Diversity and Distributions, (Diversity Distrib.) (2013) **19**, 1235–1247

A Journal of Conservation Biogeography
Diversity and Distributions

BIODIVERSITY RESEARCH

Predicting biological invasions in marine habitats through eco-physiological mechanistic models: a case study with the bivalve *Brachidontes pharaonis*

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ABSTRACT

Aim We used a coupled biophysical ecology (BE)-physiological mechanistic modelling approach based on the Dynamic Energy Budget theory (DEB, *Dynamic energy budget theory for metabolic organisation*, 2010, Cambridge University Press, Cambridge; DEB) to generate spatially explicit predictions of physiological performance (maximal size and reproductive output) for the invasive mussel, *Brachidontes pharaonis*.

Location We examined 26 sites throughout the central Mediterranean Sea.

Methods We ran models under subtidal and intertidal conditions; hourly weather and water temperature data were obtained from the Italian Buoy Network, and monthly CHL-*a* data were obtained from satellite imagery.

Results Mechanistic analysis of the *B. pharaonis* fundamental niche shows that subtidal sites in the Central Mediterranean are generally suitable for this invasive bivalve but that intertidal habitats appear to serve as genetic sinks.

Main conclusions A BE-DEB approach enabled an assessment of how the physical environment affects the potential distribution of *B. pharaonis*. Combined with models of larval dispersal, this approach can provide estimates of the likelihood that an invasive species will become established.

Keywords
Bivalves, Dynamic Energy Budget model, fundamental niche, invasive species, life-history traits, Mediterranean Sea.

INTRODUCTION

The ability to predict the physiological performance and fitness (Stearns, 1992) of invasive species is crucial for understanding the dynamics of biological invasions in marine ecosystems. The likely spread and establishment of a non-native species in a new habitat is the product of the likelihood that adults, juveniles or larvae of the invader are transported to the new location, the physiological suitability of that habitat for the potential invader and the ways in which these organisms interact with native species (Sarà *et al.*, in press-b). Recent studies have emphasized that while extreme environmental conditions can serve as important barriers to range edges, sublethal effects such as reproductive failure may also play a key role (e.g. Petes *et al.*, 2007). Most approaches to predicting species invasions in use today are parameterized using correlations between current range edges and environmental parameters at those locations. Especially in the case of potential invasive species, existing range boundaries (i.e. realized niche space) may not always serve as an effective indicator of that species physiological limits (fundamental niche space). For example, several studies have pointed to the importance of local environmental conditions, which can over-ride larger-scale geographic gradients in parameters such as temperature, and which can lead to high levels of heterogeneity over latitudinal scales (Helmuth *et al.*, 2006; Mislan *et al.*, 2011).

The ability to quantitatively predict levels of growth and reproduction by invasive species is especially important in the context of climate change (Lika *et al.*, 2011), which has the potential to open previously uncolonized areas to invasion as environmental conditions change, or as new modes of transport such as ship ballast water arise (Simberloff, 2009). Many factors affect a species' metapopulation

DOI: 10.1111/ddi.12074
http://wileyonlinelibrary.com/journal/ddi

dynamics, including patterns of larval dispersal, the amount of time that larvae in the water column remain competent to settle (O'Connor *et al.*, 2007) and the local density and spatial distribution of reproductive adults. Thus the body size, number of reproductive bouts and time to reproductive maturity (puberty; Roff, 1992) are crucial life-history parameters affecting the larval dispersal of most marine organisms (Hughes *et al.*, 2005), and the local persistence of populations over time (Simberloff, 2009; Kearney *et al.*, 2010). While considerable progress has been made predicting patterns of larval competency and dispersal (e.g. Menge & Olson, 1990; McQuaid & Phillips, 2006; Dong *et al.*, 2012), understanding and predicting the spatial distribution of physiologically suitable habitat and larval production has remained problematic.

Recent mechanistic eco-physiological models such as Dynamic Energy Budget approaches (DEB; Kooijman, 2010) can potentially provide a powerful tool for predicting patterns of reproduction and other sublethal responses to environmental change, especially when coupled with spatially and temporally explicit predictions of how the physical environment affects organismal parameters such as body temperature (BT; Kearney *et al.*, 2010). Such methods are important because recent studies have emphasized that the first impacts of climate change may lie in sublethal responses such as changes in growth and reproduction (Monaco & Helmuth, 2011; Wethey *et al.*, 2011) and that evidence of these impacts has been found well inside species ranges (Beukema *et al.*, 2009). The mechanistic nature of the DEB theory provides an exceptionally powerful tool to predict organismal function according to physical principles (Kearney, 2012). Several recent studies have shown that coupled heat budget (biophysical ecology, BE) and DEB modelling approaches can be used effectively to predict population-level responses to environmental change. However, such methods have yet to be applied to invasive marine species.

Here, using a mechanistic approach based on coupled BE-DEB theory, we modelled the fitness of an invasive Lessepsian bivalve, the Pharaonic mussel *Brachidontes pharaonis* at multiple sites throughout the Italian Mediterranean. *Brachidontes pharaonis* entered the Mediterranean from the Red Sea after the Suez canal opened in 1869 (Safriel & Sasson-Frostig, 1988; Sarà *et al.*, 2000, 2008; Rilov *et al.*, 2004; Sarà, 2006). This species is considered to be intertidal, as it has been reported in the Mediterranean in lower intertidal (Rilov *et al.*, 2004) and shallow subtidal environments such as lagoons (Sarà *et al.*, 2000; Cilia & Deidun, 2012). *Brachidontes pharaonis* is listed among the 100 worst invasive species in the Mediterranean (Galil, 2007). This species has a cosmopolitan distribution (Sarà *et al.*, 2003; Sarà & De Pirro, 2011) and colonizes valuable ecosystems like *Dendropoma* reefs (Chemello & Silenzi, 2011) outcompeting native gastropods and bivalves (Rilov *et al.*, 2004).

The specific aims of this study were: (1) to quantitatively predict differences in reproductive output in *B. pharaonis*, in subtidal and intertidal (+35 cm above Mean Lower Low Water) populations; (2) to identify the localities where *B. pharaonis* would reach maximal fitness and null fitness (i.e. reproductive failure) throughout the central Mediterranean and (3) predict patterns of suitable habitat and thus possible colonization routes in the near future that will likely result from environmental change.

METHODS

Study area and environmental inputs

We ran DEB models with BT and food as forcing drivers of life history of *B. pharaonis* (Sarà *et al.*, in press-b) throughout the central Mediterranean Sea (Fig. 1). In particular, we performed DEB simulations using food and water temperature datasets from 26 sites around the Italian Peninsula, from the Gulf of Tigullio northernmost (LAT *c.* 44°) up to the Gulf of Gabes (LAT *c.* 33°; Tunisia) southernmost and from the western Sardinia (LONG *c.* 8°) to the eastern part of the Adriatic Sea (LONG *c.* 19°).

Dynamic Energy Budget models (Fig. 2) were run simulating both subtidal (i.e. always immersed) and intertidal (e.g. immersed at low tide and submerged at high tide) conditions. BT for submerged animals (subtidal or intertidal at high tide) was assumed to be the same as water temperature (Lima *et al.*, 2011). We used the hourly seawater temperatures (1 January 2006–31 December 2009) measured about 1 m below the surface by the Italian Oceanographic Buoy Network maintained at ISPRA (http://www.mareografico.it/).

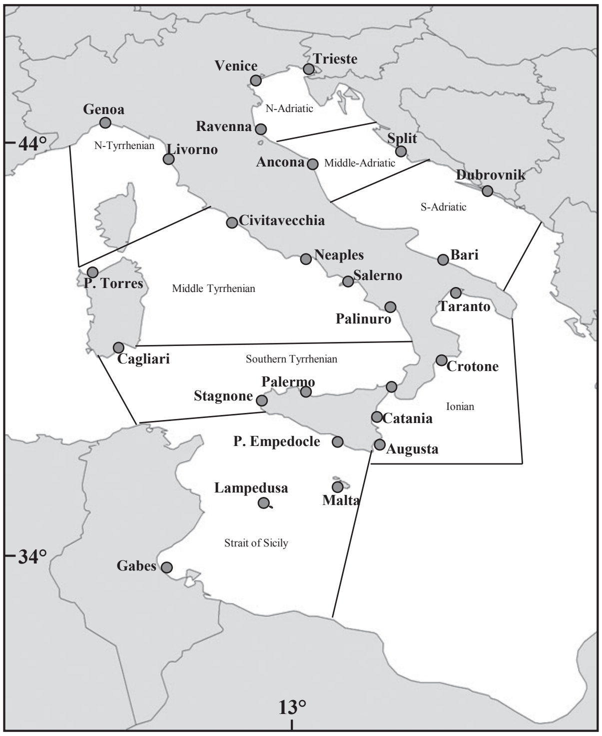

Figure 1 Map showing all sites considered in this study.

During aerial exposure at low tide, BT is driven by multiple environmental factors, and is moreover affected by the body size and morphology of the organism (Helmuth, 1998). We used a BE heat budget model (see Kearney *et al.*, 2010; Helmuth *et al.*, 2011 for details) that was integrated with the DEB model so that the output of the BE model served as the source for the BT in the DEB routine for intertidal conditions (Kearney *et al.*, 2010; Sarà *et al.*, 2011, in press-b). Hourly weather data for the BE model (hourly air temperature, tide amplitude, wind speed) were obtained from the ISPRA Buoy Network; daily irradiance data were downloaded from the European Commission Joint Research Centre (2012; http://re.jrc.ec.europa.eu/pvgis/apps4/pvest.php; for details on biophysical models and recent applications in a DEB context, see Helmuth *et al.*, 2011; Kearney *et al.*, 2010, 2012; Sarà *et al.*, 2011; Kearney, 2012).

Water temperatures were obtained for the Gulf of Gabes (Tunisia), Dubrovnik and Split (Croatia) using datasets of the closest Italian buoys (Lampedusa, Bari and Ancona, respectively; Fig. 1) as there are no local, continuous hourly temporal series for Tunisia and Croatia yet available.

Chlorophyll-*a* (CHL-*a*) from satellite imagery was used to estimate the amount of food available to suspension feeders (Kearney *et al.*, 2010; Sarà *et al.*, 2011, 2012, in press-b). We used monthly data for CHL-*a* ($\mu g\ l^{-1}$) from January 1998 to December 2007 (i.e. 120 point-months) from the EMIS website (http://emis.jrc.ec.europa.eu). We downloaded data from a horizontal grid spacing of 30 km positioned on the sea around every ISPRA oceanographic station. Areas were *c.* 10 km from the coast to avoid the interference of reflectance due to the presence of the landmass. We obtained 12 mean values (January–December) for every location using 10 years data (1998–2007). The lack of high resolution CHL-*a* data is therefore a potential limitation to our approach, and the use of averages therefore ignores any potential effects of interannual variability in CHL-*a*. We therefore focus on the effects of changes in BT.

Our model assumed that at low tide, mussels could not feed except during wave splash, which was estimated by integrating wind and wave height into a biophysical model (see Sarà *et al.*, 2011). Thus, under subtidal conditions, we assumed that the feeding time occurred constantly, while under intertidal the feeding time was a function of low-tide-exposure time modified by wave splash. We assumed that temperature-dependent physiological rates during aerial exposure were the same as those during submersion, except for food intake (Kearney *et al.*, 2010; Sarà *et al.*, 2011). Simulations were run for 4 years (1 January 2006–31 December 2009) using *Brachidontes* DEB parameters (Table 1) at each location both under subtidal and intertidal conditions, using food and temperature parameters as described above. Outputs were (Sarà *et al.*, in press-b): (1) the maximum theoretical total shell length (TL, cm) reached by mussels; (2) maturation time, in days; (3) the number of reproductive events (RE, *n*) throughout the simulated 4-year period; (4) the total reproductive outputs (TRO, *n*) i.e. the number of eggs produced per biomass unit (dry weight) throughout 4 years; and (5) the number of eggs produced *per* reproductive event (i.e. TRO/RE).

DEB model validation

Throughout the 2009 and 2010, we collected more than 1000 animals from the saltpan of the close Stagnone di Marsala where this species has established highly dense populations (Sarà *et al.*, 2000). We estimated the age of each animal through the analysis of shell rings using the technique described in Peharda *et al.* (2012; Sarà *et al.*, in press-b), longitudinally cutting shells with a Dremel rotary tool (Series 4000; Robert Bosch Tool Corporation Inc., Stuttgart, Germany).

We sampled bi-monthly (six samples per year) water and sediments and estimated the amount phyto-pigments (chlorophyll-*a*) according to methods reported in Pusceddu *et al.* (1997) and Sarà (2009). Temperature and food density (as expressed by the concentration of chlorophyll-*a*) were used to run DEB models of *B. pharaonis* in the Stagnone di Marsala. With these local data, we obtained the Von Bertalanffy infinite size through DEB models and compared it

Table 1 Parameters used for the Dynamic Energy Budget models (Palmeri, 2011; Sarà *et al.*, in press-b; parameters are posted at: http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/index.php)

Parameter	Unit	*Brachidontes pharaonis*
$\{\dot{J}Xm\}$, Maximum surface area-specific ingestion rate	$J\ cm^{-2}\ h^{-1}$	17.88
$[\dot{p}M]$, Volume-specific maintenance cost	$J\ cm^{-3}\ h^{-1}$	9.29
$[E_m]$, Maximum storage density	$J\ cm^3$	1,967
$[E_G]$, Volume-specific cost of growth	$J\ cm^3$	1,118
κ, Fraction of mobilized reserve spent on soma	–	0.9874
δm, Shape coefficient	–	0.288
V_b, Structural volume at birth	cm^3	0.00000049
V_p, Structural volume at puberty	cm^3	0.01008
A_e, Assimilation efficiency	–	0.75
X_k, Saturation coefficient	μg chl-*a* l^{-1}	0.62
k_R, Fraction reproductive energy fixed	–	0.95
T_A, Arrhenius temperature	°K	8232
T_L, Lower boundary of tolerance range	°K	284
T_H, Upper boundary of tolerance range	°K	305
T_{AL}, Rate of decrease at lower boundary	°K	17,957
T_{AH}, Rate of decrease at upper boundary	°K	6005

against the ultimate size estimated with the analysis of age obtained from animals collected in the field. Data of this validation exercise are presented in Appendix A.

Statistical analysis

Data from DEB models (i.e. fitness variables) were analysed to test the null hypothesis that there is no difference in fitness of *B. pharaonis* between subtidal and intertidal habitats across all sectors (Fig. 1) of the study area using a two-way analysis of variance (ANOVA). The 26 sites were grouped into eight sectors to examine the null hypothesis that variability between sectors was greater than that within a sector; is that sites would cluster based on proximity. Thus, habitat (Hab; two levels) and sector (Sect; eight levels) were treated as fixed factors in the analysis. Sites *per* sector were replicates in the analysis; this implied that our design was unbalanced [i.e. having different numbers of replicates (i.e. = sites)] within the groups or cells. This made tests less robust to heterogeneity of variances within groups (tested *a priori* by the Cochran's *C* test). The Student–Newman–Keuls (SNK) test allowed the appropriate means comparison. When no homogeneous variances were rendered with any type of transformation such as in the case of two fitness variables (RE and ROB; Table 2), the significance level was set at 0.01 instead of 0.05, as ANOVA can withstand variance heterogeneity, reducing the possibility of a Type I error (Ruiz *et al.*, 2010).

To verify the amount of corrected occurrences predicted by DEB models of mussels, we adopted the Manel *et al.* (2001) method. We estimated the Sensitivity Index (%, proportion of true presences correctly predicted throughout the 26 sites of this study) and the Specificity Index (%, proportion of true absences correctly predicted throughout the 26 sites of this study). Model performance (% true) was tested combining the first two metrics by calculating the percentage of all cases that were correctly predicted (true presences plus true absences divided by total cases). For this analysis, we made the simplifying assumption that reproductive failure could be considered as equivalent to species absence. This assumption is likely to be violated in populations that serve as genetic sinks (such as was predicted to occur in intertidal populations). However, this assumption allowed us to generate a more rigorous test of model predictions beyond what would have been possible using only presence data. In cases where the information was not present, we could not apply the analysis, and thus we considered those cases as not applicable (n.a.). Sensitivity analysis results are reported in Appendix 2 (Fig B1, Table B1). Statistical analyses were performed by PRIMER 6 (Anderson, 2001) and STATISTICA 6.0 (StatSoft, Inc., Tulsa, OK, USA).

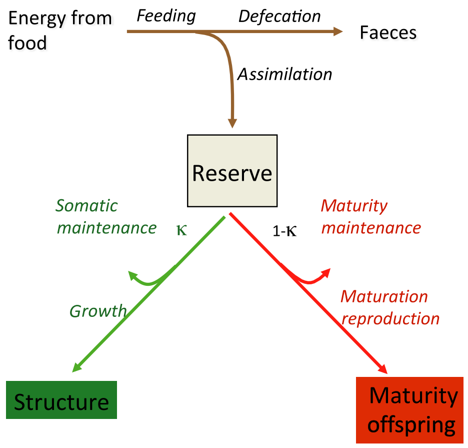

Figure 2 Schematic representation of the κ-rule Dynamic Energy Budget (DEB) model. A portion of ingested material is assimilated (absorbed) and indigestible material is lost as faeces. Assimilated products enter the reserve compartment. A fixed fraction (κ) of flux from the reserves is spent on maintenance and growth (with maintenance as the priority), the remainder goes to maturity (for embryos and juveniles), reproduction (for adults) and maturity maintenance (from Kooijman, 2010, modified).

RESULTS

Mussels experienced a broader range of BTs in intertidal (Fig. 3a) than subtidal (Fig. 3b; from values < 0 °C in winter to values higher than 45–50 °C in summer throughout the study area) although the overall subtidal mean BT was higher than intertidal BT by about 0.6–1.0 °C; southern sectors (Ionian, Southern Tyrrhenian and Strait of Sicily) showed higher BT than northern according to a latitudinal gradient. The feeding time in the intertidal zone was more than 80% lower than in the subtidal due to the emersion times which had repercussions for the hourly amount of food available for animals. Consequently, under subtidal conditions food density was significantly higher than in the intertidal (more than 80% of difference; Fig. 4). Food density was higher in the Northern Adriatic and in the Gulf of Gabes than in Southern sites (Ionian and Tyrrhenian) where water masses were almost ultra-oligotrophic (CHL-*a* $< 0.1\ \mu g\ l^{-1}$) throughout the study years. As a main consequence, not surprisingly, estimated fitness of the Pharaonic mussel throughout the study area was significantly higher under subtidal than intertidal conditions. For example, the infinite total length potentially reachable under subtidal conditions was more than two times larger than that reachable under intertidal conditions (ANOVA, $P < 0.05$; Table 2; Fig. 5a). The same was true for the amount of eggs produced per life span (Fig. 5c,d) largely because the time to maturation (Fig. 5b) was much longer under intertidal conditions. Under intertidal conditions, the estimated gamete production per reproductive event was negligible or null (ANOVA, $P < 0.05$; Fig. 5d) as compared to subtidal conditions. Fitness of *Brachidontes* was generally several times higher, both under subtidal and intertidal conditions (ANOVA $P > 0.05$), in the Northern Adriatic and Strait of Sicily (Table 2; Fig. 6a–d) than other simulated sectors.

Table 2 ANOVA performed on fitness response variables to test the difference between habitat (subtidal versus intertidal), sectors (see Fig. 1) and their interaction

		TL			MT		
	d.f.	MS	*F*	*P*	MS	*F*	*P*
Habitat (Hab)	1	4.07	66.19	***	25.58	7.05	*
Sector (Sect)	7	0.16	2.62	*	1.31	0.36	n.s.
Hab × Sect	7	0.03	0.52	n.s.	0.66	0.18	n.s.
Residuals	40	0.06			3.63		
Cochran's C				n.s.(†)			n.s.(†)

		TRO			RE		
	d.f.	MS	*F*	*P*	MS	*F*	*P*
Habitat (Hab)	1	681.11	148.31	***	18.83	42.82	***
Sector (Sect)	7	22.01	4.79	***	2.56	5.83	***
Hab × Sect	7	9.04	1.97	n.s.	2.28	5.19	***
Residuals	40	4.59			0.44		
Cochran's C				n.s.(tr)			*(†)

		ROB		
	d.f.	MS	*F*	*P*
Habitat (Hab)	1	467.74	148.69	***
Sector (Sect)	7	10.42	3.31	**
Hab × Sect	7	2.48	0.79	n.s.
Residuals	40	3.15		*(†)

TL, cm = total length; TW = total weight, g; MT = maturation time, days; TRO = total reproductive output as expressed by total amount of eggs emitted in 4 years; RE = number of reproductive events in 4 years; ROB = reproductive output per bout; n.s. = not significant difference.

**P* < 0.05; ***P* < 0.01; ****P* < 0.001.

†Data log-transformed [ln (*x* + 1].

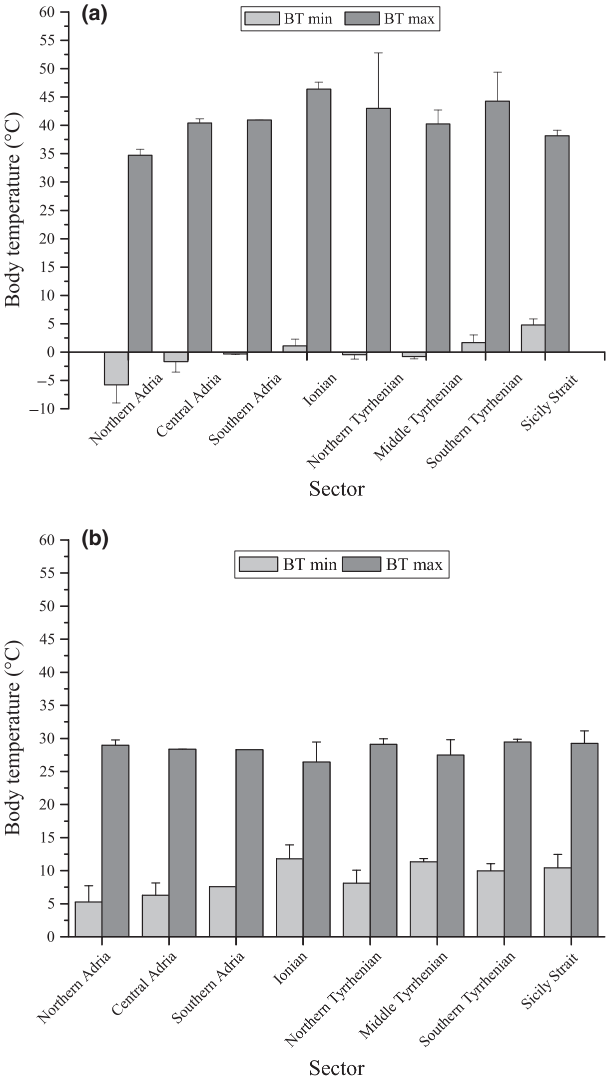

Figure 3 Maximum and minimum body temperatures throughout the study area under (a) intertidal conditions and (b) subtidal conditions.

DISCUSSION

The ability to predict the potential permissible habitat where an invasive species may be able to find suitable environmental conditions that permit persistence *via* continual reproduction is highly significant in a context of biological invasions. Apart from very large-scale experiments and surveys (e.g. Wethey *et al.*, 2011) which are often very expensive, to date, there have been few reliable tools to predict, across broad spatial and temporal scales (> 10–50 km and > 1-year), the potential reproductive output of marine invasive species. For example, classical correlative species distribution models which are mostly based on Geographic Information Systems (GIS) data are unable to predict sublethal responses, especially in novel environments (Hampe, 2004). While these models are able to provide qualitative indications of where habitat conditions should allow the presence of a certain species (Kearney, 2012), they do not produce direct, spatially explicit information on whether conditions in new environments will probably allow species reproduction, because predictions are based only on presence and absence. These approaches therefore cannot predict the presence, absence or change in the number of 'stepping stones' which may be a key to metapopulation dynamics (Leibold, 2009). Moreover, because they are generally based on environmental correlates at a species existing (realized niche) distribution, they may not be particularly effective when examining species with rapidly changing distributions, such as invasive species (Jeschke & Strayer, 2008; Kearney *et al.*, 2008).

Specifically, in biological invasion science, a critical factor in determining the success of an invasive species is understanding its ability to tolerate new environmental conditions and to identify features of the habitat that meet its requirements (Galil, 2008). Our mechanistic models, based on the study of eco-physiological tolerance limits and on the functional traits of the fundamental niche (Kearney *et al.*, 2010), enabled an assessment of the factors involved in *Brachidontes* distribution and potential spread.

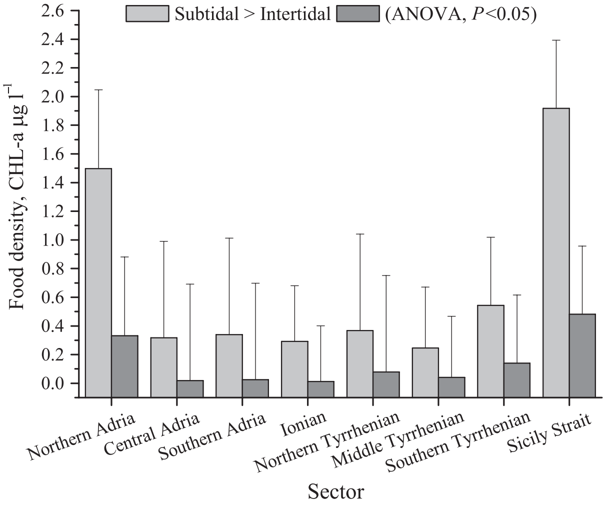

Figure 4 Amount of chlorophyll-*a* throughout the study area both under subtidal and intertidal conditions.

Many studies (mostly indirect and rarely successful; *sensu* Simberloff, 2009) have tried to provide estimates of gamete pressure from correlated and measured variables (e.g. Schneider *et al.*, 1998; Colautti *et al.*, 2003; Semmens *et al.*, 2004) to infer the distribution of invasive species. Nevertheless, if the factors of a successful colonization are: (1) the number of larvae/propagules produced by source populations, (2) temporal and spatial patterns of larval dispersal and delivery and (3) the ability of larvae to settle, survive and successfully colonize habitats, then mechanistic models like DEB seem to be a good candidate to predict many parameters associated with invasion success. The accurate prediction of number of eggs per life span combined with the number of RE per every site should help in understanding more about possible strategies to be adopted in mitigating biological invasions (Simberloff, 2009), especially when combined with information on dispersal and species interactions.

Habitat preference of *Brachidontes pharaonis* in the Central Mediterranean

Some important aspects emerged from our mechanistic analysis of the *B. pharaonis* fundamental niche: (1) in the Central Mediterranean conditions are generally suitable for *B. pharaonis*, (2) the main larval reservoir of this species is in subtidal habitat and (3) intertidal habitats appear to serve as sinks for larvae coming from subtidal habitats.

These findings are significant as this species has been always considered an intertidal organism by past research (e.g. Safriel & Sasson-Frostig, 1988) with the implicit presumption that the main gamete source should be in the intertidal zone. Our findings are corroborated indirectly by Rilov *et al.* (2004) who found most *B. pharaonis* along the

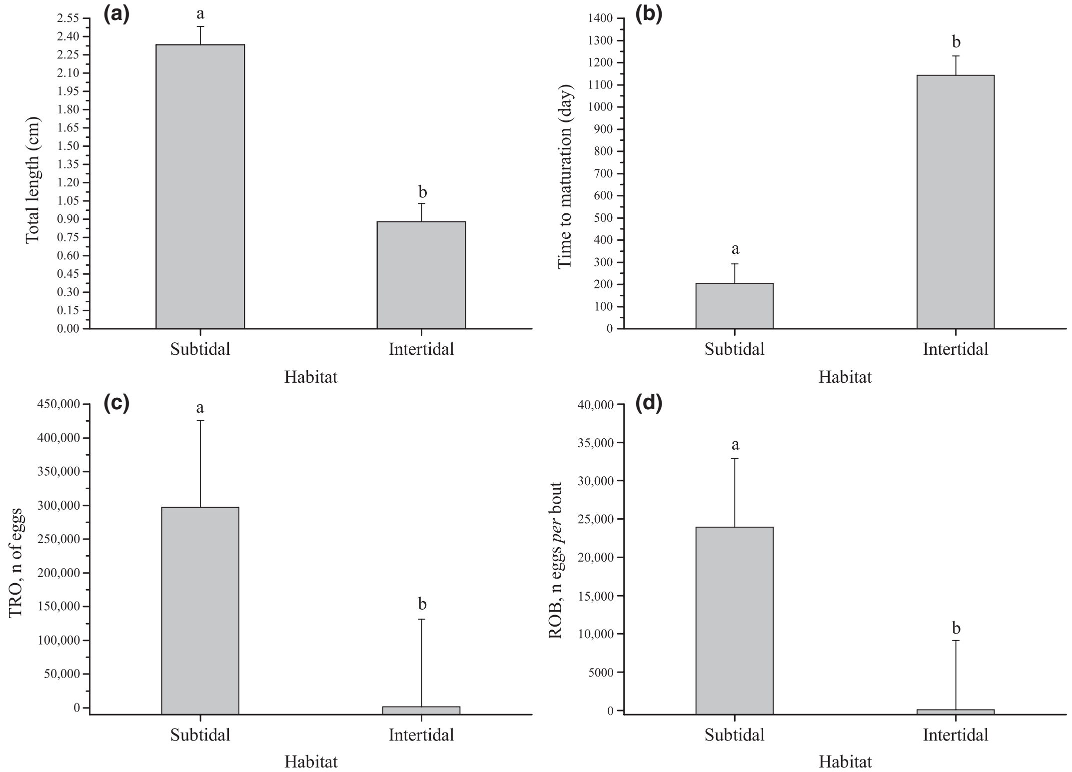

Figure 5 Fitness variables as a function of the habitat (upper left = total length, cm; upper right = Time to maturation, day; bottom left = Total Reproductive Output [TRO], *n* of eggs; bottom right = Reproductive Output per every Bout [ROB], *n* eggs *per* bout).

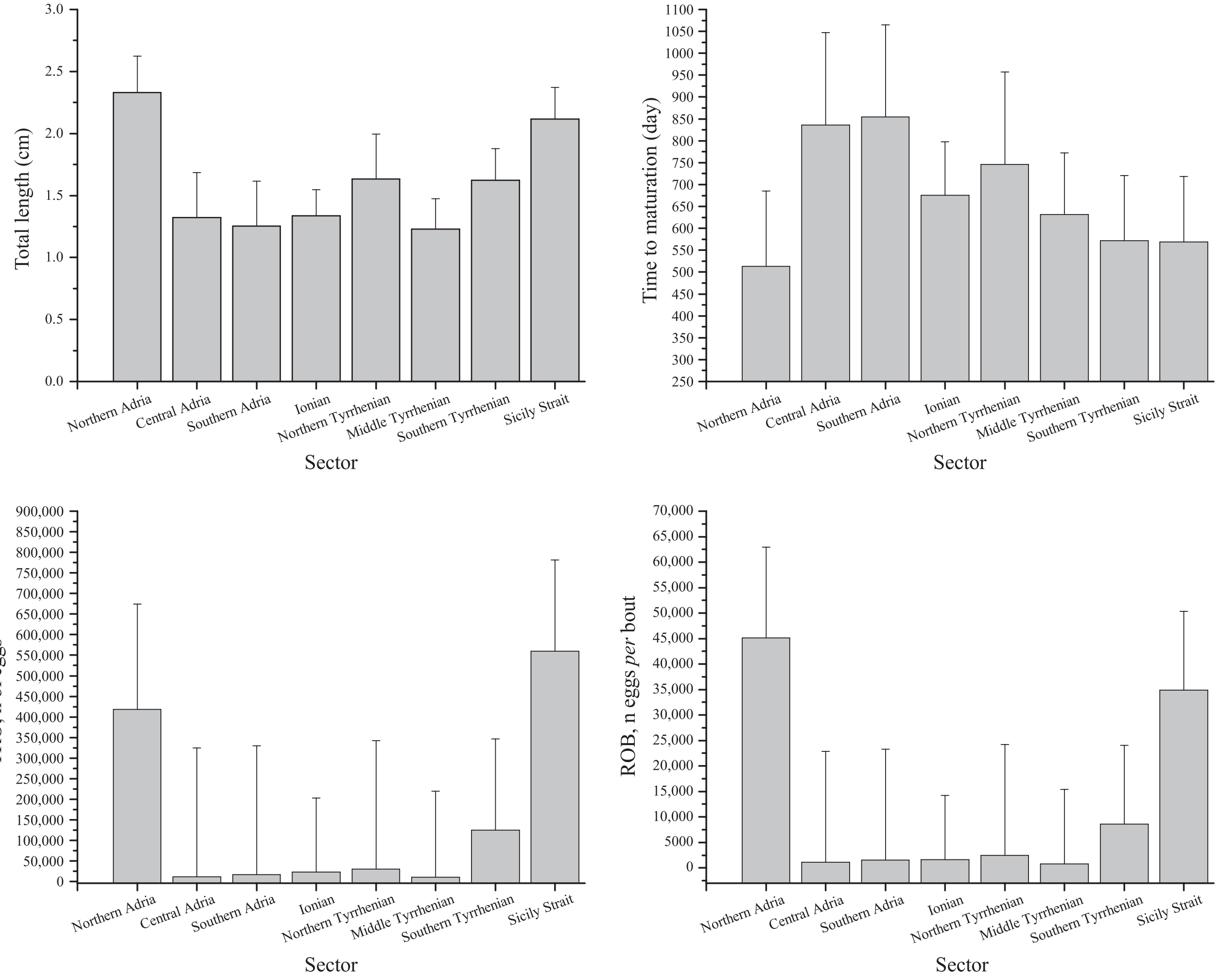

Figure 6 Fitness variables as a function of the habitat (upper left = total length, cm; upper right = Time to maturation, day; bottom left = Total Reproductive Output [TRO], *n* of eggs; bottom right = Reproductive Output per every Bout [ROB], *n* eggs *per* bout).

Israeli coasts lower in the intertidal or on submerged hard substrate, as well as by Cilia & Deidun (2012) who reported similar results for Malta populations. Our previous observations in western Sicily also confirmed this result. Sarà *et al.* (2000, 2008) found higher densities of Pharaonic mussels below the low tide lower mark than on intertidal surfaces and more recently, Garaventa *et al.* (2012) reported this species from lower mid-littoral artificial surfaces of industrial plants of Southern Sicily (Siracusa and Augusta).

Such findings are in theoretical contrast with what Mediterranean intertidal characteristics might superficially suggest. Here, intertidal conditions may be usually considered less harsh than those of oceans such as the Northern Atlantic (Sarà *et al.*, 2007) or along the Pacific coasts of North America (Helmuth *et al.*, 2006), where wave forces can be much greater and tidal ranges greater. Mediterranean tides indeed are smaller in amplitude than in these regions (a few decimetres as opposed to several metres). Nevertheless, in oceanic habitats, larger tidal amplitudes are often associated with water masses that may be trophically richer with large amounts of suspended food for intertidal filter feeders like along the Pacific of North America or the Southern Iceland where suspended chlorophyll-*a* concentrations have spikes of over than 30 μg l^{-1} (e.g. Petes *et al.*, 2007; Sarà *et al.*, 2007). Subsequently, although the intertidal feeding time in mid-intertidal zones is often not more than 50% of the total time in more oceanic regimes, at the re-immersion at high tide, organisms can rely on large amounts of food. In the Central Mediterranean, although overall the intertidal feeding time is greater than that of oceanic coasts worldwide (more than 80%), at the re-immersion at low tide, animals rely on water masses that are nearly oligotrophic, with less 0.5 μg l^{-1} in many sites throughout the study area examined here. Thus, even given the small amplitude of tides in the Mediterranean, food levels are sufficiently depauperate that reduced feeding time leads to reproductive failure. Therefore, under intertidal conditions, *Brachidontes* need to cope with highly variable BTs closer to thermal tolerance limits (Sarà *et al.*, 2011) and scant food to compensate those intertidal thermal conditions.

Predicting future patterns of colonization

Our results suggest that intertidal life for *B. pharaonis* along the central coasts of the Mediterranean is suboptimal for this species. DEB showed the largest fitness of *B. pharaonis* in (1) the Northern Adriatic (De Min & Vio, 1997; but see Appendix B for sensitivity analysis) where water masses are largely influenced by large terrigenous-continental inputs from Po River, (2) in the most polluted areas of the Mediterranean, the Gulf of Gabes and Augusta, (3) in the trophically enriched waters of the saltpan system in the western Sicily (Sarà *et al.*, 2000) and around Malta (Cilia & Deidun, 2012).

Such an insight is consistent with first records of *B. pharaonis* in western Mediterranean. It was first recorded on the shores of Malta (Lanfranco, 1975) and Southern-east Sicily, Augusta and Catania (Di Geronimo, 1971), then recorded in western Sicily (Sarà *et al.*, 2000) and successively in other northern sites (Zangara, 2007). Thus, our results are consistent with the likely entrance routes of this invasive species in the western Basin. This is crucial finding for the accuracy of our mechanistic approach and represents an important indirect validation which further supports the validation exercise carried out experimentally in the Stagnone di Marsala (Appendix 1A).

This also implies that, in theory, *B. pharaonis* should be able to survive anywhere in the western Basin provided a mechanism of larval dispersal. *Brachidontes pharaonis* is indeed reported as an organism able to move through the Mediterranean by ship transportation through ballast waters or as a fouler of ship keels (Shefer *et al.*, 2004; Sirna-Terranova *et al.*, 2006; Occhipinti-Ambrogi *et al.*, 2010). Consequently, the speed of colonization by this mechanism and its ability to reach novel environments throughout the western Mediterranean basin should be limited to ships carrying larvae to coastal areas far from the points of origin (e.g. Augusta harbour, Gulf of Gabes or Malta). Nevertheless, once a significant flux of larvae reaches any hard substrata in the central Mediterranean, they could substantially establish a population able to reproduce and persist over time. Subtidal populations in new locations should thereby work as a source to assure sufficient larvae to diminish the impacts of environmental and demographic stochasticities during colonization of new sites. Such a fact should enhance the likelihood that an initial introduction would establish on-going populations (e.g. MacArthur & Wilson, 1967) in sites far from where gametes are produced (Simberloff, 2009).

In conclusion, while at present stage, there is not sufficient theory and research to derive insights on how biotic relationships may quantitatively affect niche dimensions (according to the concept of realized niche; *sensu* Hutchinson, 1957), this DEB exercise successfully provides a means of estimating the fundamental niche of this species and thus identify where it could potentially colonize (*sensu* Kearney and Porter 2009). Our approach was able to investigate, in a mechanistic way and through a very limited number of simple parameters (cf. Kearney, 2012), the ability of *B. pharaonis* to exploit energy from food (Sarà *et al.*, 2011, 2012) under both subtidal and intertidal conditions throughout the Central Mediterranean Sea. This mechanistic approach, which has been already used with success in terrestrial habitats with lizards (Kearney, 2012) and for Mytilid mussels (Kearney *et al.*, 2010; Sarà *et al.*, 2011, 2012), crustaceans and fish (Jusup *et al.*, 2011; Pecquerie *et al.*, 2011), seems a good candidate to predict distributions of invasive organisms starting from their functional traits and from a few mechanistic rules (Kooijman, 2010). This information will be important when assessing the future potential expansion of invasive species under conditions of future warming in the Mediterranean Sea, as a result of global climate change (Sarà *et al.*, in press-a), where tropical thermo-tolerant invasive species may have distinct advantage over native species, affecting global patterns of biodiversity.

ACKNOWLEDGEMENTS

This paper has been sustained by INTERMED, one of the CIRCLE Med projects funded by EU in the framework of Circle ERA Net project (which is funded by the European Commission 6th Framework Programme). This research was in part funded to G.S. and B.H. by a Visiting Scholar Award made by the Office of the Provost at the University of South Carolina. We thank all collaborators and students from EEB lab at UNIPA. We are especially grateful to Mike Kearney to have addressed our effort in DEB modelling, providing us the first Excel routine to run DEB models, John Widdows to have allowed the fine tuning of our experimental lab work to measure eco-physiological variables in bivalves.

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BIOSKETCH

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Author contributions: G.S. conceived the idea, elaboration, led the writing and funding; V.P. and A.R. data collection and elaboration; V.M. collected the data, elaboration and writing; B.H. conceived the idea and writing.

Editor: Wilfried Thuiller

APPENDIX A

Materials and Methods

Throughout the 2009 and 2010, we collected more than 1000 animals from the saltpan of the close Stagnone di Marsala (Western Sicily, Italy) where this species has established highly dense populations (Sarà *et al.*, 2000). We estimated the age through the analysis of shell rings proposed in Peharda *et al.* (2012) cutting shells by a Dremel rotary (Series 4000; Robert Bosch Tool Corporation Inc. Germany) and reading the number of rings through an stereomicroscope Leica Z4 (Leica Microsystems GmbH, Wetzlar, Germany).

Results

Brachidontes maximal length (3.7 cm, both in 2009 and 2010) was reached after 4 years in the field (Fig. A1), while that predicted by DEB under real environmental conditions was *c.* 3.9 cm at the end of 2009. DEB model estimates deviated from reality by *c.* 5.6% in 4 years (a yearly error of less than *c.* 1.5%).

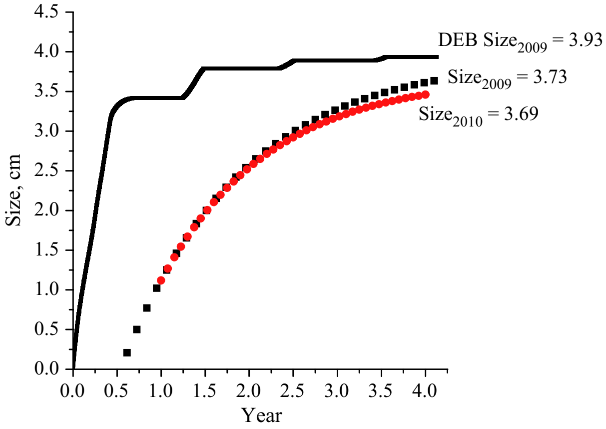

Figure A1 Age-size curves as estimated through the DEB and as validated (2009 and 2010) in the field through experimental procedures.

APPENDIX B

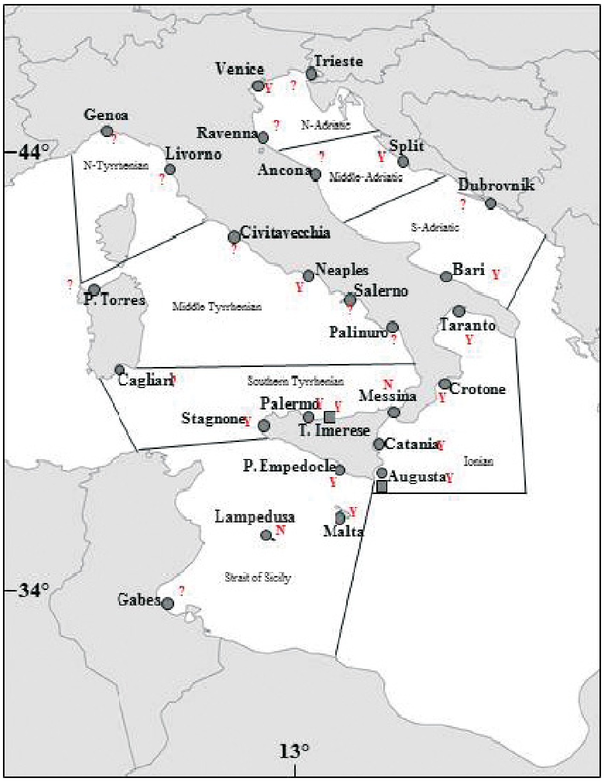

Figure B1 Map of all sites investigated in the present paper throughout the Central Mediterranean reporting presence (Y), absence (N) of *Brachidontes pharaonis* using data from literature or personal communications as reported in the table below. Presences/absences are indicated *per* single site. A question mark indicates the lack of information or suspects about the presence, but currently there is no evidence about it.

Table B1 *Brachidontes pharaonis*: literature or personal communications reporting presence or absence of the species throughout study area

Sector	Location	Occ	Author	Year	Title	Journal reference
Northern Adria	Ravenna	?	No record	–	–	–
Northern Adria	Trieste	?	De Min R, Vio E	1997	Molluschi conchiferi del litorale sloveno	*Ann Istran Med Stud, Koper, Historia naturalis*, **11**, 241–258
Northern Adria	Venezia	Y	G. Sarà, personal communication	2009		
Central Adria	Ancona	?	No record	–	–	–
Central Adria	Split	Y	G. Sarà, personal communication	2010		
Southern Adria	Bari	Y	G. Sarà, personal communication	2010		
Southern Adria	Dubrovnik	?	No record	–	–	–
Ionian	Augusta	Y	Garaventa *et al.*	2012	Settlement of the alien mollusc Brachidontes pharaonis in a Mediterranean industrial plant: bioassays for antifouling treatment optimization and management	*Marine Environmental Research*, **76**, 90–96
Ionian	Augusta Power Plant	Y	Garaventa *et al.*	2012	Settlement of the alien mollusc Brachidontes pharaonis in a Mediterranean industrial plant: bioassays for antifouling treatment optimization and management	*Marine Environmental Research* **76**, 90–96
Ionian	Catania	Y	G. Sarà, personal communication	2011		
Ionian	Crotone	Y	G. Sarà, personal communication	2011		
Ionian	Messina	N	Cosentino *et al.*	2009	The CSI of the Faro Coastal lake (Messina): a natural observatory for the incoming of marine alien species	Poster, 40° Congresso della Societá Italiana di Biologia Marina
Ionian	Taranto	Y	Crocetta *et al.*	2009	New distributional and ecological data of some marine alien molluscs along the southern Italian coasts	*Marine Biodiversity Records*, **2**, e23
Northern Tyrrhenian	Genova	?	No record	–	–	–
Northern Tyrrhenian	Livorno	?	No record	–	–	–
Middle Tyrrhenian	Civitavecchia	?	No record	–	–	–
Middle Tyrrhenian	Napoli	Y	Crocetta *et al.*	2009	New distributional and ecological data of some marine alien molluscs along the southern Italian coasts	*Marine Biodiversity Records*, **2**, e23
Middle Tyrrhenian	Palinuro	?	No record	–	–	–
Middle Tyrrhenian	Porto Torres	?	No record	–	–	–
Middle Tyrrhenian	Salerno	?	No record	–	–	–
Southern Tyrrhenian	Cagliari	?	No record	–	–	–
Southern Tyrrhenian	Palermo	Y	Terranova *et al.*	2006	Population structure of *Brachidontes pharaonis* (P. Fisher, 1870) (Bivalvia, Mytilidae) in the Mediterranean Sea, and evolution of a novel mtDNA polymorphism	*Marine Biology*, **150**, 89–101
Southern Tyrrhenian	Stagnone di Marsala	Y	Sarà *et al.*	2000	The new lessepsian entry Brachidontes pharaonis (Fischer P., 1870) (Bivalvia, Mytilidae) in the western Mediterranean: a physiological analysis under varying natural conditions	*Journal of Shellfish Research*, **19**, 967–977

Table B1 Continued.

Sector	Location	Occ	Author	Year	Title	Journal reference
Southern Tyrrhenian	Stagnone di Marsala	Y	Sarà *et al.*	2006	A new Lessepsian species in the western Mediterranean (Brachidontes pharaonis Bivalvia: Mytilidae): density, resource allocation and biomass	*Marine Biodiversity Records*, **1**, e8
Southern Tyrrhenian	Termini Power Plant	Y	Terranova *et al.*	2006	Population structure of *Brachidontes pharaonis* (P. Fisher, 1870) (Bivalvia, Mytilidae) in the Mediterranean Sea, and evolution of a novel mtDNA polymorphism	*Marine Biology*, **150**, 89–101
Sicily Strait	Gabes	?	No record	–	–	–
Sicily Strait	Lampedusa	N	G. Sarà, personal communication	2009		
Sicily Strait	Malta	Y	Mifsud & Cilia	2009	On the presence of a colony of Brachidontes pharaonis (P. Fischer, 1870) (Bivalvia: Mytilidae) in Maltese waters (central Mediterranean)	*Triton*, **20**, 20–22
Sicily Strait	Malta	Y	Zammit *et al.*	2009	Occurrence of Paraleucilla magna Klautau *et al.*, 2004 (Porifera: Calcarea) in Malta	*Mediterranean Marine Science*, **10**, 135–138
Sicily Strait	Malta	Y	Cilia and Diedun	2012	Branching out: mapping the spatial expansion of the Lessepsian invader mytilid Brachidontes pharaonis (Fischer, 1870) around the Maltese Islands	*Marine Biodiversity Records*, **5**, 1–8
Sicily Strait	P. Empedocle	N	G. Sarà, personal communication	2009		