higher chlorophyll 415 concentrations.

416 The role of genetic variability may also help explain our results. For models seeking to describe physiological processes subject to plasticity and local adaptation, like individual-417 418 based energy budget models, model skill is additionally determined by the capacity of the 419 parameters to capture variability in traits across time and space (Woodin et al. 2013; 420 Valladares et al. 2014; Montalto et al. 2015). By comparing populations from vastly 421 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 422 423 growth for one region but not the other suggests that traits can be flexible. In order to 424 perform well at a global scale, this DEB model needs to incorporate such flexibility in its 425 parameters. The notion that species exhibit phenotypic plasticity and local adaptation has, 426 of course, existed for a long time. Different populations coping with disparate environmental conditions can have different sensitivities to these drivers (Sinervo and 427 428 Adolph 1994). Little work has, however, been done on the incorporation of genetic 429 variability into predictive models applied across distant populations (but see Buckley 2008). 430 Previous DEB modelling efforts to capture differences in physiological performance 431 between distant sites have taken two approaches: (1) maintaining parameter values by

432 assuming stationarity (Montalto et al. 2015), or (2) modifying key parameters based on 433 specific conditions (Alunno-Bruscia et al. 2011), i.e. non-stationarity. As a third approach 434 (not discussed here), we could consider independent DEB parameterizations done by 435 separate studies/researchers; however, because these efforts are uncoordinated, their 436 parameter values and predictions are not easily comparable. Our results revealed that the 437 first alternative was not viable for this inter-hemispheric model application. Therefore, we 438 explored the possibility that simple adjustments of parameter values controlling food 439 ingestion (X_{κ}) and temperature sensitivity (T_A) could improve our predictions, offering a 440 '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 441 442 different sites with contrasting food quality/quantity conditions along the French coastline. 443 By allowing X_{κ} to vary freely they significantly improved model fits at each site. This 'quick 444 fix', however, did not yield better predictions for our data.

445 The most parsimonious explanation for our poor predictions in South Africa is that 446 the greater distance between populations in our study than in that of Alunno-Bruscia et al. (2011) prohibits genetic connectivity, allowing genetic divergence drift and through 447 448 adaptation to local conditions. This explanation is partly supported at a local scale in Italy by 449 the fact that the model performed better at sites closer to the location where it was first 450 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 451 452 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 453 454 environmental similarity alone does not explain model skill.

455 The assumption that evolutionary relatedness among species is reflected in similarity 456 in parameter values is a fundamental tenet in DEB theory. While DEB models are commonly 457 built for a 'species', the theory maintains that the continuum in parameter values could be 458 followed down to population and individual levels (Nisbet et al. 2000; Kooijman 2010; Sousa 459 et al. 2010). Theoretically then, one could envision different sets of parameter values for 460 different individuals and populations. In practice however, this is not feasible for realistic ecological application, and parameterizations are typically conducted to the species level. 461 462 The underlying mechanisms that orchestrate phenotypic plasticity and local 463 adaptation at the genome level are complex and still poorly understood in many model 464 species. While flexibility in traits or parameter values due to existing genetic variance can 465 be exposed experimentally (Lesser et al. 2010; Pespeni et al. 2013), plastic responses may 466 not be obvious unless properly tested. Context dependence can complicate the issue to the 467 point that it is impossible to recommend general solutions. Instead, we suggest that a 468 better approach is to expend the necessary effort in identifying the traits that drive poor 469 performance of the model. For instance, because feeding in bivalves depends on several 470 behavioural and physiological responses (filtration efficiency, particle selection, assimilation 471 efficiency) that vary with the environment (Bayne et al. 1993), some DEB models have 472 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 473 parameters appears to be the only way to maintain the mechanistic nature of this approach. 474 475 Alternatively, one may re-parameterize the model using locally collected data, but this 476 implies ignoring the processes driving differences between regions, therefore incurring similar drawbacks to those of correlative models (Buckley 2008). 477

478

479 **Conclusions and future directions**

480 Mechanistic models hold great potential for anticipating species physiological and ecological 481 performance across increasingly large spatial scales (Kearney and Porter 2004). However, 482 when working with cosmopolitan species at global scales, notably invasive generalists, 483 ecologists must test the assumption of model stationarity. This study reveals that spatial 484 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 485 486 model's failure can be categorized as either 'unaccounted environmental or biological 487 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 488 489 tailored experiments. Furthermore, explicit consideration of the relevant factors that vary 490 amongst populations requires moving beyond the standard DEB model used here to more 491 specialized formulations (Kooijman 2010).

492 Physiological ecologists have warned about the dangers of predicting species 493 distributions in the future based on habitat conditions experienced by populations today (i.e. a 'climate envelope' approach). Although climate envelope models may accurately 494 495 predict responses under conditions within the realized niche of a species, they perform 496 poorly in scenarios that lie outside of the envelope (Kearney 2006). Therefore, unless 497 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' 498 499 fundamental niche, they could be considered safe from this problem. However, as we have 500 shown, when used across large geographical scales, mechanistic models can also provide 501 flawed predictions. Progress in the critical endeavour of predicting species' responses to

502 climate change requires addressing the issues responsible for poor predictive power rather

503 than ignoring them.

504

505 List of items in the supplementary material

- 506 Appendix S1. *Mytilus galloprovincialis* Dynamic Energy Budget (DEB) parameter values used
- 507 to perform model simulations.
- 508 Appendix S2. Linear regression coefficients from relationships between satellite-derived sea
- 509 surface temperature and *in situ* measurements (data available in Appendix S5).
- 510 Appendix S3. Linear regression coefficients from relationship between weather station air
- 511 temperature (www.weatherunderground.com/weather/api) and *in situ* measurements
- 512 taken with aerially exposed "robomussels" (data available in Appendix S6).
- 513 Appendix S4. Dynamic Energy Budget (DEB) model scrip for *Mytilus galloprovincialis*.
- 514 Appendix S5. Satellite-derived sea surface temperature and *in situ* measurements used to
- 515 estimate submerged mussel body temperature.
- 516 Appendix S6. Weather station air temperature and *in situ* "robomussels" measurements
- 517 used to estimate aerially exposed mussel body temperature.
- 518 Appendix S7. Site-specific environmental data used to run the DEB models. Columns are:
- 519 region, site, local time (SAST or CEST), estimated body temperature in water (°C), estimated
- body temperature in air (°C), *chlorophyll-a* concentration (μ g/L), tide height (m), and tide
- 521 flag (1=mussel submerged, 0=mussel exposed to air).

- 523 **Conflict of interest**. The authors declare that they have no conflict of interest.
- 524

525 Ethical approval. All applicable international, national, and/or institutional guidelines for the526 care and use of animals were followed.

528	References
529	Alunno-Bruscia M, Bourlès Y, Maurer D, Robert S, Mazurié J, Gangnery A, Goulletquer P,
530	Pouvreau S (2011) A single bio-energetics growth and reproduction model for
531	the oyster Crassostrea gigas in six Atlantic ecosystems. J Sea Res 66: 340-348 doi
532	10.1016/j.seares.2011.07.008
533	Anestis A, Lazou A, Pörtner HO, Michaelidis B (2007) Behavioral, metabolic, and
534	molecular stress responses of marine bivalve Mytilus galloprovincialis during
535	long-term acclimation at increasing ambient temperature. American Journal of
536	Physiology - Regulatory, Integrative and Comparative Physiology 293: R911-
537	R921 doi 10.1152/ajpregu.00124.2007
538	Bayne BL, Iglesias JIP, Hawkins AJS, Navarro E, Heral M, Deslous-Paoli JM (1993)
539	Feeding behaviour of the mussel, Mytilus edulis: responses to variations in
540	quantity and organic content of the seston. J Mar Biol Assoc UK 73: 813-829 doi
541	doi:10.1017/S0025315400034743
542	Branch GM (1981) The biology of limpets: physical factors, energy flow, and ecological
543	interactions Oceanography and Marine Biology: An Annual Review. Aberdeen
544	University Press/Allen & Unwin, London, pp 235-380
545	Brown PC (1992) Spatial and seasonal variation in chlorophyll distribution in the upper
546	30 m of the photic zone in the southern Benguela/Agulhas ecosystem. S Afr J Mar
547	Sci 12: 515-525 doi 10.2989/02577619209504722
548	Buckley LB (2008) Linking traits to energetics and population dynamics to predict
549	lizard ranges in changing environments. Am Nat 171: E1-E19

550	Buckley LB (2013) Get real: putting models of climate change and species interactions
551	in practice. Ann N Y Acad Sci 1297: 126-138 doi 10.1111/nyas.12175
552	Bustamante RH, Branch GM, Eekhout S, Robertson B, Zoutendyk P, Schleyer M, Dye A,
553	Hanekom N, Keats D, Jurd M, McQuaid C (1995) Gradients of intertidal primary
554	productivity around the coast of South Africa and their relationships with
555	consumer biomass. Oecologia 102: 189-201 doi 10.2307/4220948
556	Carrington E (2002) The ecomechanics of mussel attachment: from molecules to
557	ecosystems. Integr Comp Biol 42: 846-852
558	Colella S, Falcini F, Rinaldi E, Sammartino M, Santoleri R (2016) Mediterranean Ocean
559	Colour chlorophyll trends. PLoS One 11: e0155756 doi
560	10.1371/journal.pone.0155756
561	Demarcq H, Barlow RG, Shillington FA (2003) Climatology and variability of sea surface
562	temperature and surface chlorophyll in the Benguela and Agulhas ecosystems as
563	observed by satellite imagery. Afr J Mar Sci 25: 363-372 doi
564	10.2989/18142320309504022
565	Denny M, Helmuth B (2009) Confronting the physiological bottleneck: a challenge from
566	ecomechanics. Integr Comp Biol 49: 197-201 doi <u>10.1093/icb/icp070</u>
567	Gilman SE (2017) Predicting indirect effects of predator-prey interactions. Integr Comp
568	Biol icx031 doi doi.org/10.1093/icb/icx031
569	Grant BW, Porter WP (1992) Modeling global macroclimatic constraints on ectotherm
570	energy budgets. Am Zool 32: 154-178 doi 10.1093/icb/32.2.154
571	Harley CDG, Helmuth BST (2003) Local- and regional-scale effects of wave exposure,
572	thermal stress, and absolute versus effective shore level on patterns of intertidal
573	zonation. Limnol Oceanogr 48: 1498-1508

574	Helmuth B, Choi F, Matzelle A, Torossian JL, Morello SL, Mislan KAS, Yamane L,
575	Strickland D, Szathmary PL, Gilman SE, Tockstein A, Hilbish TJ, Burrows MT,
576	Power AM, Gosling E, Mieszkowska N, Harley CDG, Nishizaki M, Carrington E,
577	Menge B, Petes L, Foley MM, Johnson A, Poole M, Noble MM, Richmond EL,
578	Robart M, Robinson J, Sapp J, Sones J, Broitman BR, Denny MW, Mach KJ, Miller
579	LP, O'Donnell M, Ross P, Hofmann GE, Zippay M, Blanchette C, Macfarlan JA,
580	Carpizo-Ituarte E, Ruttenberg B, Peña Mejía CE, McQuaid CD, Lathlean J, Monaco
581	CJ, Nicastro KR, Zardi G (2016) Long-term, high frequency in situ measurements
582	of intertidal mussel bed temperatures using biomimetic sensors. Scientific Data
583	3: 160087 doi 10.1038/sdata.2016.87
584	Helmuth BST (1998) Intertidal mussel microclimates: predicting the body temperature
585	of a sessile invertebrate. Ecol Monogr 68: 51-74
586	Hijmans RJ (2016) raster: Geographic Data Analysis and Modeling. R package version
587	2.5-8. https://CRAN.R-project.org/package=raster
588	Hochachka PW, Somero GN (2002) Biochemical Adaptation: Mechanism and Process in
589	Physiological Evolution. Oxford University Press, New York
590	Hofmann GE, Gaines SD (2008) New tools to meet new challenges: emerging
591	technologies for managing marine ecosystems for resilience. Bioscience 58: 43-
592	52 doi 10.1641/B580109
593	Hölker F, Mehner T (2005) Simulation of trait- and density-mediated indirect effects
594	induced by piscivorous predators. Basic Appl Ecol 6: 289-300 doi
595	doi.org/10.1016/j.baae.2004.10.001
596	Holling CS (1959) Some characteristics of simple types of predation and parasitism. Can
597	Entomol 91: 385-398

- Hothorn T, Müller J, Schröder B, Kneib T, Brandl R (2011) Decomposing environmental,
- spatial, and spatiotemporal components of species distributions. Ecol Monogr
 81: 329-347 doi 10.1890/10-0602.1
- 601 Izaguirre C, Méndez FJ, Menéndez M, Losada IJ (2011) Global extreme wave height
- 602 variability based on satellite data. Geophys Res Lett 38 doi
- 603 10.1029/2011GL047302
- Jimenez AG, Alves S, Dallmer J, Njoo E, Roa S, Dowd WW (2016) Acclimation to elevated
 emersion temperature has no effect on susceptibility to acute, heat-induced lipid
 peroxidation in an intertidal mussel (*Mytilus californianus*). Mar Biol 163: 55 doi
- peroxidation in an intertidal mussel (*Hythas cullormanus*). Mar bior 105.
- 607 10.1007/s00227-016-2828-8
- Kaehler S, McQuaid CD (1999) Use of the fluorochrome calcein as an in situ growth
- 609 marker in the brown mussel *Perna perna*. Mar Biol 133: 455-460 doi
- 610 10.1007/s002270050485
- 611 Karasov WH, Martínez del Rio C (2007) Physiological Ecology: How Animals Process
- 612 Energy, Nutrients, and Toxins. Princeton University Press, Princeton
- 613 Kearney M (2006) Habitat, environment and niche: what are we modelling? Oikos 115:
- 614 186-191 doi 10.1111/j.2006.0030-1299.14908.x
- Kearney M, Porter WP (2004) Mapping the fundamental niche: physiology, climate, and
 the distribution of a nocturnal lizard. Ecology 85: 3119-3131
- 617 Kerr JT, Ostrovsky M (2003) From space to species: ecological applications for remote
- 618 sensing. Trends Ecol Evol 18: 299-305 doi 10.1016/S0169-5347(03)00071-5
- 619 Kitazawa D, Tabeta S, Kato T, Ruardij P (2008) A comparative study of the biomass-
- based and individual-based models of blue mussels. Ecol Modell 215: 93-104 doi
- 621 10.1016/j.ecolmodel.2008.02.014

- 622 Klok C, Wijsman JWM, Kaag K, Foekema E (2014) Effects of CO2 enrichment on cockle
- shell growth interpreted with a Dynamic Energy Budget model. J Sea Res 94:

624 111-116 doi 10.1016/j.seares.2014.01.011

625 Kooijman SALM (2010) Dynamic Energy Budget Theory For Metabolic Organization.

626 Cambridge University Press, Cambridge

627 Kupfer J, Farris C (2007) Incorporating spatial non-stationarity of regression

628 coefficients into predictive vegetation models. Landsc Ecol 22: 837-852

629 Lathlean JA, Ayre DJ, Minchinton TE (2011) Rocky intertidal temperature variability

along the southeast coast of Australia: comparing data from in situ loggers,

- 631 satellite-derived SST and terrestrial weather stations. Mar Ecol Prog Ser 439: 83-632 95
- 633 Lavaud R, Flye-Sainte-Marie J, Jean F, Emmery A, Strand Ø, Kooijman SALM (2014)
- 634Feeding and energetics of the great scallop, *Pecten maximus*, through a DEB

635 model. J Sea Res 94: 5-18 doi 10.1016/j.seares.2013.10.011

636 Lesser MP (2016) Climate change stressors cause metabolic depression in the blue

mussel, *Mytilus edulis*, from the Gulf of Maine. Limnol Oceanogr 61: 1705-1717
doi 10.1002/lno.10326

639 Lesser MP, Bailey MA, Merselis DG, Morrison JR (2010) Physiological response of the

640 blue mussel Mytilus edulis to differences in food and temperature in the Gulf of

- 641 Maine. Comparative Biochemistry and Physiology Part A: Molecular &
- 642 Integrative Physiology 156: 541-551
- Mancuso SG, Morgan VA, Mitchell PB, Berk M, Young A, Castle DJ (2015) A comparison

of schizophrenia, schizoaffective disorder, and bipolar disorder: results from the

645 second Australian national psychosis survey. J Affect Disord 172: 30-37 doi

646 10.1016/j.jad.2014.09.035

647	Marquet N, Nicastro KR, Gektidis M, McQuaid CD, Pearson GA, Serrão EA, Zardi GI
648	(2013) Comparison of phototrophic shell-degrading endoliths in invasive and
649	native populations of the intertidal mussel Mytilus galloprovincialis. Biol
650	Invasions 15: 1253-1272 doi 10.1007/s10530-012-0363-1
651	McQuaid CD, Lindsay TL (2000) Effect of wave exposure on growth and mortality rates
652	of the mussel Perna perna: bottom up regulation of intertidal populations. Mar
653	Ecol Prog Ser 206: 147-154 doi 10.3354/meps206147
654	Monaco CJ, Helmuth B (2011) Tipping points, thresholds and the keystone role of
655	physiology in marine climate change research. Adv Mar Biol 60: 124-154
656	Monaco CJ, McQuaid CD (2018) Applicability of Dynamic Energy Budget (DEB) models
657	across steep environmental gradients. Sci Rep 8: 16384 doi 10.1038/s41598-
658	018-34786-w
659	Monaco CJ, Wethey DS, Helmuth B (2014) A dynamic energy budget (DEB) model for the
660	keystone predator <i>Pisaster ochraceus</i> . PLoS One 9: e104658 doi
661	10.1371/journal.pone.0104658
662	Montalto V, Rinaldi A, Sarà G (2015) Life history traits to predict biogeographic species
663	distributions in bivalves. Sci Nat 102: 1-12 doi 10.1007/s00114-015-1313-4
664	Nicastro KR, Zardi GI, McQuaid CD (2010) Differential reproductive investment,
665	attachment strength and mortality of invasive and indigenous mussels across
666	heterogeneous environments. Biol Invasions 12: 2165-2177 doi
667	10.1007/s10530-009-9619-9
668	Nisbet RM, Muller EB, Lika K, Kooijman SALM (2000) From molecules to ecosystems
669	through dynamic energy budget models. J Anim Ecol 69: 913-926
670	Peharda M, Ezgeta-Balić D, Radman M, Sinjkević N, Vrgoč N, Isajlović I (2011) Age,
671	growth and population structure of Acanthocardia tuberculata (Bivalvia:

- 672 Cardiidae) in the eastern Adriatic Sea. Sci Mar 76: 59-66 doi
- 673 10.3989/scimar.03257.21A
- 674 Pespeni MH, Sanford E, Gaylord B, Hill TM, Hosfelt JD, Jaris HK, LaVigne M, Lenz EA,
- 675 Russell AD, Young MK, Palumbi SR (2013) Evolutionary change during
- experimental ocean acidification. Proc Natl Acad Sci 110: 6937-6942 doi
- 677 10.1073/pnas.1220673110
- 678 Pierce D (2015) ncdf4: Interface to Unidata netCDF (Version 4 or Earlier) Format Data
- 679 Files. R package version 1.15. https://CRAN.R-project.org/package=ncdf4
- 680 Pincebourde S, Woods HA (2012) Climate uncertainty on leaf surfaces: the biophysics of
- 681 leaf microclimates and their consequences for leaf-dwelling organisms. Funct
- 682 Ecol 26: 844-853 doi 10.1111/j.1365-2435.2012.02013.x
- Potter KA, Woods HA, Pincebourde S (2013) Microclimatic challenges in global change
 biology. Glob Chang Biol 19: 2932–2939 doi 10.1111/gcb.12257
- 685 R Core Team (2016) R: A Language and Environment for Statistical Computing. R
- 686 Foundation for Statistical Computing, Vienna, Austria
- 687 Sanford E, Kelly MW (2011) Local adaptation in marine invertebrates. Annual Review of
- 688 Marine Science 3: 509-535 doi <u>10.1146/annurev-marine-120709-142756</u>
- 689 Sarà G, Kearney M, Helmuth B (2011) Combining heat-transfer and energy budget
- 690 models to predict thermal stress in Mediterranean intertidal mussels. Chem Ecol
- 69127: 135-145 doi 10.1080/02757540.2011.552227
- 692 Sarà G, Palmeri V, Montalto V, Rinaldi A, Widdows J (2013) Parameterisation of bivalve
- 693 functional traits for mechanistic eco-physiological dynamic energy budget (DEB)
- 694 models. Mar Ecol Prog Ser 480: 99-117 doi 10.3354/meps10195
- 695 Sarà G, Reid G, Rinaldi A, Palmeri V, Troell M, Kooijman S (2012) Growth and
- 696 reproductive simulation of candidate shellfish species at fish cages in the

697	Southern Mediterranean: Dynamic Energy Budget (DEB) modelling for
698	integrated multi-trophic aquaculture. Aquaculture 324: 259 - 266
699	Saraiva S, van der Meer J, Kooijman SALM, Sousa T (2011) Modelling feeding processes
700	in bivalves: a mechanistic approach. Ecol Modell 222: 514-523 doi
701	10.1016/j.ecolmodel.2010.09.031
702	Saulquin B, Gohin F, Garrello R (2011) Regional objective analysis for merging high-
703	resolution MERIS, MODIS/Aqua, and SeaWiFS Chlorophyll-a data from 1998 to
704	2008 on the European Atlantic shelf. IEEE Transactions on Geoscience and
705	Remote Sensing 49: 143-154
706	Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P,
707	Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-
708	Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H,
709	Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J,
710	Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R,
711	Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P,
712	Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species
713	worldwide. Nature Communications 8: 14435 doi 10.1038/ncomms14435
714	Sinervo B, Adolph SC (1994) Growth plasticity and thermal opportunity in Sceloporus
715	lizards. Ecology 75: 776-790 doi 10.2307/1941734
716	Smit AJ, Roberts M, Anderson RJ, Dufois F, Dudley SFJ, Bornman TG, Olbers J, Bolton JJ
717	(2013) A coastal seawater temperature dataset for biogeographical studies: large
718	biases between in situ and remotely-sensed data sets around the coast of South
719	Africa. PLoS One 8: e81944 doi 10.1371/journal.pone.0081944

Sokolova IM (2013) Energy-limited tolerance to stress as a conceptual framework to
 integrate the effects of multiple stressors. Integr Comp Biol 53: 597-608 doi
 10.1093/icb/ict028

Sousa T, Domingos T, Poggiale J-C, Kooijman SALM (2010) Dynamic energy budget

- theory restores coherence in biology. Philosophical Transactions of the Royal
- 725 Society B: Biological Sciences 365: 3413-3428 doi 10.1098/rstb.2010.0166
- 726 Stenseth N, Ottersen G, Hurrell J, Mysterud A, Lima M, Chan K-S, Yoccoz N, Adlandsvik B

727 (2003) Studying climate effects on ecology through the use of climate indices: the

North Atlantic Oscillation, El Nino Southern Oscillation and beyond. Proc R Soc
 Lond B 270: 2087 - 2096

730 Tagliarolo M, McQuaid C (2015) Sub-lethal and sub-specific temperature effects are

better predictors of mussel distribution than thermal tolerance. Mar Ecol Prog
Ser 535: 145-159 doi 10.3354/meps11434

733 Tagliarolo M, Montalto V, Sarà G, Lathlean JA, McQuaid CD (2016) Low temperature

trumps high food availability to determine the distribution of intertidal mussels *Perna perna* in South Africa. Mar Ecol Prog Ser 558: 51-63

736 Valladares F, Matesanz S, Guilhaumon F, Araújo MB, Balaguer L, Benito-Garzón M,

737 Cornwell W, Gianoli E, Kleunen M, Naya DE (2014) The effects of phenotypic

738 plasticity and local adaptation on forecasts of species range shifts under climate

739 change. Ecol Lett 17: 1351-1364

- van der Meer J, Klok C, Kearney MR, Wijsman JWM, Kooijman SALM (2014) 35 years of
 DEB research. J Sea Res 94: 1-4 doi 10.1016/j.seares.2014.09.004
- 742 Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-
- 743 Guldberg O, Bairlein F (2002) Ecological responses to recent climate change.
- 744 Nature 416: 389-395

- 745 Widdows J, Johnson D (1988) Physiological energetics of *Mytilus edulis*: Scope for
- 746Growth. Mar Ecol Prog Ser 46: 113-121
- 747 Wilcox RR (2012) Introduction to robust estimation and hypothesis testing.
- 748 Elsevier/Academic Press, Amsterdam
- 749 Woodin SA, Hilbish TJ, Helmuth B, Jones SJ, Wethey DS (2013) Climate change, species
- 750 distribution models, and physiological performance metrics: predicting when
- biogeographic models are likely to fail. Ecol Evol 3: 3334-3346 doi
- 752 10.1002/ece3.680
- 753 Zardi GI, McQuaid CD, Nicastro KR (2007) Balancing survival and reproduction:
- seasonality of wave action, attachment strength and reproductive output in
- indigenous *Perna perna* and invasive *Mytilus galloprovincialis* mussels. Mar Ecol
- 756 Prog Ser 334: 155-163 doi 10.3354/meps334155

758 Tables

759 Table 1. Error statistics (RMSE = Root Mean Square Error, MAE = Mean Absolute Error) to

760 compare Dynamic Energy Budget model mussel shell length (g) predictions against

observations of size at age. The number (N) of individuals aged as 1 and 2 years old is

762 provided.

Region/SiteN age 1N age 2		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		

763

765 Table 2. Bootstrapped one-way ANOVA results testing the effect of region (Mediterranean

766 Sea vs. South African coast) on *Mytilus galloprovincialis* DEB model skill (absolute error).

Source	SS	df	F	95% CI	р
Region	64.69	1	987.35	782.16 - 1236.35	< 0.001
Residuals	53.53	817			

769 Figures captions

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 (M.S. = Mediterranean Sea). 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

778 (http://www.simplemappr.net).

Fig. 2 Dynamic Energy Budget model soma dry weight (g) growth simulations for 1 (grey)

and 2 (black) year old *Mytilus galloprovincialis* (using original parameter values and local

781 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

783 cluttering. The scale differs between panels. Panels (A)-(D) correspond to Mediterranean

784 Sea populations, and (E)-(H) South African populations.

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

787 from the Mediterranean Sea in grey (GA = Gaeta, OTRA = Otranto, ANCO = Ancona, TRI =

788 Trieste) and non-native South African populations (HB = Hondeklip Bay, PA = Paternoster, BR

789 = 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

792	range. Different letters above the violins reflect significant differences between sites
793	(bootstrapped ANOVA, post hoc pairwise comparison with Bonferroni correction).
794	Fig. 4 Environmental conditions, (A) chlorophyll-a, (B) submerged body temperature, and
795	(C) aerial body temperature experienced by mussel populations at each site over a period of
796	2 years. Data are given in violin plots and separated by region as in Fig. 3. Correlations
797	between Mean Absolute Error (MAE) and mean environmental variables (D) chlorophyll-a
798	concentration, (E) submerged body temperature, and (F) aerial body temperature.
700	

800 Fig. 1







806 Fig. 3





