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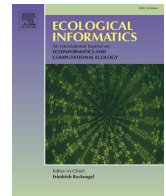
DEBEcoMod: A dynamic energy budget R tool to predict life-history traits of marine organisms across time and space

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ABSTRACT

DEBEcoMod is an open-source R script designed to apply Dynamic Energy Budget (DEB) theory to predict life-history traits of marine organisms under various environmental and anthropogenic stressors. It presents a novel approach to overcoming the computational and scale limitations of previous DEB applications, enabling the generation of spatially explicit outputs. DEBEcoMod is intended to predict traits such as maximum size, reproductive output, and life-history traits across different temporal and spatial scales. It utilises parameters from the AddMyPet database for various species and environmental time series to simulate the past, present, and future performance of organisms. The tool also includes a module for spatio-temporal representation, producing clear and accessible maps for stakeholders. The document highlights DEBEcoMod's application in invasion biology, marine spatial planning, integrated multi-trophic aquaculture, and marine ecology, drawing on published examples of spatial applications to demonstrate its versatility and potential in ecological research and adaptive management. Furthermore, the code has been cross-validated with the official DEBtool to ensure its accuracy and reliability. DEBEcoMod is available for download on GitHub, enhancing its accessibility and utility for a wide range of ecological and conservation applications.

1. Introduction

Anthropogenic climate change is a key driver of increased environmental variability, demanding enhanced predictive capabilities across the ecological hierarchy to inform effective management and conservation strategies (De Bello et al., 2021). Within this framework, the evaluation of organisms' ecological niches through process-based, mechanistic models becomes critically important (Kearney, 2012; Kearney et al., 2010, 2012; Mangano et al., 2020, 2023; Nisbet et al., 2012; Sarà et al., 2018; Schuwirth et al., 2019).

However, the application of mechanistic models is often hindered by challenges such as the absence or incompleteness of data, the need to estimate numerous model parameters, and significant computational demands, particularly when applied across large spatial scales and environmental gradients. As a result, scientists frequently turn to correlative models, such as those utilising presence-absence databases to run established routines (e.g., the BIOMOD implementation of the Maxent algorithm; Phillips et al., 2006) (Bosch-Belmar et al., 2021; Cecino et al., 2021). However, an over-reliance on statistical models, at the expense of mechanistic ones, represents a key limitation, as doing so, only connects implicitly to the underlying processes. This limitation undermines the ability to estimate the impacts of unprecedented environmental variability on functional and life-history traits (Ezgeta-Balić et al., 2011; Pacifici et al., 2017; Prusina et al., 2014; Sarà et al., 2014).

Understanding how environmental variability influences life-history traits is crucial, as it aids in predicting whether species can persist in specific locations, thereby enhancing our comprehension of potential community shifts following the loss of dominant, subdominant, or competitively weak species (Leibold and Chase, 2018). Such insights also assist conservationists and managers in implementing proactive resource management strategies to improve the sustainability of fisheries and aquaculture (Giacoletti et al., 2021, 2024; Haberle et al., 2024; Mangano et al., 2020, 2023), as well as in preventing the local proliferation of invasive species (Sarà et al., 2000), which, if not addressed, could severely impact ecosystem functionality (Tan et al., 2021). This approach has also been recently applied to Environmental Risk Assessments (ERA) and Environmental Impact Assessments (EIA) to evaluate the sustainability of industrial anthropogenic activities (Martins et al.,

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This study presents a novel approach to overcoming some of the primary challenges in forecasting species distributions through time and space using mechanistic models. We utilised Dynamic Energy Budget (DEB) theory (Kooijman, 2010) alongside recent computational advancements to develop a new DEB-based R tool. This tool is designed to assess the effects of environmental changes—arising from climatic or anthropogenic disturbances—on key ecological and resource management questions (e.g., Mangano et al., 2023). DEB theory, which adheres to the laws of thermodynamics (Sousa et al., 2008), provides a comprehensive framework for linking environmental conditions with the physiological performance of organisms, encompassing growth, maturation, reproduction, and survival metrics (Nisbet et al., 2000; Sousa et al., 2010). It is a universally applicable approach, as demonstrated by the Add_my_Pet (AmP) database, which catalogues DEB parameters for thousands of species (AmP, 2024; Marques et al., 2018).

The R environment, initially designed for statistical computation, has evolved into a powerful platform for complex scientific simulations. This includes ecological modelling, exemplified by the recent development of NicheMapR, a tool that facilitates mechanistic modelling of heat, water, energy, and mass exchange between ectothermic organisms and their environments, as well as microclimate calculations (Kearney et al., 2010; Kearney et al., 2018).

This versatility inspired us to implement our own mechanistic framework based on DEB Theory, leading to the development of DEBEcoMod. This script provides a standardised approach for multiple species, enabling the prediction and spatial representation of species distribution under conditions of greater-than-historical environmental variability. DEBEcoMod also serves as an important open-source tool for evaluating present and future aquaculture performance and impact at a highly detailed scale, translating complex computational modelling results into easily interpretable maps.

DEBEcoMod adheres to the KISS (Keep It Simple, Stupid) engineering principle, recognising that complex systems are more prone to failure and harder to repair. As often attributed to Albert Einstein, "everything should be made as simple as possible, but not simpler." Jager et al. (2013) effectively applied the KISS principle to modelling life-history traits of animals through a straightforward DEB energy-budget approach, known as DEB-KISS, while following Einstein's advice.

Here, we outline the methodology behind DEBEcoMod, present three illustrative applications of the script, and discuss the results within a broader ecological and marine resource management context.

2. Methods

DEBEcoMod was coded in R version 4.3.2 (R Core Team, 2023). The script calculates the performance of a selected species in terms of growth, maturation, and reproduction under specified environmental conditions. The mechanistic basis for these computations is provided by Dynamic Energy Budget (DEB) theory (Jusup et al., 2017; Kearney, 2012; Kooijman, 2010; Sousa et al., 2008, 2010), specifically through the standard DEB model, which tracks how individual organisms utilise energy from food to meet various metabolic needs. DEBEcoMod is freely available for download on GitHub (https://github.com/DEBE coMod/DEBEcoMod.git).

2.1. Model description

The standard DEB model (Kooijman, 2010) divides an organism into two conceptual compartments: structure and reserve. Structure represents all tissues that sustain the organism's life. Structural tissue requires maintenance and, in principle, cannot be metabolised for energy. Reserve includes all tissues that buffer the organism from environmental variability. Reserve tissue is maintenance-free and can be metabolised for energy.

The standard DEB model incorporates three main state variables:

reserve E (J), structure V (cm^3) and maturity E_H (J). Once the individual reaches puberty, an additional state variable, the reproductive buffer E_R (J) is included. The model tracks changes in state variables across three primary life stages: embryo ($E_H < E_H^b$), juvenile ($E_H^b < E_H < E_H^p$), and adult ($E_H = E_H^p$). During the embryo stage, individuals use reserve energy for development and growth. After birth, feeding begins, and food availability affects the ingestion ($\dot{p}_X$) and the assimilation of energy from food into reserve ($\dot{p}_A$). Energy from the reserve is mobilised to meet the organism's metabolic needs ($\dot{p}_C$) and is divided between somatic and reproductive needs according to the κ-rule. The fraction $0 < κ < 1$ is allocated to somatic maintenance ($\dot{p}_S$) and growth ($\dot{p}_G$), while the fraction 1 - κ is used for development ($\dot{p}_R$) if the individual has not yet reached puberty ($E_H < E_H^p$), or for the reproductive buffer upon maturation ($E_H = E_H^p$). Development includes maintenance termed maturity maintenance ($\dot{p}_J$). The relationships between the state variables and energy flows are detailed in Table 1.

The metabolism of all living organisms depends on body temperature (Sousa et al., 2010), a relationship well described by the Van't Hoff-Arrhenius equation. Table 2 lists the primary parameters required to predict the dynamics of the main state variables, along with additional parameters needed to model thermal responses, feeding rates, and other compound parameters.

2.1.1. Extensions of the standard DEB model

Animal diversity is represented by a family of related DEB models, all of which are straightforward extensions of the simplest model: the standard (std) DEB model. The std. DEB model is based on a single type of food, reserve, and structure, assuming isomorphy throughout the organism's entire life cycle and modelling three main life stages: embryo, juvenile, and adult. Among these, abj-models are a one-parameter extension of std-models, incorporating acceleration between birth (E_H^b) and metamorphosis (E_H^j), following the V1-morphy rules. This model type is used for species undergoing metamorphosis (Marques et al., 2018). After metamorphosis, an abj-model resembles a std-model but includes a permanent gradual increase in energy assimilation $\left\{\dot{p}_{Am}\right\}$ and energy conductance $\dot{v}$ (Kooijman, 2014), which are adjusted by multiplying them with the acceleration factor.

In its current form, our script, DEBEcoMod, is designed to compute the performance of both the standard (std) DEB model and its one-parameter extension, the abj-model. This versatility allows for the modelling of species that undergo metamorphosis, incorporating acceleration between birth and metamorphosis, while maintaining compatibility with the simpler std. model framework.

Table 1
The relationships between the state variables and energy flows.

Energy flow	Units	Formula
Assimilation	J d^{-1}	$\dot{p}_A = f(X)\left\{\dot{p}_{Am}\right\}V^{\frac{2}{3}}$
Mobilisation	J d^{-1}	$\dot{p}_C = E\left(\frac{[E_G]\dot{v}V^{\frac{2}{3}}+\dot{p}_S}{\kappa E + [E_G]V}\right)$
Somatic maintenance	J d^{-1}	$\dot{p}_S = [\dot{p}_M]V + \{\dot{p}_T\}V^{\frac{2}{3}}$
Maturity maintenance	J d^{-1}	$\dot{p}_J = \dot{k}_J E_H$
Growth	J d^{-1}	$\dot{p}_G = \kappa\dot{p}_C - \dot{p}_S$
Maturation/reproduction	J d^{-1}	$\dot{p}_R = (1-\kappa)\dot{p}_C - \dot{p}_J$
State variables		
Reserve energy, E	J	$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$
Structural volume, V	cm^3	$\frac{dV}{dt} = \frac{\dot{p}_G}{[E_G]}$
Maturity energy, E_H	J	$\frac{dE_H}{dt} = \dot{p}_R$ when $E_H < E_H^p$
Reproductive buffer, E_R	J	$\frac{dE_R}{dt} = \dot{p}_R$ when $E_H \geq E_H^p$

Table 2

DEB parameters for *B. pharaonis* (AmP version 2016/01/10), *M. galloprovincialis* (AmP version 2018/09/17), *D. labrax* (AmP version 2018/05/11), *Sparus aurata* (AmP version 2016/10/15, refined by Haberle et al. 2019 in bold).

Symbol	Description	Units	*B. pharaonis*	*M. galloprovincialis*	*Dicentrarchus labrax*	*Sparus aurata*
		Primary parameters				
$\left\{\dot{p}_{Am}\right\}$	Maximum surface area-specific assimilation rate	J cm^{-3} d^{-1}	8.202124	7.13375	84.99644	**16.8191**
κ	Fraction of utilised energy spent on maintenance and growth	–	0.983	0.47679	0.56524	**0.9378**
kap_X	Assimilation efficiency	–	0.75	0.7	0.68	**0.805**
kap_R	Reproduction efficiency	–	0.95	0.95	0.95	0.9542
$\dot{v}$	Energy conductance	cm^{-3} d^{-1}	0.01868	0.023785	0.041587	**0.0453**
$[\dot{p}_M]$	Volume-specific maintenance cost	J cm^{-3} d^{-1}	14.24	9.0477	19.4366	**12.5144**
$\{\dot{p}_T\}$	Surface-specific maintenance cost	J cm^{-2} d^{-1}	0	0	0	0
$[E_G]$	Volume-specific cost of growth	J cm^3	2478	2380.6249	5230	**5265.8**
k_J	Maturity maintenance rate coefficient	1/d	0.002	0.002	0.002	0.002
E_H^b	Maturity at birth	J	3.938e-06	5.63e-05	1.599	**0.0589**
E_H^j	Maturity at metamorphosis	J	3.31e-05	0.0403	513.8	**385.9**
E_H^p	Maturity at puberty	J	2163	1587	2.469e06	145,400
		Temperature effect				
T_A	Arrhenius temperature	K	8232	14,821.191	8144.1978	**8414**
T_L	Lower boundary of tolerance range	K	–	293.15	273.654	–
T_H	Upper boundary of tolerance range	K	–	303.2494	302.7369	–
T_{AL}	Rate of decrease at lower boundary	K	–	−0.001021	57,351.7881	–
T_{AH}	Rate of decrease at upper boundary	K	–	31,292.8769	84,842.0831	–
		Auxiliary and compound parameters				
z	Zoom factor	–	0.5662	0.37593	2.4718	1.253
δ_M	Shape coefficient of adult	–	0.33	0.23035	0.14841	**0.2525**
δ_{MB}	Shape coefficient at birth	–	–	0.0.23287	–	–
s_M	Acceleration factor	–	2.030585	8.93448	6.823139	18.70099
$[E_m]$	Maximum storage density	J cm^3	439.0859	299.9265	2043.822	575.7761

2.2. Model inputs and outputs

DEBEcoMod processes the main state variables, mapping them as functions of time across a specified study area. This area is digitally represented as an extensive mosaic of spatial "pixels," with granularity typically constrained by the resolution of the available data. For its operation, DEBEcoMod requires inputs of food abundance and hourly sea-surface temperature (SST) data, drawing on foundational guidance from studies by Thomas et al. (2011, 2016). In our research, chlorophyll-a (Chl-a) is used as a proxy for food availability specific to bivalves (Handå et al., 2011; Lavaud et al., 2014), though the model's utility extends to a diverse array of organisms. Our application of DEBEcoMod focused on suspension feeders, including bivalves, and utilised both Chl-a and SST datasets available from online repositories such as the Copernicus Marine Environment Monitoring Service (CMEMS), the National Oceanic and Atmospheric Administration (NOAA), the National Aeronautics and Space Administration (NASA), NASA's Jet Propulsion Laboratory (JPL), and the European Space Agency (ESA). These datasets generally offer daily temporal resolution, requiring an up-sampling process to enable simulations at hourly intervals, as demonstrated in Sarà et al. (2018) and Mangano et al. (2019, 2023). The spatial resolution of the data typically ranges from 0.04° (approximately 4 km × 4 km) to 0.01° (approximately 1 km × 1 km), ensuring a detailed representation of the study area suitable for accurate and comprehensive ecological simulations. For cultivated fish species, a daily food intake scale was applied based on the body weight estimated by the DEB model at that specific time. Food intake was determined using common feeding schemes employed by farmers (Hossu et al., 2005). Specifically, for *S. aurata*, we used data from Sicilian farms (Mangano et al., 2023), and for *D. labrax*, we referenced data from Sarà et al., 2018 (Table S3). The DEBEcoMod framework incorporates both historical data and future projections, including scenarios outlined by the Intergovernmental Panel on Climate Change (IPCC). A commonly modelled timeframe spans four years, as documented in studies by Pethybridge et al. (2013), Sarà et al. (2013a), Mangano et al. (2019, 2020), and Giacoletti et al.

(2021, 2024). However, this duration is flexible and can be tailored to suit the specific needs of the investigation, the availability of data, or to reflect the typical lifespan of the species under study, as suggested by Tan et al. (2021). Despite the common limitations of mechanistic modelling, such as being time-consuming and requiring large amounts of data, once DEB species models are calibrated, validated, and tested for skill and stationarity (Helmuth et al., 2014), there are minimal obstacles to their large-scale use in exploring the performance of both cultivated and wild species across a wide range of ecological and environmental contexts.

DEBEcoMod saves biological forecasts in a .csv output file, with one row for each pixel, and a column for each desired output. Basics outputs may include: i) pixel number, ii) maximum length, iii) maximum body mass, iv) number of eggs, v) timing of reproductive events, vi) egestion, vii) time to commercial size (for aquaculture) or time to catch size (in the wild), etc. A selection of the main model outcomes is then automatically represented by accurate, high-resolution, stakeholder-friendly maps through the ggplot2 package (Wickham, 2016).

3. DEBEcoMod applications

Here, we present three distinct case studies demonstrating how DEBEcoMod predicts the life-history traits of marine organisms ranging from the invasive mussel *Brachidontes pharaonis* to two aquaculture fishes (*Dicentrarchus labrax* and *Sparus aurata*), and the Mediterranean mussel *Mytilus galloprovincialis* reared under natural or multi-trophic aquaculture (IMTA) conditions. Readers are encouraged to download the code from the GitHub repository, obtain species-specific parameters (for std. or abj models) from the AmP database, download the relevant forcing variables, and conduct their own simulations. For details on converting DEB parameters, please refer to the Supplementary Information. It is crucial to validate the link between environmental drivers and species through in-situ growth experiments and ensure that predictions undergo a validation phase. The predictions generated by the code here are tailored to include ultimate length, cumulative

reproductive output, and time to reach commercial size in both aquaculture and wild settings. Details on the validation of model outputs and cross-validation with the official DEBTool are also provided in the Supplementary Information.

3.1. Application of DEBEcoMod to predict invasive species habitat selection – insight for informing spread and tailoring local monitoring activities

The first case study investigates the performance of the invasive species *Brachidontes pharaonis* (Fischer, 1870), in terms of growth and reproductive output across three sites. The first site is Stagnone di Marsala, the largest lagoon in Sicily, located within the nature reserve "Isole dello Stagnone di Marsala" (Fig. 1c; ITA010026, EU Habitat Directive 927437EEC). The second site is the Ettore salt flats, one of the most studied environments within the reserve (Sarà et al., 2000; Sarà et al., 2003; Sarà et al., 2008). The third site is located off the coast of Marsala, a town near the reserve. Input data for the first two sites were provided by the University of Palermo's Ecology laboratory (*E*-Lab), specifically its near-term ecological forecasting network of thermal sensors (Sarà et al., 2021). Input data for the third site are sourced from CMEMS (resolution 0.04° × 0.04°; MEDSEA_ANALYSIS_FORECAST_PHY_006_013; Clementi et al., 2021).

Model projections indicate that by the end of the fourth year, *B. pharaonis* reaches a similar size across all three environments (Fig. 1a). Additionally, the species produces approximately 14 % more eggs at the Ettore Pond and Stagnone di Marsala sites compared to the Marsala site (Fig. 1b). These findings highlight the significance of marine lagoons as key hotspots that facilitate the spread of invasive species across larger regions.

3.2. Application of DEBEcoMod to assess aquaculture farming success on a basin scale – insight for future market trends and local farming practices

The second case study demonstrates the application of DEBEcoMod to predict the time required for fish to reach commercial size in three geographically distinct Mediterranean countries: Italy, Egypt, and Tunisia (representing 2282, 1026, and 3315 pixels respectively, cut on a 50 m bathymetry). The fish species in question are the European sea bass *Dicentrarchus labrax* (Giacoletti et al., 2021; Sarà et al., 2018) and the Gilthead sea bream *Sparus aurata* (Serpa et al., 2013a), which are the two primary cultured species in the Mediterranean Sea (STECF, 2018–2019). Input data are sourced from CMEMS. Fig. 2 illustrates that *S. aurata* is predicted to reach commercial size (400 g, FAO) in a shorter time than *D. labrax* (500 g, FAO), (30 % less in Egypt and Italy and up to 33 % less in Tunisia), despite noticeable variability within specific countries. This predictive capability enables aquaculture operators to better plan their cultivation cycles and secure the necessary funding to ensure successful cultivation.

3.3. Application of DEBEcoMod to evaluate the effectiveness of IMTA aquaculture for mussel farming at Mediterranean basin scale – insight for sustainable practice in a climate change context

The third case study assesses the growth of the mussel *Mytilus galloprovincialis* in Integrated Multi-Trophic Aquaculture (IMTA) compared to its growth in the natural environment. *M. galloprovincialis* was selected as a model species because it is the primary cultured bivalve in the Mediterranean Sea (STECF 2018–2019). As in the previous case study, the time to reach commercial size was used as the key performance indicator. Input data were sourced from CMEMS, covering 10,102 pixels at a resolution of 0.04° x 0.04° representing a total surface-area of 161,632 km^2. We assumed that aquaculture contributes to a CHL-a enrichment of +2 µg l^{-1} (Sarà et al., 2012).

The results are presented for four Mediterranean subregions: the
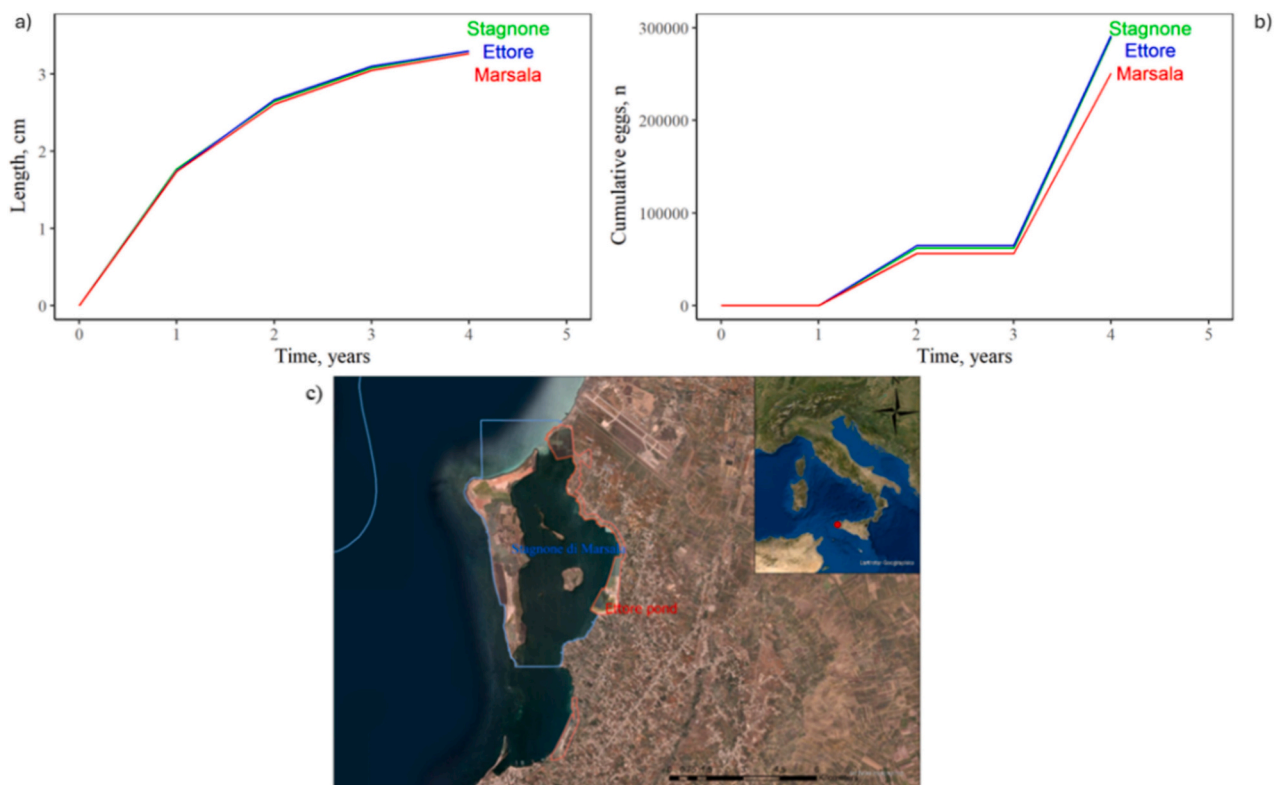
Fig. 1. Predicted a) growth (expressed as Length, cm) and b) cumulative reproductive output (n° of eggs). In c) particular of the "Stagnone di Marsala" lagoon (blue selection) and salt flats (red selection). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
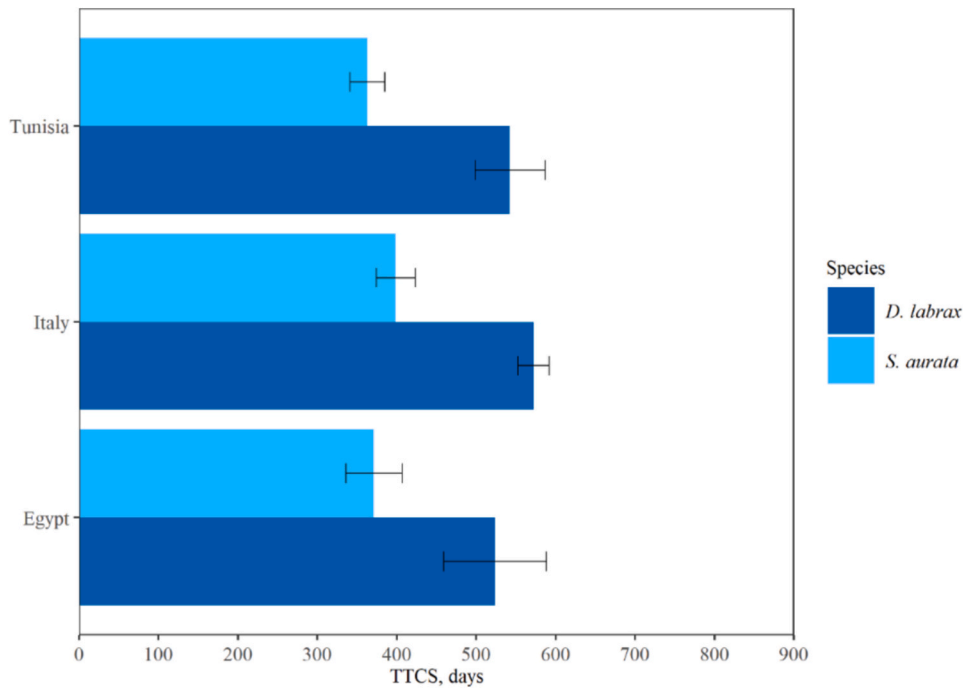
Fig. 2. Predicted Time To reach the Commercial Size (expressed as TTCS, days ± standard deviation) of two different species in three different Mediterranean sites. Error bars provide a visual representation of spatial heterogeneity in environmental trophic and thermal conditions as inputs in the current model.
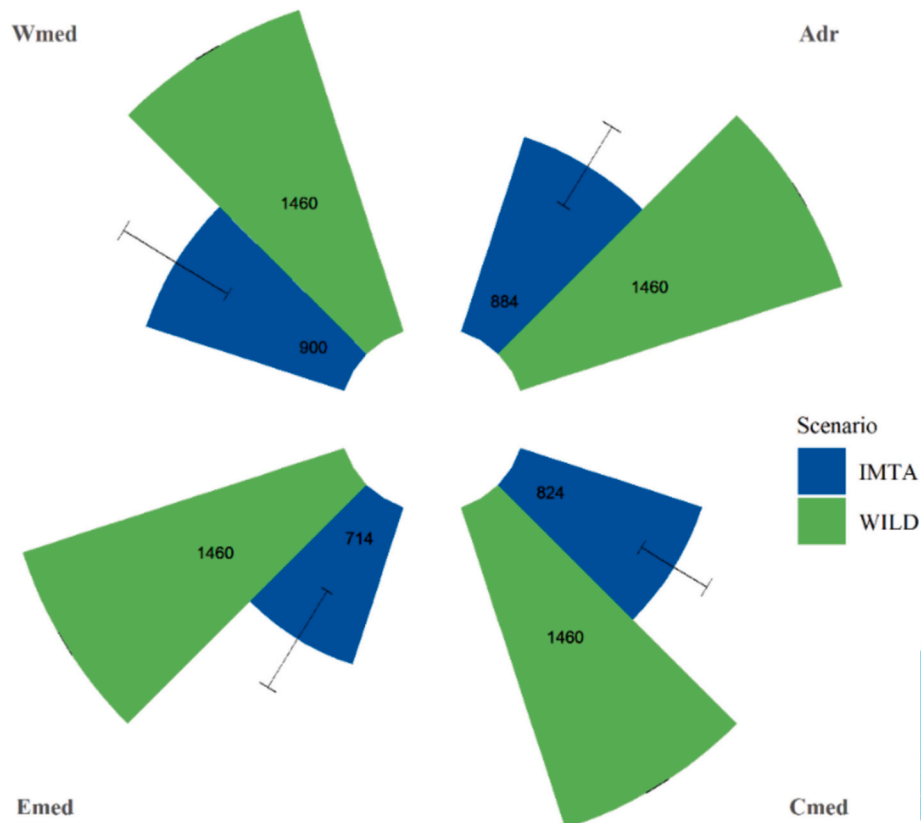

Fig. 3. Predicted current Time To reach the Commercial Size (expressed as TTCS, days ± standard deviation) in two different trophic scenarios across Mediterranean sectors simulating environmental food (WILD) and the trophic enrichment derived from IMTA. (Wmed = western, Cmed = central and Emed = eastern Mediterranean; Adr = Adriatic Sea). Error bars provide a visual representation of spatial heterogeneity in environmental trophic and thermal conditions as input of current model.
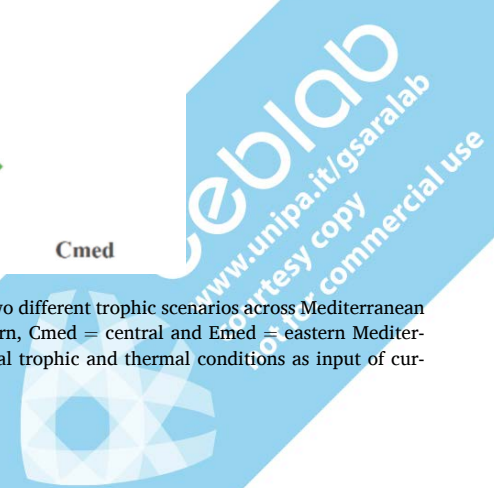
Western Mediterranean (Wmed), Central Mediterranean (Cmed), Eastern Mediterranean (Emed), and the Adriatic Sea (Adr), following the standard division by the FAO's General Fisheries Commission for the Mediterranean (GFCM). DEBEcoMod reveals a significantly longer time to reach commercial size for wild mussels compared to those cultivated in integrated multi-trophic aquaculture (Fig. 3). The differences between the Mediterranean subregions are relatively minor.

We also extended simulations to include the Representative Concentration Pathway (RCP) 4.5 and 8.5 scenarios provided by the IPCC, across an area encompassing 1536 pixels at a resolution of 0.1° x 0.1°, covering a total surface area of 185,856 km^2 (POLCOM-ERSEM 15.06, Butenschön et al., 2016). Specimens of *M. galloprovincialis* reared under IMTA conditions show a shorter average time to commercial size (TTCS) compared to wild-grown specimens that feed solely on environmental food, across all four Mediterranean sectors. Under the climate scenarios mentioned, the time to reach commercial size is significantly reduced compared to default conditions. The RCP8.5 scenario shortens the time to reach commercial size in both scenarios, with a more pronounced effect in integrated multi-trophic aquaculture (Fig. 4).

The outcomes of DEBEcoMod are spatially contextualised in Fig. 5 using the ggplot2 package (Wickham, 2016).

4. Discussion

Biodiversity plays a crucial role in shaping ecosystem structure and function, essential for conservation and environmental management. In this context, Dynamic Energy Budget (DEB) theory emerged as a key framework for understanding biodiversity through its diverse characteristics and functionalities (Marques et al., 2018). Over four decades of development, DEB theory has gained increasing recognition for its foundational assumptions and inherent simplicity, which are unparalleled by alternative models (Kooijman, 2020).

The AmP (Add-my-Pet) project, originated in 2009, operates as a comprehensive database, including referenced data, parameter values and associated properties related to animal energetics derived from DEB theory models (Kooijman, 2001, 2010; Sousa et al., 2008). Developed collaboratively by 193 authors (as of 04 October 2024), AmP facilitates the comparison of species based on these parameters. However, species comparison is just one aspect of the AmP website's broader utility. Anticipating the impacts of global change (Thomas et al., 2016), comprehending the geographic distribution of species (Montalto et al., 2015; Schwarzkopf et al., 2016; Tagliarolo et al., 2016), evaluating the effects of toxic chemical compounds (Baas and Kooijman, 2015; Kooijman et al., 2007; Martins et al., 2024; Robinson et al., 2017; Sussarellu et al., 2016), enhancing bio-production (e.g., in aquaculture and agriculture) (Kooijman and Lika, 2014; Serpa et al., 2013a, 2013b), effectively managing stocks, reintroducing endangered species, and mitigating

invasive species (Montalto et al., 2014) are instances where detailed understanding of species energetics in a DEB context proves invaluable.

Among the several tools freely available on the AmP project portal, we highlight the following:

- **AmPtool** (GitHub): A collection of Matlab functions for visualizing and analysing patterns in the parameter values of the Add-my-Pet (AmP) collection;
- **DEBtool** (GitHub): A Matlab software package focused on extracting parameter values from data and testing model predictions;
- **DEBsea Shiny app** (link) and **DEB Shiny app** (link): Applications that compute various DEB predictions using sea surface temperatures from geographic locations;
- **DEB Tox** (DEBtox): A flexible model platform package used to analyse toxicity data;
- **DEB micro trait** (GitHub): A genome-informed, trait-based microbial DEB modelling package.

Several years later, the Italian DEB research group at the University of Palermo (Laboratory of Ecology) began developing an R-based script to replace an earlier routine from Microsoft Excel (Microsoft Corporation, 2010) described in Sarà et al. (2013b). This transition was motivated by the need to overcome the computational limitations of Microsoft Excel, but also the ones encountered in Matlab, particularly to enable spatially explicit output generation. While R was originally used for statistical computations, it has evolved into a robust platform for complex scientific simulations, including ecological modelling. Additionally, R is completely free, whereas Matlab requires a costly license. This versatility justified the decision to create an independent code that integrates a DEB-based mechanistic framework within R. The model, which was progressively refined, soon demonstrated its capability to manage multiple pixels efficiently (Mangano et al., 2019). Although an initial update incorporating a macro provided a minor improvement by facilitating programme loading, it was insufficient for supporting multi-pixel simulations effectively. Consequently, the experience from Monaco et al. (2019) led to a comprehensive optimisation of the code.

Meanwhile, Kearney et al. (2018) described the NicheMapR microclimate modelling routines. This model included a suite of programs for the mechanistic modelling of heat and mass exchange between organisms and their environments. The integration of biophysical models with Dynamic Energy Budget (DEB) Theory into the R package was detailed in Kearney and Porter (2020), offering a comprehensive view of heat, water, energy, and nutritional budgets and their associated life-history consequences across different environments.

DEBEcoMod's parallel development adheres to the KISS principle while following DEB Theory, with the primary goal of creating a straightforward and reliable R script that focuses on performance and
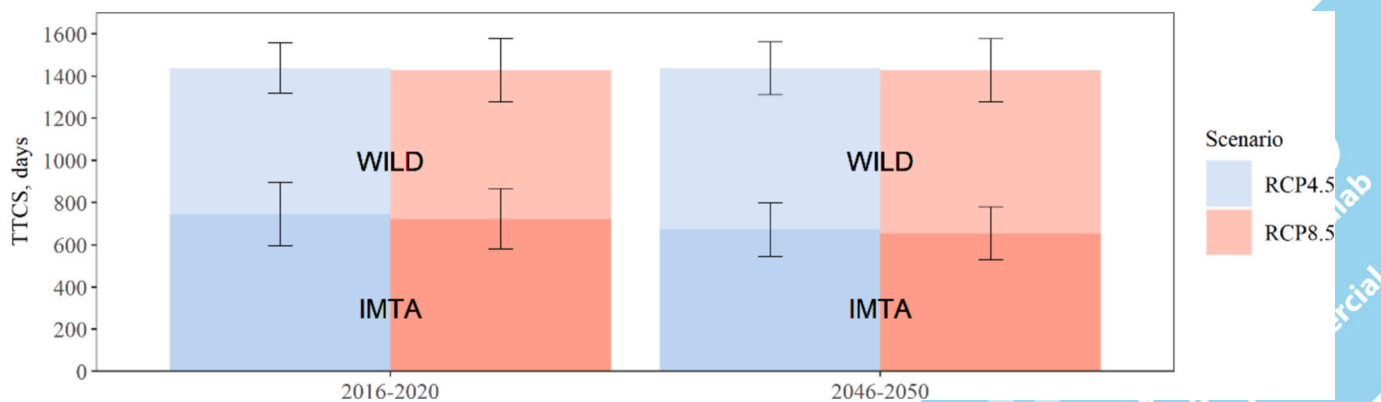

Fig. 4. Predicted Time To reach the Commercial Size (expressed as TTCS, days) in two different IPCC scenario (RCP 4.5 and 8.5) simulating environmental food (WILD) and trophic enrichment derived from multitrophic aquaculture (IMTA). Error bars provide a visual representation of spatial heterogeneity in environmental trophic and thermal conditions as input of current model.
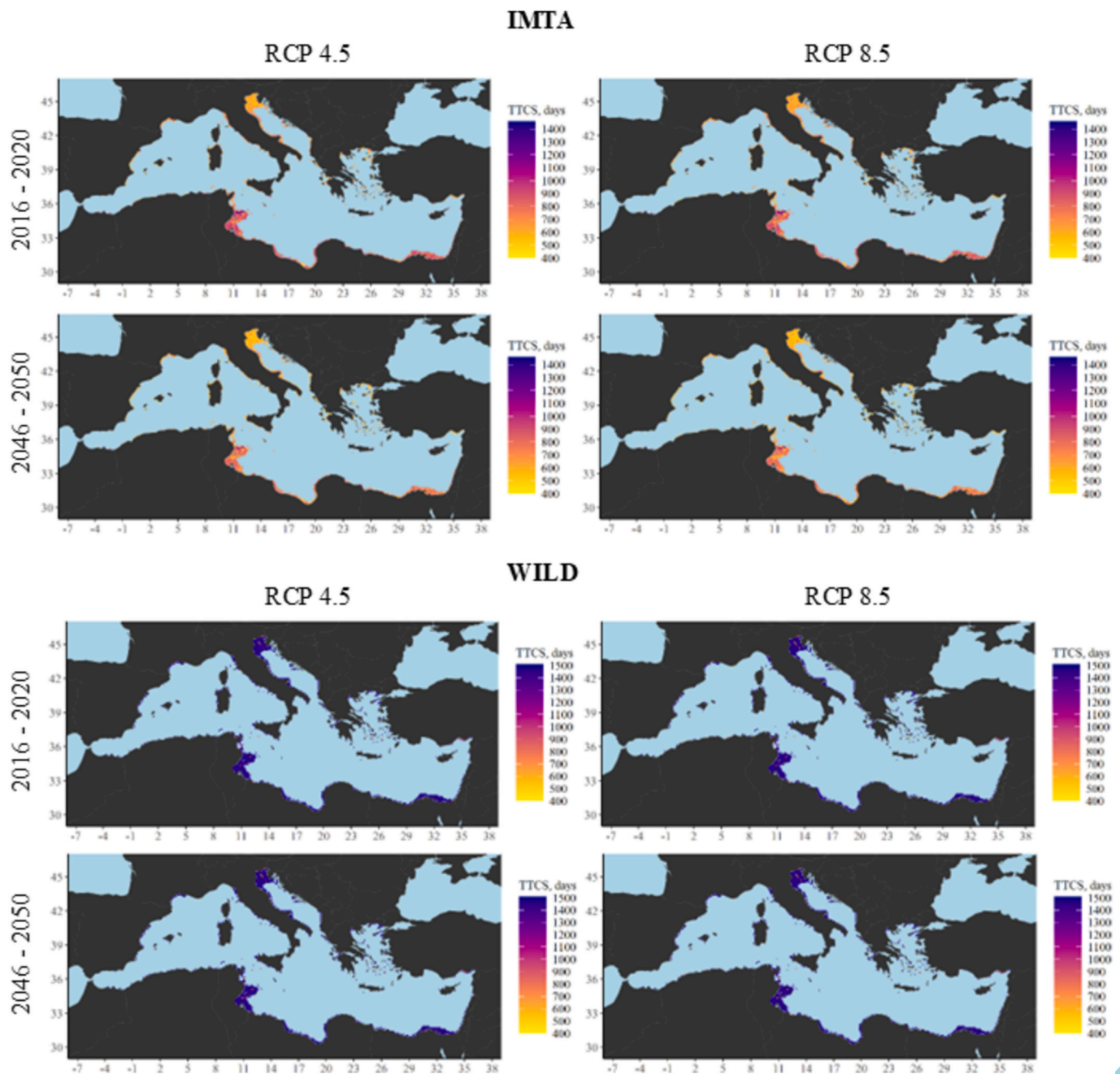
Fig. 5. Maps representing the Time To reach Commercial Size (TTCS, days) for each RCP scenario (4.5 and 8.5) and for the two considered time periods (2016–2020 and 2046–2050). Total number of cells = 1536, cell resolution 11 × 11 km. WILD = environmental food, IMTA = trophic enrichment derived from integrated multitrophic aquaculture.

capability. Unlike NicheMapR, DEBEcoMod omits detailed microclimate, heat, water, and other advanced features. This new code has been continuously refined and tested; equations were checked for consistency with NicheMapR, resulting in increasingly sophisticated predictions across various scales, from the Sicilian Channel to the entire Mediterranean basin (Giacoletti et al., 2021; Mangano et al., 2020; Mangano et al., 2023).

The development of DEBEcoMod revealed previously overlooked issues related to energy conservation, as highlighted by Monaco et al. (2019) and discussed in the Supplementary Information. Both the code from Monaco et al. (2019) and our earlier version required modifications, particularly in modelling the fate of gametes at temperatures exceeding spawning thresholds. Additionally, the Monaco et al. (2019)

code inaccurately allowed reproduction when the growth flux ($\dot{p}G$) was zero or negative; an unrealistic scenario. After addressing these issues, all the energy fluxes assimilation ($\dot{p}_A$), mobilisation ($\dot{p}_C$), growth ($\dot{p}_G$), somatic maintenance ($\dot{p}_S$), maturation ($\dot{p}_R$) and maturity maintenance ($\dot{p}_J$) were thoroughly re-evaluated according to Kooijman (2010).

Notably, the model now excludes mineral flux computations to streamline future module integration, allowing for a complete DEB simulation of a single pixel in an average of 3–4 s on standard research lab PCs (tested on a 13th generation Intel Core™ i7 CPU with 32 GB of RAM, running Microsoft Windows 11™). The current code supports simulations across the Mediterranean Sea, completing an analysis of approximately 10,000 cells (at a 0.1° × 0.1° resolution) in about 11 h, and nearly 20,000 cells (at a finer 0.04° × 0.04° resolution) in around

20 h, all without requiring specialised computing resources beyond a standard laptop. In comparison, the previous Excel routine took between 14 and 28 days to simulate 10,000 and 20,000 cells, respectively. DEBEcoMod also includes a fully customisable spatial module, which facilitates the automatic generation of spatially contextualised outputs, such as maximum length, fecundity, and time to reach commercial size, thus enhancing the tool's utility and accessibility for ecological researchers.

4.1. Strengths, limitations and future developments

DEBEcoMod represents a significant advancement in ecological modelling by offering an easy-to-use code based on the R software platform, renowned for its robust statistical and graphical capabilities. This mechanistic ecological model excels in providing detailed and versatile predictions, crucial for effective marine resource management and conservation. The tool can predict life-history traits such as maximum length, body mass, reproductive output, time to commercial size, and ecological responses across a wide range of organisms, which is essential for both aquaculture and ecological management.

In Giacoletti et al. (2021), DEBEcoMod facilitated the investigation of performance and environmental impact across Mediterranean countries with varying seeding sizes. In Mangano et al. (2023), it assessed the sustainability of single and multi-species multi-trophic aquaculture systems. Additionally, Giacoletti et al. (2024) utilised the tool to examine the effects of cage cleaning practices on the life-history traits of cultured mussels at a regional scale and under different IPCC scenarios.

DEBEcoMod harnesses R's extensive libraries and user-friendly coding environment, which simplifies the user experience and makes the tool accessible to a wide range of practitioners and researchers. By leveraging R's capabilities, DEBEcoMod is designed to be particularly user-friendly for Master's students and Ph.D. students, enabling them to manipulate data, run complex simulations, and visualise results with minimal programming effort. Its innovative features and intuitive interface streamline the process of generating accurate and comprehensive ecological forecasts, thereby enhancing decision-making and policy development in marine environments.

However, DEBEcoMod does have some limitations. These include its dependency on data quality, the accuracy of model parameter estimates, computational demands, and the need for further enhancements. The accuracy of model predictions is closely tied to the availability and resolution of input data, such as food abundance and sea-surface temperature (SST). Therefore, using the highest available spatial (from 0.04° to 0.01°) and temporal (daily to hourly) resolution is highly recommended.

Accurately estimating numerous model parameters is challenging, and any inaccuracies can affect the reliability of predictions. While DEBEcoMod itself does not estimate model parameters, the DEBtool package, available freely at https://github.com/add-my-pet/DEBtool_M/, can assist with this. DEBtool uses the covariation method to estimate DEB parameters, as outlined by Lika et al. (2011).

Other limitations are represented by its current exclusion of mineral flux computations and the need for future enhancements. The potential for variation in size at maturity due to differing food levels is noted; however, this does not depend on the code and may affect only a limited number of species. As the field of ecological modelling advances, ongoing developments will focus on incorporating additional modules and improving the tool's versatility and accuracy to address emerging research needs and environmental challenges.

Despite optimisations, running the model across extensive spatial scales and environmental gradients, including simulations of climate change scenarios or multiple stressors, can still be computationally intensive. This is often constrained by the availability of dedicated hardware required for these computations. Future applications of DEBEcoMod encompasses a broad range of topics, including the study of carrying capacity in coastal environments (Filgueira et al., 2014),

nutrient cycling (Kotta et al., 2023), and the conservation of species particularly sensitive to climate change (Lavaud et al., 2021a). It can also be used to improve growth cycles and reproduction timing (Bourles et al., 2009), assess product quality (Duarte et al., 2012), enhance management strategies (Lavaud et al., 2021b), and aid in site selection for restoration projects (Stechele et al., 2023).

4.2. Model validation and cross validation with DEBTool

DEBEcoMod's outputs, in terms of key state variables, fluxes, and zero variates, were compared with DEBTool's predictions as reported in each AmP entry. Furthermore, the outputs for each case study were validated using literature data, field data, or data from real aquaculture facilities. Detailed comparisons are provided in the Supplementary Information.

Ensuring compatibility between our tool and DEBTool is crucial for enhancing the reliability and broader applicability of DEBEcoMod in Ecological modelling and spme specific applications such as aquaculture. DEBTool, widely used and trusted within the scientific community, provides well-validated predictions for a range of biological processes. By cross-validating DEBEcoMod's outputs with DEBTool's predictions, we can ensure consistency across models, which strengthens the credibility of DEBEcoMod's results. This compatibility serves as a major advantage, allowing users to benefit from both tools' strengths while promoting seamless integration across platforms. In future efforts, extending validation across diverse taxa and scenarios will be a key focus, further ensuring robust, generalizable applications of DEBEcoMod in both research and practical settings.

5. Conclusion

Our research, supported by a range of case studies, highlights the utility of our code in addressing critical applied ecological questions relevant to marine resource management, including fisheries and aquaculture. By generating predictions for key species such as mussels, oysters, clams, and cockles, our modelling tool provides valuable insights into both current and future states of aquaculture. It assesses various stressors, such as climate change and anthropogenic disturbances, facilitating the identification of critical environmental thresholds where organisms may struggle to meet their metabolic needs, affecting their development. Projecting the growth and performance of ecosystem engineers is essential for estimating biodiversity loss and understanding its impacts on ecosystem functioning and service provision.

The role of bivalves in maintaining water quality and biomass production underscores the broader ecological questions our tool can address beyond aquaculture productivity (Maynou et al., 2020; Sarà et al., 2021). DEBEcoMod is designed to support the sustainable advancement of modern fisheries and aquaculture, which is vital for reducing hunger, improving nutrition, combating poverty, fostering economic growth, and ensuring the sustainable exploitation of natural resources globally (FAO, 2018). Initially, DEBEcoMod has proven effective in generating species- and site-specific predictions on aquaculture performance and its environmental impacts, particularly for the European seabass (*D. labrax*). It aids in farm management decisions, such as determining optimal seeding sizes and selecting sites for maximum growth rates (Giacoletti et al., 2021; Mangano et al., 2023; UNEP, 2023).

Future enhancements for DEBEcoMod will include integrating mineral flux calculations, scenario analysis modules, population dynamics modules, and mechanisms to explore egg and larval connectivity. These advancements aim to improve the tool's applicability in ecological, fishery, and aquaculture research, enhancing our understanding and management of environmental stressors' impacts on marine ecosystems and organisms.

In summary, DEBEcoMod's development as a sophisticated,

automated mechanistic model holds significant potential for scientists, managers, conservationists, and practitioners across diverse fields. It can be integrated with socio-economic models for comprehensive marine resource management, improved with machine learning for enhanced predictive capabilities, and updated with real-time environmental data for dynamic predictions and adaptive management. Additionally, it has the potential to inform policy and governance decisions and engage the public and stakeholders through user-friendly interfaces or educational modules, promoting a broader understanding of marine ecology and sustainable practices.

Author statements

AG wrote the original version of the ms. and together with GS and MCM conceptualized the idea; AG performed modelling and handled data visualization. SB revised the code. GDB with AG both supervised and prepared the code for the upload to online repository. GS, MBB, MCM and SB both contributed to the supervision, review and editing process of the manuscript. GS funded the study and all the authors reviewed and commented on the final version of the manuscript.

Code availability

Codes for model running and mapping generated outputs are freely available on GitHub.com repository at https://github.com/DEBEcoMod/DEBEcoMod.git on a GPL-3.0 license.

CRediT authorship contribution statement

A. Giacoletti: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **M. Bosch-Belmar:** Writing – review & editing, Supervision. **G. Di Bona:** Software, Data curation. **M.C. Mangano:** Writing – review & editing, Supervision, Conceptualization. **B. Stechele:** Writing – review & editing, Visualization, Validation, Software. **G. Sarà:** Supervision, Review & editing, Conceptualizaion, Funding.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data supporting the findings of this study are available from the corresponding author on reasonable request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoinf.2024.102897.

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