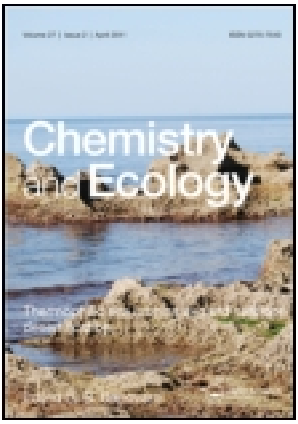

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Combining heat-transfer and energy budget models to predict thermal stress in Mediterranean intertidal mussels

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Recent studies have emphasised that organisms can experience physiological stress well within their geographic range limits. Developing methods for mechanistically predicting the presence, absence and physiological performance of organisms is therefore important because of the ongoing effects of climate change. In this study, we merged a biophysical–ecological (BE) model that estimates the aquatic (high tide) and aerial (low tide) body temperatures of *Mytilus galloprovincialis* with a Dynamic Energy Budget (DEB) model to predict growth, reproduction and mortality of this Mediterranean mussel in both intertidal and subtidal environments. Using weather and chlorophyll-*a* data from three Mediterranean sites along the Italian coasts, we show that predictions of sublethal and lethal (acute) stress can potentially explain the observed distribution (both presence and absence) of mussels in the intertidal and subtidal zones, and the maximum size of animals in the subtidal zones. Importantly, our results suggest that different mechanisms limit the intertidal distribution of mussels, and that these mechanisms do not follow a simple latitudinal gradient. At the northernmost site (Palermo), *M. galloprovincialis* appears to be excluded from the intertidal zone due to persistent exposure to lethal aerial temperatures, whereas at the southernmost sites (Porto Empedocle and Lampedusa) sublethal stress is the most important driver of mussel intertidal distribution. Our predictions provide a set of hypotheses for future work on the role of climate change in limiting intertidal distribution of mussels in the Mediterranean.

Keywords: biophysical ecology; Dynamic Energy Budget models; intertidal zone, mussel; *Mytilus galloprovincialis*; Mediterranean Sea

1. Introduction

For over a century, intertidal ecosystems have served as a natural laboratory for exploring the roles of weather and climate in driving local and geographic patterns of species distributions [1–3]. Subsequently, intertidal invertebrates and algae have increasingly become the focus of studies exploring the potential impacts of climate change on natural ecosystems. These studies are particularly numerous for North American and European oceanic coasts [4–7] where tidal ranges are often large and the duration of exposure to air experienced by intertidal organisms can last many hours. Emersion at low tides is particularly stressful and aquatic organisms have adopted various behavioural (e.g. shading, valve gaping, timing of foraging and reproduction)

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and physiological mechanisms to reduce the effects of thermal and desiccation stresses [8,9]. Nevertheless, many intertidal organisms live very close to their physiological limits, particularly in the upper intertidal zone [10].

Our understanding of the limits to zonation remains incomplete because of the complex interaction of factors such as aerial body temperature, desiccation and reduction in feeding time, all of which increase with increasing tidal elevation. Moreover, large-scale mortality due to lethal exposure is known to occur in intertidal ecosystems [11,12], yet an increasing number of studies have demonstrated the importance of sublethal stress in driving patterns of abundance and distribution [13]. Importantly, these studies have shown that organisms are often living close to their physiological limits well within their geographic range edges, suggesting that increases in physiological stress could potentially lead to the collapse of populations even when there is currently no evidence of mortality [13,14]. It is therefore crucial that we develop tools that allow us not only to predict species presence (as it is commonly done using 'climate envelope' models [15]), but that we also find ways of predicting patterns of physiological performance, population abundance, productivity and species absences [16].

In this study, we investigated the role of aerial body temperature, chlorophyll-*a* (Chl-*a*) and feeding time on the geographic distribution of the common intertidal mussel *Mytilus galloprovincialis* (Lamarck 1819) in the southern Mediterranean by developing an approach that permits an exploration of both lethal and sublethal processes. Although the methods we use are potentially applicable to other, more common mussels in the region (e.g. *Mytilaster minimus*), we focus on *M. galloprovincialis* because of the wider availability of physiological data for this species. Although we recognise the key roles that desiccation stress, larval recruitment, species interactions and physically induced disturbance play in determining the distribution of intertidal organisms, our specific goal is to explore the potential role of thermal stress, exposure time and food supply under typical Mediterranean Sea intertidal conditions. To achieve our objective, we used three southern Mediterranean locations as our model sites. Despite a huge amount of physical data available for the worldwide coastal oceans, the effects of weather, climate and future climate change on intertidal habitats in the Mediterranean Sea remain largely unknown [17]. For example, current models predicting climate change impacts on intertidal habitats for several oceanic regions [18–21] are almost entirely not available for the microtidal Mediterranean Sea [22].

Although much more work is needed to understand how the physical environment affects fitness via the modification of functional traits [16,23], recent advances and access to data have allowed the application of biophysical–ecological (BE) models to describe the climatic niche of intertidal organisms [19,24] using large-scale weather and climate data archives. The climatic niche, *in ultimis*, can be defined as the combination of environmental variables setting body temperatures suitable for growth and reproduction [21]. According to the Life Laws [25], only if organisms have sufficient energy, can they grow and reproduce to form stable populations over time, which later represent a source of new propagules for further colonisation [21,26,27]. The Dynamic Energy Budget (DEB) theory provides a model of how an organism takes up and uses energy and matter throughout its life cycle [25]. In particular, DEB models allow the prediction of how (much) energy is assimilated and assigned to the different needs for life (growth, development, reproduction) under fluctuating environmental conditions, including temperature variations and ranges and the availability of food.

Body temperature represents one of the most important drivers of physiological performance, determining the amount of energy needed for growth and reproduction. Importantly, body temperature is often not equivalent to 'ambient' temperature. It can be calculated by the physics of heat and mass transfer using the BE approach. Thus, the integration of BE and DEB models offers an opportunity to understand constraints on the current distribution and abundance of intertidal sessile ectotherms, and forecasting how these may be altered under predicted scenarios of climate change [21].

In this article, under the auspices of the EU-funded INTERMED project [28], we integrated BE and DEB models to investigate the effects of thermal stress on intertidal and subtidal mussels in the southern Mediterranean Sea. Specifically, using large environmental datasets from three Sicilian sites located at different latitudes (35°N to 38°N) during the years 2006–2009; we: (1) estimated the hourly immersion and emersion times of intertidal mussels; (2) modelled the hourly body temperature experienced by mussels under either subtidal or intertidal conditions using the BE approach; (3) calculated the DEB components of mussels and the maximum theoretical total shell length reached by mussels as a function of body temperature under observed natural conditions; and (4) used a combination of BE and DEB models to estimate potential reproductive outputs expressed in terms of number of eggs produced per biomass unit (wet weight). We then compared our model results with all available data on maximum size (shell length) and presence/absence for each site as an initial test of the model outputs.

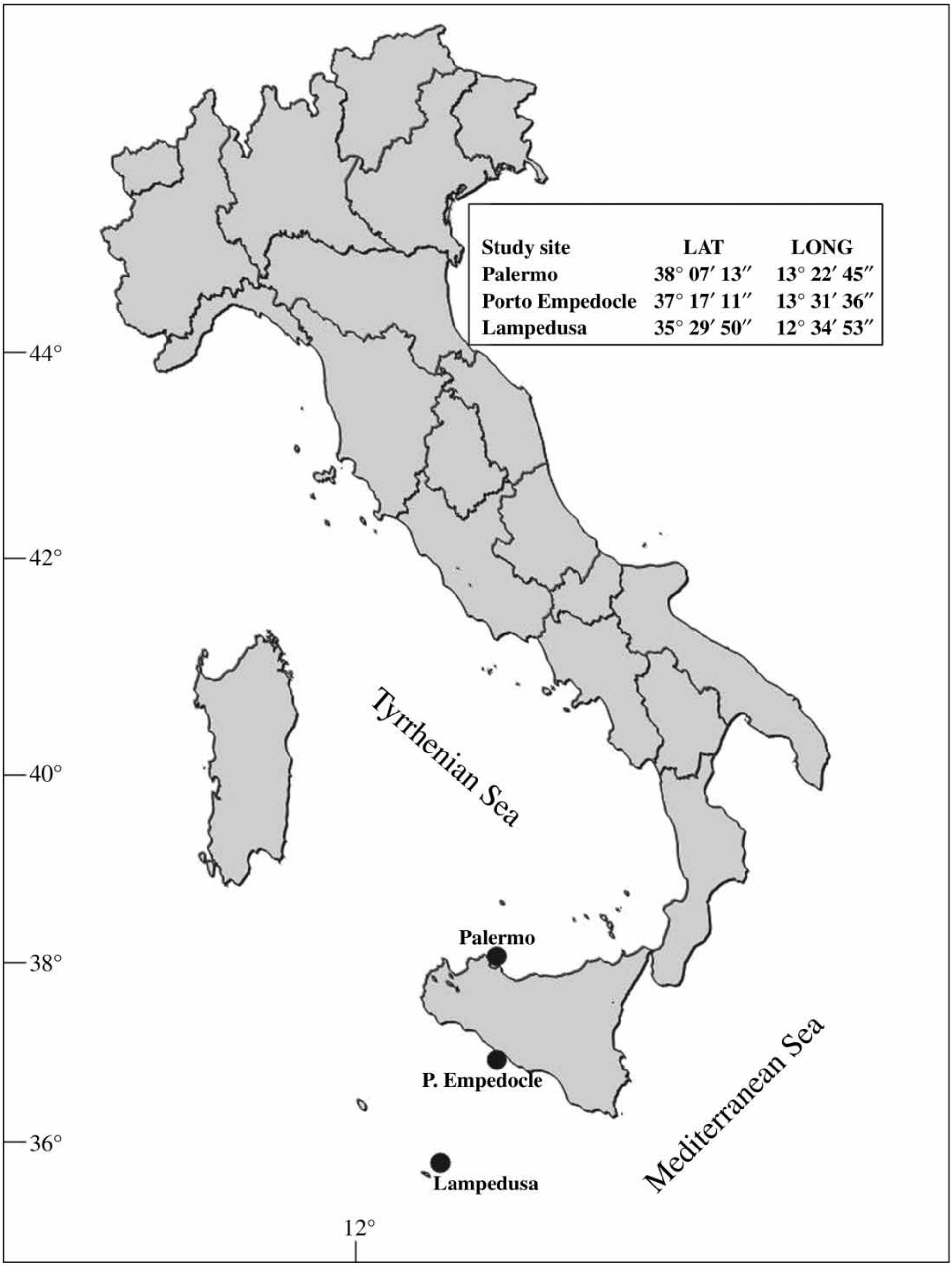
The ultimate goal of this study is to provide a framework for assessing the possible future distribution of Mediterranean mussels under conditions of increasing temperature as a result of global warming. Here, we outline the approach and make preliminary calculations based on available data for the Mediterranean Sea. However, significant data still need to be collected for animals in this region before the approach could be fully validated. We, therefore, stress that this article should be considered as a ‘first cut approximation’ due to the rather extensive assumptions made in constructing the energy budget, and the limited number of sites tested.

Previous studies have used DEB models to explore the role of temperature variations on mussel growth and survival [29,30], but most of these studies have ignored the potential role of aerial body temperature in driving physiological responses [21]. Such a simplification has generally been justified because metabolic oxygen consumption by *Mytilus* spp. during aerial exposure at low tide is often much lower (∼15–20%) than during submersion [31] (but see [32] for *Mytilus californianus*, which can be much higher). Nevertheless, aerial body temperature has been shown to have significant impacts on the growth, survival and reproduction of intertidal mussels, especially under conditions of reduced food supply [33,34]. The relevance of standard *Mytilus* spp. DEB parameters in the context of aerial exposure has yet to be explored in detail. We therefore considered thermal physiological response curves (e.g. digestive efficiency) under conditions of aerial exposure to be similar to curves during submersion, but assumed that animals fed only when submerged. However, unlike most previous studies (but see [21]), we calculated both aerial and submerged body temperatures using a biophysical model. Our goal here is thus not an exhaustive test of the approach, but rather an introduction to the general methodology so that models for this region may become better refined as we begin to better understand the impacts of aerial body temperature on physiological performance.

2. Materials and methods

2.1. *Environmental data and study sites*

Environmental data used for simulations were obtained from three sites located in the central Mediterranean Sea (Figure 1): Lampedusa Island, Porto Empedocle and Palermo. Lampedusa Island, located in the Sicily Channel and 130 km from the North African coast, is the southernmost European island and is characterised by a dominance of rocky substrates. Porto Empedocle is located in the southern part of Sicily and has a shoreline comprising both sand and rocky outcrops. Palermo, located in the northern part of the Sicily, has both rocky and sandy beaches. For all three sites, we obtained hourly data (02 January 2006 to 31 December 2009) of tidal amplitude (m), water and air temperature (°C), wind direction (°) and speed ($\mathrm{m \cdot s^{-1}}$), which were downloaded from the Italian Institute of Environmental Research (ISPRA) website (http://www.mareografico.it/).



Study site	LAT	LONG
Palermo	38° 07′ 13″	13° 22′ 45″
Porto Empedocle	37° 17′ 11″	13° 31′ 36″
Lampedusa	35° 29′ 50″	12° 34′ 53″

Figure 1. Location of the study sites.

Irradiance (global sky) data ($W \cdot m^{-2}$) calculated on an hourly basis as an average for each month of the year under clear skies, were obtained from the European Joint Research Centre (http://sunbird.jrc.it/pvgis). Chl-*a* concentrations derived from fluorescence measurements ($\mu g \cdot L^{-1}$) were downloaded from the Environmental Marine Information System (EMIS) maintained at the European Joint Research Centre website (http://emis.jrc.ec.europa.eu/).

Using a BE approach (explained in detail in [21]) we modelled, on an hourly basis, the aerial and aquatic body temperatures of both subtidal and intertidal (mean lower low water

[MLLW] +0.35 m) mussels at each site. The Mediterranean Sea is characterised by narrow tidal amplitude (not more than 30–50 cm), so that the role of wave splash, which is in turn driven by wave height, can easily overwhelm the effects of the tide in driving patterns of aerial exposure [20,21,35]. Because wave height data were not available for the investigated sites during the study period, hourly wind data from the ISPRA website were used to scale sea conditions according to the empirical Beaufort scale. We then converted Beaufort scale scores into wave heights using the following empirical formula: Beaufort = cube root of wind velocity $(\mathrm{km}\cdot\mathrm{h}^{-1})/9$, [36] assuming open-sea conditions. A Beaufort 3 (indicating a wave height of ~0.6–1.0 m) is the sea condition at which intertidal organisms positioned at MLLW + 0.35 m should experience wave splash when the still tide level is approximately at mean sea level.

Using this approach, we estimated, on an hourly basis for each site: (1) the body temperature (T_b) of both subtidal and intertidal (MLLW + 0.35 m) animals; (2) the amount of emersion and immersion time of intertidal mussels [21]; (3) the periods during which mussels experienced $T_b < 10°C$ (~4°C lower than the normal minimum winter water temperature); (4) number of exposures with $T_b > 31°C$ (~4°C higher than the normal maximum summer water temperature); and (5) the number of events during which body temperature exceeded 40°C for >3 h, conditions that are known to be lethal for *Mytilus* species [11]. We then estimated the budget of energy and matter flowing through the mussels and allocated to development, growth, maintenance and reproduction. We applied the DEB theory of Kooijman [25] based on the κ-rule. The κ-rule predicts that a fixed fraction κ of the energy/matter is allocated for growth and somatic maintenance, whereas the rest is devoted to sexual maturation and reproduction. DEB parameters (Table 1) included: the shape coefficient (δ_m), calculated experimentally for *M. galloprovincialis* using companion published data according to [25,37,38] and the absorption efficiency estimated as the Conover ratio [39] and proprietary data (Figure 2).

To validate results of the simulations by models, results were compared against measurements from each of the three sites (Palermo, Porto Empedocle and Lampedusa), as well as data from the literature. In the central Mediterranean Sea, where our study was conducted, *M. galloprovincialis* is found only rarely in the intertidal zone, and in the subtidal zone grows to

Table 1. Parameters used for the *Mytilus* Dynamic Energy Budget (DEB) model based on *Mytilus edulis* and some calculated data throughout this study.

Symbol	Description	Value	Units	Reference
V_b	Structural volume at birth	0.000001	cm^3	[25]
V_p	Structural volume at puberty	0.06	cm^3	[48]
δ_m	Shape coefficient	0.23 ± 0.04	–	This study; [48]
{JXm}	Maximum surface area-specific ingestion rate	8.20	$\mathrm{J}\cdot\mathrm{cm}^{-3}\cdot\mathrm{h}^{-1}$	[29]
Assim rate	Assimilation efficiency	0.88	–	[39]; this study
{pAm}	Maximum surface area-specific assimilation rate	7.216	$\mathrm{J}\cdot\mathrm{cm}^{-3}\cdot\mathrm{h}^{-1}$	This study
XK	Saturation coefficient	2.1	$\mu\mathrm{g}\cdot\mathrm{L}^{-1}$	[34]
[EG]	Volume-specific cost of growth	1900	$\mathrm{J}\cdot\mathrm{cm}^3$	[48]
[ES]	Volume-specific structural energy content	1350	$\mathrm{J}\cdot\mathrm{cm}^3$	[48]
[EM]	Maximum storage density	2190	$\mathrm{J}\cdot\mathrm{cm}^3$	[48]
[PM]	Volume-specific maintenance cost	1	$\mathrm{J}\cdot\mathrm{cm}^{-3}\cdot\mathrm{h}^{-1}$	[48]
κ	Fraction of utilized energy spent on maintenance plus growth	0.5	–	This study
κ_r	Fraction reproductive energy fixed	0.8	–	[48]
TA	Arrhenius temperature	5800	°K	[48]
TL	Lower boundary of tolerance range	275	°K	[48]
TH	Upper boundary of tolerance range	296	°K	[48]
TAL	Rate of decrease at lower boundary	45,430	°K	[48]
TAH	Rate of decrease at upper boundary	31,376	°K	[48]

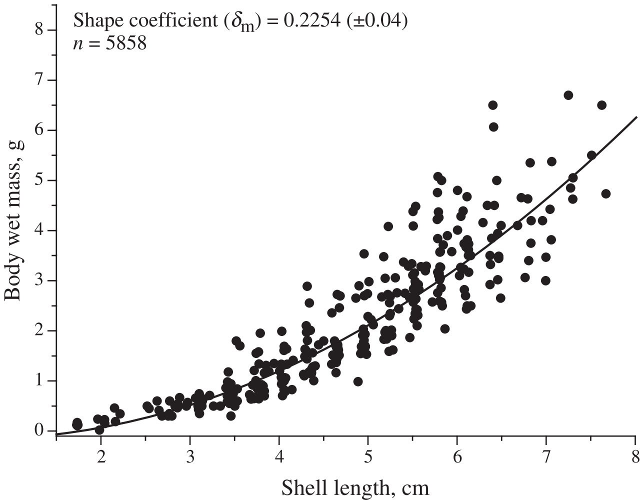


Figure 2. The relation between body wet mass and shell length for the Mediterranean mussel *Mytilus galloprovincialis*.

maximum size only in nutrient-rich areas such as near sewage outfalls or close to fish aquaculture cages [40].

3. Results

Background environmental conditions for three Mediterranean sites used in this study are summarised in Table 2. Mean water and air temperatures were quite similar across sites. Nonetheless, air temperature in Palermo showed a much wider temporal variability than in Lampedusa, whereas water temperature variability was much higher in Lampedusa than in Porto Empedocle. The amount of Chl-*a* available to mussels was highest and almost invariant in Porto Empedocle and lowest and highly variable in Lampedusa. As expected, we found no *M. galloprovincialis* at any of the three intertidal sites, and the only mussel found was the smaller *Mytilaster minimus*.

Predicted exposure to intertidal conditions and heat stress estimates are reported in Table 3. In general, at the tidal elevation examined (MLLW + 0.35 m), intertidal mussels at all of the three sites were predicted to be exposed to aerial conditions for ~75% of the time. Periods during which the mussels were exposed to stressfully cold (<10°C) or warm (>31°C) body temperatures were higher in Palermo than in Lampedusa and Porto Empedocle (Table 3). Lethal exposures to aerial intertidal conditions (40°C for at least 3 h) were predicted to have occurred at Palermo nine times during the period examined, and not at all at the other two sites (a single event lasting only one hour was predicted at Lampedusa).

Table 2. Mean environmental conditions and predicted intertidal mussel body temperatures at three Sicilian study sites.

	Water temperature (°C)				Air temperature (°C)				Intertidal body temp. (°C)				Chlorophyll-*a* ($\mu g \cdot L^{-1}$)			
Study site	Mean	±	Min	Max	Mean	±	Min	Max	Mean	±	Min	Max	Mean	±	Min	Max
Palermo	20.17	4.64	10.60	29.70	20.39	5.80	3.30	45.30	20.19	6.67	2.45	47.40	0.35	0.23	0.12	1.13
Porto Empedocle	18.97	3.18	13.50	26.40	19.05	5.37	4.00	36.00	19.63	5.80	3.14	37.40	0.44	0.21	0.17	1.01
Lampedusa	20.67	4.58	9.40	30.20	19.74	5.00	6.30	35.10	20.03	5.60	5.00	40.20	0.23	0.14	0.10	0.58

Table 3. Predicted exposure to intertidal conditions and heat stress estimates.

Study site	HM	Tot H-low	Tot H-high	H-low	H-high	Lethal h
Palermo	32,311 (74%)	854	1926	219	115	27
Porto Empedocle	33,792 (80%)	795	516	96	110	0
Lampedusa	32,647 (76%)	808	965	163	63	1

Note: HM, hours spent by mussels in total emersion, % of the total time is also reported within brackets; Tot H-low, total number of hours spent by mussels with body temperature <10°C; Tot H-high, total number of hours spent by mussels with body temperature >31°C; H-low, number of events in 3 years during which mussels experience more than three consecutive hours with body temperature <10°C; H-high, number of events in 3 years during which mussels experience more than three consecutive hours with body temperature >31°C; Lethal h, number of hours in 3 years during which body temperature >40°C.

Intertidal conditions significantly reduced predicted mussel growth and reproduction when compared with subtidal mussels at all three sites (Figure 3a–c). The intertidal conditions in Porto Empedocle resulted in predictions of extremely small maximum size of intertidal mussels; ~0.52 cm at the end of the 4 years, representing only 6% of the theoretical $L\infty$ (7.6 cm) calculated for *M. galloprovincialis* [41]. In both Lampedusa and Palermo, the estimated maximum size of intertidal mussels did not exceed 0.8 cm (~11% of the theoretical $L\infty$ [41]). However, maximum estimated size of subtidal mussels was much higher than those estimated for intertidal mussels (up to 2.5 cm in 4 years, representing ~34% of the theoretical $L\infty$ [41]). The DEB model also predicted that subtidal mussels have the potential to produce many more eggs (3624, 12,792 and 8664 per g dw in Lampedusa, Porto Empedocle and Palermo, respectively) than those estimated for intertidal mussels. The estimated age of first reproduction in Palermo was much shorter than at the other two sites.

4. Discussion

Here we have used heat transfer and Dynamic Energy Budget models to explore the potential effects of body temperature and aerial exposure time (as driven by the complex interaction of weather, tidal exposure and wave splash) on the growth and reproduction of intertidal Mediterranean Sea mussels. In essence, our approach provides a mechanistic approach for quantifying the thermodynamic constraints of this species fundamental niche [42] in both subtidal and intertidal environments using readily available weather and oceanographic data. The results of our simulations are consistent with field observations in that they predict both the absence of intertidal mussels in the study sites as well the small body size of subtidal animals. At each site, intertidal conditions as predicted by models, could not support gonad maturation, gamete production and spawning of large specimens of *M. galloprovincialis*. This result is consistent with field measurements because in all investigated sites there were no individuals of *M. galloprovincialis*. Indeed, although *M. galloprovincialis* is common at northern Mediterranean Sea latitudes and grows to large sizes (Von Bertalanffy Growth Function $L\infty$ 7–9 cm) [38,43], in the southern Mediterranean it grows to large size only under very organically enriched subtidal conditions like aquaculture facilities or close to sewage sources [40]. Our simulations are therefore consistent with what is expected under very pristine conditions, i.e. with the very low food availability typical of the southern Mediterranean Sea waters.

Importantly, our results suggest that the intertidal distribution of mussels at two of the three sites is likely set, not by exposure to lethal temperatures, but rather by chronic exposures to sublethal conditions that prevent their growth and reproduction. This result is important because it confirms that although lethal exposures can be important determinants of species range boundaries, sublethal processes can be important as well [13,14]. Our results are also significant because they

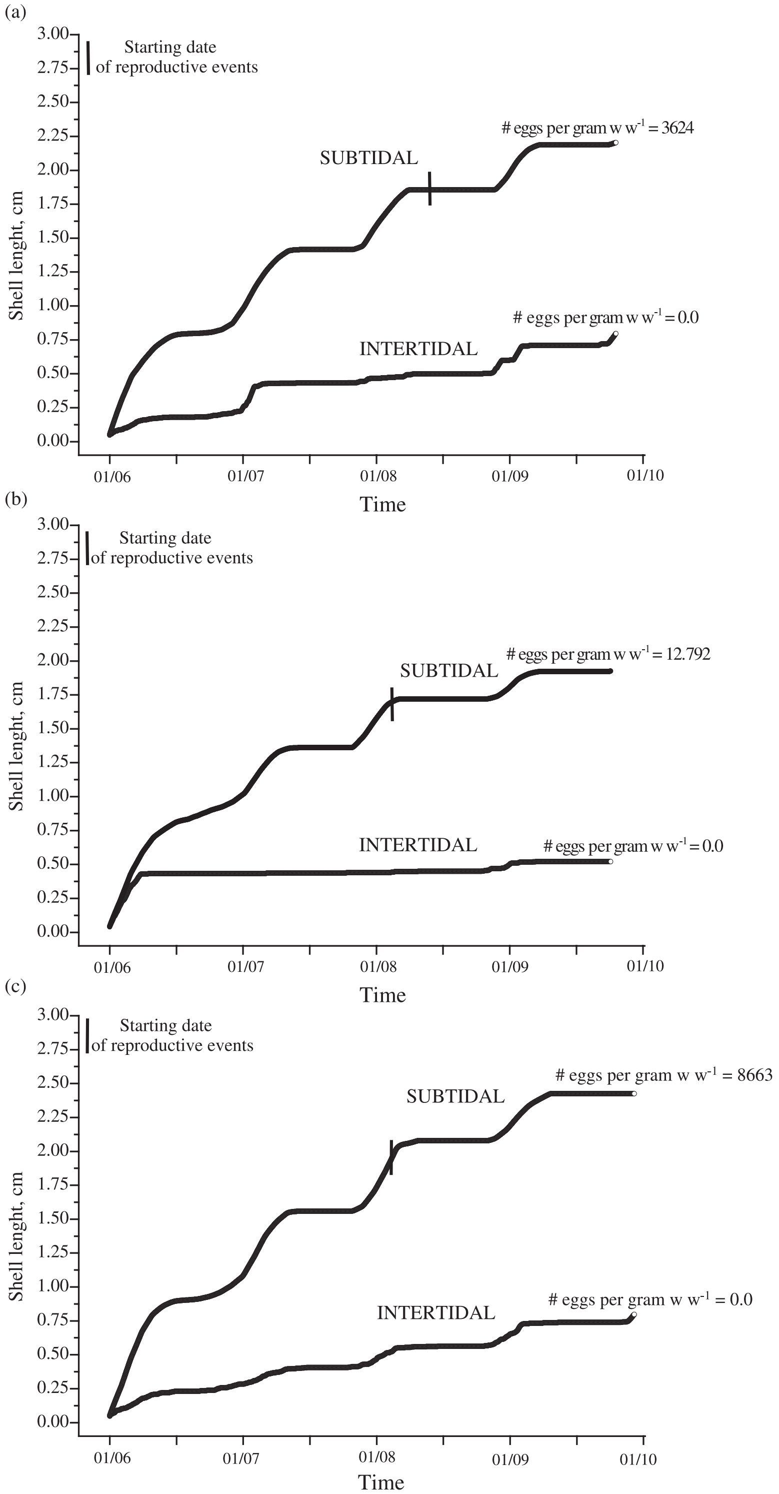


Figure 3. Predicted growth trajectory and reproductive events of *Mytilus galloprovincialis* simulated by the DEB model using the hourly dataset of temperature, tides and chlorophyll-*a* from January 2006 to December of 2009 for intertidal and subtidal organisms at (a) Lampedusa, (b) Porto Empedocle and (c) Palermo.

highlight, as have previous studies carried out in other parts of the world, that geographic patterns of stress do not always follow the latitudinal gradient [44–46]. In our study, our models predict that most of the animals at the highest latitude site (Palermo) could experience lethal events far more often than animals at the more southern sites.

Although our DEB approach worked rather well, we used a number of simplifying assumptions that require further investigation. Foremost among these is that body temperature has a similar impact on growth and reproduction during emersion as during submersion. Intertidal body temperature is, in fact, driven by a variety of terrestrial environmental variables and is less constant and more extreme than that of subtidal mussels not exposed to periodic emersion. Fluctuating and high body temperatures have been shown to induce mortality [12,34], particularly if the food supply is reduced [47]. However, it remains unclear how to parameterise a DEB model using aerial temperatures that includes changing metabolic rates during low tide. Because geographical patterns of aerial body temperature can be complex [13], including these effects may be important.

Although potentially biased by some oversimplifications, the results of this attempt at applying an integrated DEB/BE approach to model the performance of intertidal organisms under changeable climate conditions provide new perspectives for a better comprehension of the constraints on distribution and abundance of intertidal organisms. However, further work is required to better modulate and make experimental validation of the DEB model.

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