



Predicting the effect of fouling organisms and climate change on integrated shellfish aquaculture

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ARTICLE INFO

Editor: Tony R. Walker

Keywords:

Harmful cnidarian
Mussels
Functional traits
Climate-change
DEB models

ABSTRACT

Aquaculture industry represents a continuously growing sector playing a fundamental role in pursuing United Nation's goals. Increasing sea-surface temperatures, the growth of encrusting species and current cage cleaning practices proved to affect the productivity of commercial species. Here, through a Dynamic Energy Budget application under two different IPCC scenarios, we investigate the long-term effects of *Pennaria disticha* fragments' on *Mytilus galloprovincialis*' functional traits as a result of cage cleaning practices. While Climate-Change did not exert a marked effect on mussels' Life-History traits, the simulated effect of cage cleanings highlighted a positive effect on total weight, fecundity and time to commercial size. West-Mediterranean emerged as the most affected sector, with Malta, Montenegro, Morocco, Syria, Tunisia and Turkey between the top-affected countries. These outcomes confirm the reliability of a DEB-approach in projecting at different spatial and temporal scale eco-physiological results, avoiding the limitation of short-term studies and the difficulties of long-term ones.

1. Introduction

Aquaculture plays an important role inside the United Nation 2030 Agenda for Sustainable Development in pursuing Sustainable Development Goals (SDGs), and particularly the SDG 14 (Conserve and sustainably use the oceans, seas and marine resources for sustainable development). This sector is of crucial importance for the global food industry and poverty reduction, with a growing 7.5 % yearly production since 1970 (FAO, 2020). Increases in the scale and extent of human activities, including the forecasted environmental changes, are nowadays held as responsible for the environmental changes and this exacerbates potential local side-effects such as eutrophication and increasing rates of outbreak forming species, mostly encrusting colonisers, both concurring in impairing the efficiency of growth of organisms at farm level (Vitousek et al., 1997; IPCC, 2019).

Encrusting organisms colonizing hard substrates aquaculture farms are collectively called biofouling and the massive presence mainly impacts aquaculture (Sarà et al., 2007). Particularly, hydroids (sessile and

colonial stinging cnidarians) are key components of biofouling communities and are known as a significant threat for finfish mariculture due to the contact envenomation and secondary infections impacting farmed species health (Fitridge et al., 2012; Bosch-Belmar et al., 2019).

Biofouling may be a factor of further economic loss above all when increasing temperature due to global change and local eutrophication (Sarà et al., 2011) is expected to boost fouling growth and its spread among cages at local and regional level. Biofouling indeed affects farmed organisms such as shellfishes by encrusting their valves, causing physical damage, mechanical interference and biological competition and impairing finfish growth performance through restriction of water exchange, deformation of cages and facilities structures and increase disease risk (Fitridge et al., 2012). Further, the market price of biofouled valved organisms (e.g. shellfishes) is reduced doubly as affected from an aesthetic factor or due to processing or packaging methods (Willemsen, 2005). The cost of fouling management in the aquaculture industry has been estimated to affect from 5 to 10 % the total production benefits (Fitridge et al., 2012). To avoid such collective negative impacts of

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biofouling, aquaculture nets need to be periodically cleaned with high-pressure washers which is one among the most used methods in the sector, though it entails significant risks related to net-damages, contamination, health and welfare of cultured organisms causing further economic loss at farm level (Bloecher et al., 2019).

In situ net-cleaning processes usually causes hydroids fragments containing active stinging cells to be freely released in the water column. These fragments may cause severe gill injuries leading to serious pathologies and even stocks death, when inhaled (Baxter et al., 2012). Among them, the indigenous hydroid, *Pennaria disticha*, is considered a native outbreak forming species and it is identified a taxon of main concern for Mediterranean fish farms (Bosch-Belmar et al., 2017), due to the huge dimensions and robustness of its colonies, its high growth rate and stinging capabilities (Schuchert, 2006, Tezcan and Sarp, 2013, Bosch-Belmar et al., 2019).

The presence of such hydroids is exacerbated by increasing temperature and eutrophication conditions (Bosch-Belmar et al., 2022) due to local trophic augmentation exerted by cages (Sarà et al., 2011). To date, there is no research being able to design predictable management measures involving the effect of global change drivers on secondary potential threats acting at local level and to estimate their detrimental interaction on aquaculture. Current management measures indeed rely on short-term experimental analyses and results are applied day-by-day as there is a lack of a mechanistic understanding to predict how and why biofouling colonization rate change as a function of local environmental conditions and affect farmed organisms (e.g. Baxter et al., 2011, 2012; Bosch-Belmar et al., 2016, 2019). The interpretation of this kind of approaches, is basically phenomenological and based on the study of functional traits i.e. all those species-specific physiological, morphological, structural and behavioural traits that influence individual responses to environmental variability (Schoener, 1989). Short-term experimental datasets are valuable to feed projections to much broader spatial and temporal scales through correlative or mechanistic approaches (Rastetter et al., 2003), with the aim of providing reliable Life-History traits predictions (LH; e.g. habitat body size, spawning events and Darwinian fitness; Kearney et al., 2010), counteracting common difficulties encountered in experiments due to logistic limitations. Such a kind of approaches has been considered highly reliable in many fields of biology and ecology and extensively used to predict the distribution of marine organisms in face of climate change (e.g. Montalto et al., 2014; Cheng et al., 2018; Giacoletti et al., 2018). In the Mediterranean Sea, current projections predict increases in sea surface temperature of up to +2.5 °C by the end of the century under RCP 8.5 (*business as usual*) scenario (IPCC, 2019). Therefore, increasing temperature will affect aquaculture through side-effects such as circulation patterns, the frequency and severity of extreme events, sea-level rise and all the associated ecological changes (Shelton, 2014; Sarà et al., 2018c). Among the major possible concerns for both the integrity of structures (cages, nets and pontoons) and animal welfare (Douglas-Helders et al., 2003; Willemsen, 2005; Edwards et al., 2015), lies the expectation of an increased colonization by encrusting organisms (Railkin et al., 2004).

Here we provide a mechanistic exercise to assess the long-term impact of cage-cleaning on *Mytilus galloprovincialis*, one among the most farmed species in the Mediterranean Sea (STECF, 2018–2019), based on eco-physiological data collected by Bosch-Belmar et al. (2022). By applying the Dynamic Energy Budget model, we captured the effect of hydroid fragmentation on mussel functional performances, specifically respiration and clearance rates. Using the DEB model, essentially driven by temperature and food (Kooijman, 2010) we simulated future scenarios predicted by IPCC scenarios, revealing insights into potential management repercussions. This allowed us to infer on future potential management repercussions as already done in other contexts where DEB revealed a powerful tool to answer management-related questions (Mangano et al., 2019, 2020, 2023; Sarà et al., 2018c; Giacoletti et al., 2021).

This information may reveal as crucial for traditional and multi-

trophic aquaculture planning, supporting policymakers in marine spatial planning (Sarà et al., 2018c; Mangano et al., 2023) across nineteen Mediterranean coastal countries (Giacoletti et al., 2021).

2. Methods

2.1. Dynamic energy budget model

“DEB” Theory mechanistically describes the individual metabolism through the lifecycle of an organism, capturing the responses to environmental forcing variables such as temperature and food (Nisbet et al., 2000; van der Meer, 2006). The strength of metabolic theory in general and of DEB theory in particular, consists in leading to explicit quantitative prediction of LH-traits on the base of first principles (Kooijman, 2010). The standard DEB model (van der Meer, 2006; Sousa et al., 2010; Sarà et al., 2014; Jusup et al., 2017) accounts for three main state variables: reserve (E), structure (V) and maturity (E_H) and three major fluxes: ingestion (p_X), assimilation (p_A), mobilisation (p_C). Organisms are assumed to ingest and assimilate food from the environment, converting it into reserve. Following the κ -rule a fixed fraction of energy (κ) is mobilized to the somatic compartment through the maintenance (p_S) and growth (p_G) fluxes, and a fraction ($1 - \kappa$) is allocated to the reproductive branch through the maturity maintenance (p_J) and reproductive (p_R) fluxes. Growth results from the conversion of reserve into structure in the presence of oxygen, while under optimal conditions a further amount of energy from reserve is dissipated on processes that are necessary for the organism to stay alive and mature (Jusup et al., 2017).

2.2. Environmental forcing variables

Organisms take up energy and matter from the environment and allocate them into processes leading to growth and reproduction through the enhancement of individual fitness (Brown et al., 2004). Effects of an environmental forcing variable such as temperature are incorporated as a correction factor based on the Arrhenius expression $TC = \exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right)$, where T_A stands for the Arrhenius temperature, T_{ref} for the reference temperature and T for environmental temperature. The effect of food availability is instead accounted by a Type II Holling's functional response $f = \frac{X}{X+K}$ (Holling, 1959), where X represent the environmental food concentration and K the half-saturation coefficient. Simulations with *M. galloprovincialis* (Sarà et al., 2011; Giacoletti et al., 2018; Mangano et al., 2019, 2023; Monaco et al., 2019; see Table 1 for the full parameters set) were performed considering two forcing variables: sea surface temperatures (SST) and chlorophyll-a (CHL-a) concentration (as a proxy for food availability; Thomas et al., 2011; Petersen et al., 2019). Current simulations were spatially contextualized in the Mediterranean sea and restricted over a depth range from 0 to 50 m below sea level (Fig. S2), by using EMODnet bathymetry data (<http://www.emodnet-hydrography.eu/>). Daily SSTs (spatial resolution 0.1°; [c.a. 11 km]) and CHL-a (same resolution) relative to the RCP 4.5 and 8.5 IPCC scenarios (obtained from CERES and TAPAS 2017 projects; Supplementary Figs. S4–S5) were divided into five time-intervals of four years (2006–2010; 2016–2020; 2026–2030; 2036–2040 and 2046–2050). These datasets derive from the POLCOM model and contain the outputs of regionally downscaled projections for European seas generated using coupled ERSEM 15.06 hydrodynamic-biogeochemical models (Butenschön et al., 2016). In order to perform simulation on hourly time-steps each daily datum was repeated twenty-four times through the R software (R Core Team, 2023) generating a vector feature class of 1536 cells (0.1° x 0.1° [c.a. 121 km²]) covering a total surface of 185,856 km². The polygon was then restricted according to the FAO GFCM Mediterranean sub regions (Supplementary Fig. S2) and to the Economic Exclusive Zones (EEZs; Flanders Marine Institute, 2014; Supplementary Fig. S3) in order to allow a fine tailoring of results across the nineteen Mediterranean countries.

Table 1

DEB parameters for *Mytilus galloprovincialis* (1 = Monaco et al., 2019; 2 = FAO, 2009).

Symbol	Description	Units	<i>Mytilus galloprovincialis</i>	
			Value	Ref
δ_M	Shape coefficient	–	0.2133	1
$\{j_{x_m}\}$	Maximum surface area-specific ingestion rate	$J \text{ cm}^{-2} \text{ h}^{-1}$	10.62	1
ae	Assimilation efficiency	–	0.73	1
X_K	Saturation coefficient	$g \text{ l}^{-1}$	0.91	1
$[E_G]$	Volume-specific cost of growth	$J \text{ cm}^3$	5367	1
$[E_m]$	Maximum storage density	$J \text{ cm}^3$	2713	1
$[p_M]$	Volume-specific maintenance cost	$J \text{ cm}^{-3} \text{ h}^{-1}$	0.83	1
κ	Fraction of utilized energy spent on maintenance and growth	–	0.85	1
κ_r	Reproduction efficiency	–	0.95	1
T_A	Arrhenius temperature	$^{\circ}\text{K}$	5800	1
T_L	Lower boundary of tolerance range	$^{\circ}\text{K}$	275	1
T_H	Upper boundary of tolerance range	$^{\circ}\text{K}$	296	1
T_{AL}	Rate of decrease at lower boundary	$^{\circ}\text{K}$	45,430	1
T_{AH}	Rate of decrease at upper boundary	$^{\circ}\text{K}$	31,376	1
Zero-variate data used for modelling				
Symbol	Description	Units	Value	Ref
L_s	Length at seeding	cm	2	2
V_s	Structural volume at seeding	cm^3	Computed	–

2.3. Modelling strategy to investigate the effects of aquaculture practices

The rationale of this mechanistic exercise consists in exploiting the mechanistic power of the DEB model to estimate the detrimental potential of hydroid's fragments due to cage cleaning operations, that as mentioned before, causes severe gill injuries in farmed bivalves impairing two fundamental functions: the respiration and the feeding rate. Thus, our modelling strategy adopted to simulate the potential effects of fragments was through the tweaking of some DEB parameters as explained below in order to sensitively capture the magnitude of fragments' effects. Accordingly, we exploited findings from Bosch-Belmar et al. (2022) to investigate and compare the long-term effects with the short-term impairment of functional traits recorded in that companion study. To do it, recorded effects were applied on mussel's energetic maintenance costs (as expressed by the DEB $[p_M]$ parameter and estimated as a metabolic extra-cost as measured by oxygen consumption) and on food intake (as expressed by the Holling's functional response). We introduced the measured effect by tweaking the $[p_M]$ (Giacoletti et al., 2018) and the Holling f parameter in a spatially-contextualized DEB model, to investigate the potential long-term implications of aquaculture cleaning practices. Thus, we ran 1536 models, pixel-by-pixel for each RCP scenario and for each treatment (Control = CTRL and *Pennaria disticha* = PEN; TOT = 6144), simulating the presence of an Integrated Multi-Trophic Aquaculture (IMTA; Sarà et al., 2012; Sarà et al., 2018c; Mangano et al., 2019, 2023) determining a trophic enrichment in terms of chlorophyll-a (from 1 to $2.0 \mu\text{g l}^{-1}$, according to Sarà et al., 2011). The comparison of both RCP scenarios' results was used to investigate the effect of Climate-Change, while the effect of PEN was determined by comparing results of PEN and of CTRL simulations. A vector of effect on $[p_M]$ and f parameters respectively were built and applied following the effect size from Bosch-Belmar et al. (2022) (reported in Supplementary, Fig. S1), simulating the following cleaning operations calendar: 1 event on May, 3 on June, 4 on July and August, 3 on September and 1 on October based on common in situ net cleaning schedule from western Mediterranean marine aquaculture facilities (Bosch-Belmar personal communication).

3. Results

3.1. Effect at a regional scale

At a basin level our simulations at first investigated the effect of Climate Change (hereafter: CC) on mussel farming by comparing results from controls (CTRL) of both investigated Representative Concentration Pathways scenarios (RCP 4.5 and 8.5). The FT-DEB model generated outcomes in terms of: i) maximum total shell length (TL); ii) maximum wet weight (TW); iii) cumulative reproductive output (EGGS) and iv) time to reach the commercial size (TTCS). In particular, even if a positive trend is generally highlighted in Fig. 1, the more extreme (RCP 8.5) scenario did not show a marked effect on mussels' TL and TTCS (Fig. 1 and Table 2) if compared to the intermediate (RCP 4.5) scenario. The highest recorded average TL was of 11.35 cm, corresponding to a TW of 19.18 g and ~ 22 million EGGS, while the lowest average TTCS was of 366 days (Supplementary Table S2; CTRL, RCP 4.5). TW was characterized by a + 2.59 % increase under RCP 8.5 in 2026–2030 followed by a – 2.29 % decrease in the next period (2036–2040), while no effect was recorded by the last period. EGGS were positively affected by + ~ 5 % in 2026–2030 and by + ~ 2.4 % in 2046–2050 by RCP 8.5 scenario, while a – 2.8 % on EGGS was recorded in 2036–2040. The average predicted EGGS ranged between ~19 and ~ 22 million in four years (Supplementary Table S2). The simulated effect of CC on PEN organisms resulted of the same order of magnitude. A second level of investigation involved the effect of PEN on mussel farming, predicting a positive effect of PEN on all traits, with the less pronounced effect related to TL (from +1.72 % of 2006–2010 to +1.59 % of 2046–2050), a more remarkable effect on TW (from +5.17 % of 2006–2010 to +4.97 % of 2046–2050) and even more noticeable effect on EGGS (ranging from +7.76 % of 2006–2010 to +7.51 % of 2046–2050). TTCS resulted positively affected by PEN showing a – 1.8 % reduction. TL ranged between 11.25 and 11.54 cm, TW between 18.5 and 20.15 g, EGGS between ~20 and ~ 24 million, while TTCS between 360 and 376 days (Supporting Table S2). Our simulation did not highlight any remarkable difference between the two RCP scenarios.

3.2. Effect at a sector level

A positive trend is highlighted in Figs. 2 and 3, and even here RCP 8.5 did not show a marked effect of CC on mussels' LH traits (Table 3). Our simulations highlighted a positive effect of PEN on all traits (Figs. 2 and 3; Table 3). Most affected traits resulted in order: TL (from +1.49 to +1.68 %), TTCS (from –1.68 to –1.86 %), TW (from +4.64 to +5.25 %) and EGGS (from +6.79 to +7.84 %). The most affected sectors resulted in order: the western (Wmed), eastern (Emed), central (Cmed) Mediterranean and the Adriatic sea (Adr). Adr resulted for some periods (2016–2020 and 2026–2030) more affected than Cmed and Emed (with particular regards to TW and EGGS) (Figs. 2c, d and 3a, b; Table 3). Fig. 3c and d instead showed Emed as the most affected sector (in terms of TTCS) followed by Cmed, Wmed and Adr. In detail PEN is predicted to affect TL from +0.17 to +0.19 cm, TW from +0.87 to +1.05 g, EGGS from + ~ 1.4 to + ~ 1.9 million, and TTCS from ~ – 6 to ~ – 7 days among all sectors (Supplementary Table S3).

3.3. Effect at country level

CC did not show a marked effect on mussels' LH traits (Table 4), while our simulations highlighted a general positive effect of PEN on all traits: in order TL (from +1.38 to +1.9 %), TTCS (from –1.41 to –2.41 %), TW (from +4.32 to +6.03 %) and EGGS (from +6.98 to +9.44 %) when compared to CTRL (Figs. 4 and 5; Table 5). Slovenia (all LHs), Syria (all LHs), Montenegro (all LHs), Lebanon (in terms of TL, TW, EGGS) and Malta (in terms of TL and TW) were included among the five most influenced countries. The comparison of 2016–2020 and 2046–2050 periods highlighted a slightly negative temporal trend for

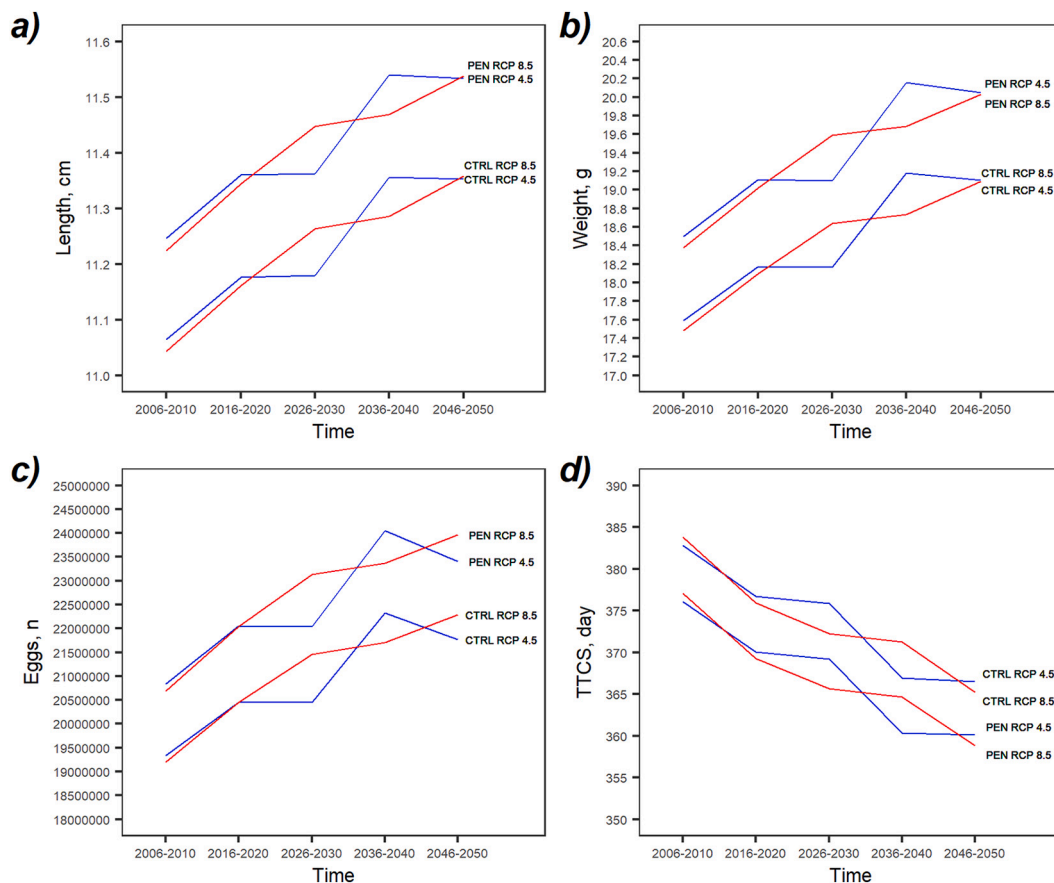


Fig. 1. Results in terms of a) Total Length (Length, cm), b) Total Wet Weight (Weight, g), c) Cumulative Eggs (Eggs, n) and d) Time To Reach the Commercial Size (TTCS, day) relative to CTRL and PEN on both RCP 4.5 and 8.5 scenarios for the Mediterranean sea.

Table 2

Percentage differences between RCP scenarios and between Control (CTRL) and *Pennaria* (PEN) simulations in terms of average Total Length (TL, cm), Total Wet Weight (TW, g), Cumulative Eggs (EGGS, n) and Time To Commercial Size (TTCS, day) for the Mediterranean sea.

Percentage effect of temperature								
Time	RCP 8.5 vs 4.5 (CTRL)				RCP 8.5 vs 4.5 (PEN)			
	TL	TW	EGGS	TTCS	TL	TW	EGGS	TTCS
2006–2010	-0.18	-0.63	-0.69	0.25	-0.27	-0.65	-0.71	0.26
2016–2020	-0.18	-0.39	0.00	-0.22	-0.18	-0.47	-0.05	-0.21
2026–2030	0.72	2.59	4.93	-0.97	0.79	2.57	4.93	-0.97
2036–2040	-0.62	-2.29	-2.81	1.18	-0.61	-2.33	-2.83	1.20
2046–2050	0.09	-0.05	2.39	-0.35	0.09	-0.10	2.37	-0.36

Percentage effect of <i>Pennaria</i>								
Time	PEN vs CTRL (RCP 4.5)				PEN vs CTRL (RCP 8.5)			
	TL	TW	EGGS	TTCS	TL	TW	EGGS	TTCS
2006–2010	1.72	5.17	7.76	-1.75	1.63	5.15	7.74	-1.75
2016–2020	1.61	5.17	7.80	-1.78	1.61	5.08	7.74	-1.77
2026–2030	1.61	5.12	7.75	-1.78	1.69	5.10	7.76	-1.78
2036–2040	1.58	5.06	7.71	-1.79	1.59	5.02	7.69	-1.77
2046–2050	1.59	4.97	7.51	-1.75	1.58	4.92	7.49	-1.76

some countries (Supplementary Figs. S16–S17): Slovenia and Croatia (TL and TW); Albania, Slovenia, France and Spain (EGGS); Slovenia, Croatia, Libya, Italy, France and Spain (TTCS).

4. Discussion

Present integrated mechanistic approach model the alteration of

individual functional traits, represented here by oxygen consumption and food intake (as reported by Bosch-Belmar et al., 2022). This investigation spans a large spatial and temporal scale to assess the effects on mussel's performances resulting from cage cleaning operations and the subsequent dispersal of *Pennaria disticha* fragments dispersal at farm level.

Looking at the effect-size representation (Supplementary Fig. S1a)

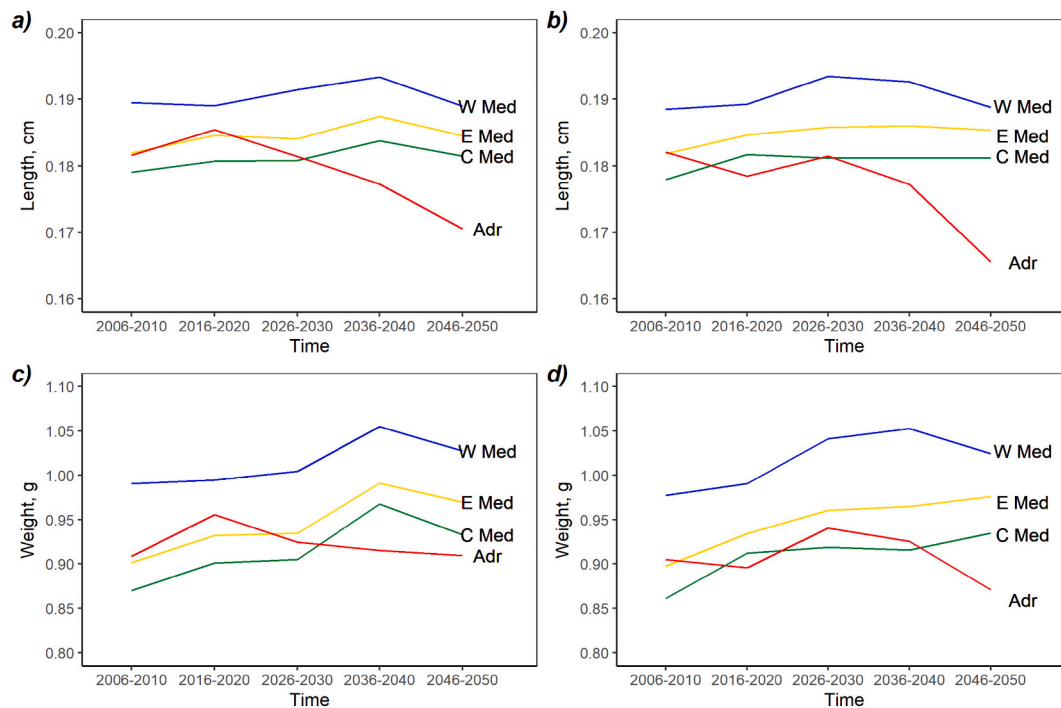


Fig. 2. Average differences (PEN - CTRL) for each of the four GFCM Mediterranean sectors in terms of Total Length (Length, cm) and Total Wet Weight (Weight, g) relative to both RCP 4.5 and 8.5 scenarios.

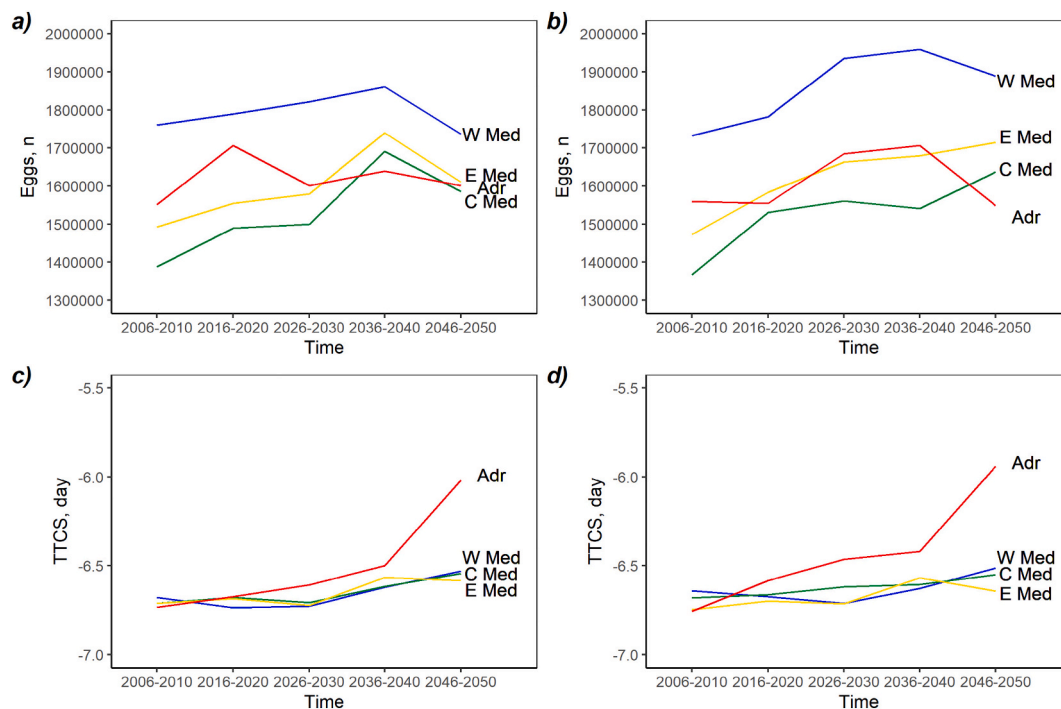


Fig. 3. Average differences (PEN - CTRL) for each of the four GFCM Mediterranean sectors in terms of Cumulative Eggs (Eggs, n) and Time To Reach the Commercial Size (TTCS, day) relative to both RCP 4.5 and 8.5 scenarios.

respiration and clearance rates modulates with a short fist part dominated by higher RRs, accompanied by lower CRs, followed by a longer part characterized by lower RRs, that translates in lower metabolic costs and higher food ingestion. The recorded short term-effects, applied on mussel's DEB parameters, generate on a long temporal scale different results, that were not quantifiable within a short experimental session.

Current DEB outcomes showed that increasing temperatures within

predicted CC scenarios will determine a general Mediterranean positive trend of both growth (TL, TW) and fecundity (EGGS), coupled with a general shortening of cultivation time (TTCS) for the more extreme (RCP 8.5) scenario that, however, did not show a marked effect on mussels' LH traits if compared to the intermediate (RCP 4.5) scenario. As metabolic rates of ectotherms are known to be strictly dependent on body temperature (Brown et al., 2004; Sarà et al., 2012), the expected increased

Table 3

Percentage differences between *Pennaria* and Control simulations in terms of average Total Length (TL, cm), Cumulative Eggs (EGGS, n) and Time To Commercial Size (TTCS, day) per each GFCM Mediterranean sector.

Time	Sector	RCP	TL	TW	EGGS	TTCS	RCP	TL	TW	EGGS	TTCS
2006–2010	Wmed	4.5	1.67	5.24	7.81	−1.82	8.5	1.67	5.22	7.78	−1.8
2016–2020	Wmed	4.5	1.66	5.22	7.79	−1.84	8.5	1.67	5.23	7.78	−1.83
2026–2030	Wmed	4.5	1.68	5.25	7.82	−1.86	8.5	1.68	5.24	7.84	−1.87
2036–2040	Wmed	4.5	1.68	5.24	7.84	−1.86	8.5	1.67	5.22	7.79	−1.85
2046–2050	Wmed	4.5	1.64	5.13	7.35	−1.85	8.5	1.64	5.11	7.62	−1.85
2006–2010	Cmed	4.5	1.64	5.12	7.63	−1.72	8.5	1.63	5.1	7.56	−1.71
2016–2020	Cmed	4.5	1.64	5.11	7.66	−1.74	8.5	1.64	5.12	7.62	−1.75
2026–2030	Cmed	4.5	1.63	5.12	7.64	−1.75	8.5	1.63	5.09	7.72	−1.75
2036–2040	Cmed	4.5	1.63	5.08	7.57	−1.79	8.5	1.63	5.09	7.59	−1.74
2046–2050	Cmed	4.5	1.62	5.05	7.52	−1.75	8.5	1.61	5.03	7.56	−1.76
2006–2010	Emed	4.5	1.65	5.15	7.69	−1.75	8.5	1.65	5.16	7.68	−1.75
2016–2020	Emed	4.5	1.66	5.18	7.71	−1.77	8.5	1.66	5.18	7.71	−1.79
2026–2030	Emed	4.5	1.65	5.16	7.7	−1.78	8.5	1.65	5.16	7.72	−1.8
2036–2040	Emed	4.5	1.65	5.16	7.62	−1.79	8.5	1.65	5.14	7.66	−1.77
2046–2050	Emed	4.5	1.63	5.08	7.38	−1.79	8.5	1.63	5.1	7.6	−1.82
2006–2010	Adr	4.5	1.63	5.1	7.6	−1.8	8.5	1.64	5.1	7.63	−1.8
2016–2020	Adr	4.5	1.64	5.13	7.69	−1.82	8.5	1.6	4.98	7.43	−1.78
2026–2030	Adr	4.5	1.61	5.03	7.46	−1.8	8.5	1.6	5	7.46	−1.78
2036–2040	Adr	4.5	1.57	4.89	7.25	−1.8	8.5	1.56	4.85	7.29	−1.78
2046–2050	Adr	4.5	1.49	4.64	6.79	−1.68	8.5	1.45	4.51	6.76	−1.66

occurrence of extreme thermal events due to climate change will undoubtedly impact the future growth of this sector. This influence will affect species' performance, leading to repercussions on overall production and yield (Rosa et al., 2012). Several studies applied DEB models to disentangle the effect of CC on growth and reproduction of different bivalves (Monaco and McQuaid, 2018, 2019; Cheng et al., 2018; Chowdhury et al., 2018; Steeves et al., 2018; Mangano et al., 2019, 2023; Tan et al., 2021). However, a mechanistic investigation that integrates eco-physiological data to predict the effects of aquaculture practices on *M. galloprovincialis* cultured in an IMTA context, has never been performed before. Our main results suggest that DEB is useful in helping the near future of the aquaculture sector, especially for disentangling the effect experimentally-measurable human activities, such as the one investigated in the present study, from that of CC.

The effect of PEN at a Mediterranean scale follows the same positive trend of CC and potentiates the effect of increasing temperatures on mussels' performance in a synergistic combination (sensu Gunderson et al., 2016; Sarà et al., 2018a, 2018b). Looking deeply into the four GFCM Mediterranean sectors, DEB outcomes highlights the same trend. In particular, a peak in most of the outcomes was identified in correspondence of the 2036–2040 period and is not correlated to any temperature or chlorophyll variation (see Supplementary Figs. S4 to S15). When zooming at a single country scale, DEB outcomes showed Lebanon, Malta, Montenegro, Syria and Slovenia coasts may be more influenced as suggested for the main performance aquaculture traits. Similarly, TTCS was lower in Albania, Israel, Montenegro, Slovenia and Spain, while Spain, Italy and France appear to be in line with the above cited countries for all LHs except for TTCS. A negative trend was not identifiable from our results at a basin scale, and neither at a sector scale, except for the Adriatic (all traits) and for the Western Mediterranean one (TL of both scenarios and EGGS of RCP 4.5) highlighting the importance of investigating at such a small scale. These results solely reflect the impact of environmental forcing variables on energy acquisition and fluxes within the model, as it does not consider any other environmental parameters. This is why the spatial translation of FT-DEB outcomes can easily lead to identify site and species-specific management strategies, representing a useful tool to pursue the sustainable development of Mediterranean aquaculture and test the effect of husbandry practices.

An interesting strategy is represented by the integration of FT-DEB with the current ecosystem-approach to aquaculture (FAO, 2010), that emphasizes the need to integrate aquaculture with other sectors promoting conservation and sustainability in order to not alter ecosystem functioning and its related services (Lacoste et al., 2020). Further, it

could represent an important tool when selecting species to be cultivated in an IMTA context using a biological habitat suitability indicator as represented by mechanistic predictions. This particular field of aquaculture was tested in Mangano et al. (2019, 2023) as a potential management solution able to provide tailored management measures based on ecological and mechanistic principles. The use of FT-DEB modelling for an aquaculture site selection was already developed by Giacoletti et al. (2021), with the purpose of identifying potential suitable zones for aquaculture development, part of an adaptive process able to support decision making within the integrated coastal zone management (ICZM) process. The main limitation of such a modelling approach consist in the resolution and amount of environmental forcing variables needed to run the models, on species parameterisation and on the computational effort needed to test different scenarios. However, unless the effort needed in gathering and processing high resolution environmental data FT-DEB models offer an impressive improvement of the temporal and spatial resolution of simulations, in order to feed regional management strategies with reliable outcomes. This tool has so far proven to be extremely powerful and reliable and its integration with local socio-economic layers could support policymakers in developing management plans that are adaptable under future climate change scenarios (IPCC, 2019).

5. Conclusions

The present study results, as outputs of a validated mechanistic modelling approach, can represent a useful quantitative risk indicator that can be discussed among scientists, policy makers and stakeholders for the evaluation of existing or new management plans across different spatial and temporal scales. Further, through the integration of biological traits, it permits to test the effect of current CC processes or specific husbandry practices, to develop adaptation and mitigation solutions at biologically- and ecologically-relevant spatio-temporal scales. Even if the purpose of the present study was not to analyse the potential economic implications induced by such stressors our tool can help the resilience of future economies to face current processes of CC.

Code availability

Codes for model running and mapping are available from the corresponding author on reasonable request.

Table 4

Percentage differences between *Pennaria* and Control simulations in terms of average Total Length (TL, cm), Wet Weight (TW, g), Cumulative Eggs (EGGS, n) and Time To Commercial Size (TTCS, day) per each Mediterranean country.

Country	Time	RCP	TL	TW	EGGS	TTCS	RCP	TL	TW	EGGS	TTCS
Albania	2006–2010	4.5	1.69	5.25	7.73	−1.93	8.5	1.68	5.27	7.76	−1.91
Albania	2016–2020	4.5	1.71	5.34	7.97	−1.94	8.5	1.70	5.27	7.75	−1.99
Albania	2026–2030	4.5	1.70	5.30	7.83	−1.98	8.5	1.68	5.28	7.85	−1.91
Albania	2036–2040	4.5	1.73	5.38	7.02	−2.03	8.5	1.72	5.34	7.98	−2.00
Albania	2046–2050	4.5	1.69	5.23	7.29	−1.88	8.5	1.69	5.25	7.67	−1.99
Algeria	2006–2010	4.5	1.59	5.04	7.46	−1.74	8.5	1.59	5.03	7.42	−1.68
Algeria	2016–2020	4.5	1.59	5.01	7.47	−1.81	8.5	1.60	5.06	7.58	−1.84
Algeria	2026–2030	4.5	1.60	5.03	7.40	−1.82	8.5	1.61	5.05	7.61	−1.73
Algeria	2036–2040	4.5	1.60	5.06	8.60	−1.86	8.5	1.61	5.05	7.52	−1.79
Algeria	2046–2050	4.5	1.58	5.00	7.45	−1.80	8.5	1.62	5.06	7.46	−1.79
Croatia	2006–2010	4.5	1.59	4.99	7.49	−1.75	8.5	1.61	5.03	7.53	−1.76
Croatia	2016–2020	4.5	1.59	4.97	7.46	−1.72	8.5	1.53	4.76	7.08	−1.69
Croatia	2026–2030	4.5	1.57	4.87	7.26	−1.73	8.5	1.55	4.85	7.27	−1.73
Croatia	2036–2040	4.5	1.48	4.61	6.93	−1.65	8.5	1.47	4.57	6.92	−1.65
Croatia	2046–2050	4.5	1.38	4.32	6.48	−1.60	8.5	1.33	4.13	6.31	−1.53
Cyprus	2006–2010	4.5	1.62	5.10	7.62	−1.79	8.5	1.63	5.10	7.54	−1.69
Cyprus	2016–2020	4.5	1.64	5.17	7.76	−1.98	8.5	1.64	5.15	7.82	−1.88
Cyprus	2026–2030	4.5	1.65	5.12	7.72	−1.86	8.5	1.61	5.06	7.59	−1.90
Cyprus	2036–2040	4.5	1.67	5.18	7.88	−1.95	8.5	1.67	5.17	7.83	−1.89
Cyprus	2046–2050	4.5	1.63	5.10	7.72	−1.83	8.5	1.61	5.10	7.60	−1.89
Egypt	2006–2010	4.5	1.64	5.12	7.66	−1.67	8.5	1.64	5.13	7.65	−1.67
Egypt	2016–2020	4.5	1.66	5.18	7.75	−1.72	8.5	1.65	5.17	7.74	−1.71
Egypt	2026–2030	4.5	1.64	5.11	7.68	−1.71	8.5	1.64	5.13	7.72	−1.72
Egypt	2036–2040	4.5	1.64	5.14	7.70	−1.74	8.5	1.64	5.11	7.66	−1.72
Egypt	2046–2050	4.5	1.62	5.05	7.59	−1.74	8.5	1.64	5.11	7.64	−1.75
France	2006–2010	4.5	1.73	5.37	8.17	−1.91	8.5	1.70	5.31	8.01	−1.84
France	2016–2020	4.5	1.66	5.22	7.77	−1.83	8.5	1.64	5.17	7.69	−1.85
France	2026–2030	4.5	1.71	5.38	8.14	−1.87	8.5	1.73	5.39	8.09	−1.94
France	2036–2040	4.5	1.67	5.22	7.55	−1.85	8.5	1.66	5.22	7.75	−1.84
France	2046–2050	4.5	1.63	5.08	7.14	−1.76	8.5	1.63	5.07	7.70	−1.84
Greece	2006–2010	4.5	1.66	5.20	7.73	−1.82	8.5	1.67	5.21	7.73	−1.85
Greece	2016–2020	4.5	1.69	5.27	7.83	−1.88	8.5	1.68	5.25	7.78	−1.91
Greece	2026–2030	4.5	1.68	5.24	7.72	−1.87	8.5	1.67	5.22	7.75	−1.86
Greece	2036–2040	4.5	1.69	5.27	7.60	−1.90	8.5	1.69	5.25	7.80	−1.88
Greece	2046–2050	4.5	1.65	5.12	6.92	−1.87	8.5	1.62	5.06	7.47	−1.84
Israel	2006–2010	4.5	1.67	5.26	7.98	−1.88	8.5	1.67	5.21	7.88	−1.90
Israel	2016–2020	4.5	1.64	5.15	7.67	−1.65	8.5	1.67	5.26	7.71	−1.67
Israel	2026–2030	4.5	1.66	5.24	7.97	−1.94	8.5	1.69	5.30	7.98	−1.90
Israel	2036–2040	4.5	1.69	5.23	7.82	−1.74	8.5	1.68	5.22	7.67	−1.72
Israel	2046–2050	4.5	1.62	4.98	7.56	−2.01	8.5	1.62	5.03	7.63	−1.99
Italy	2006–2010	4.5	1.65	5.16	7.66	−1.82	8.5	1.65	5.15	7.67	−1.81
Italy	2016–2020	4.5	1.66	5.18	7.74	−1.85	8.5	1.64	5.12	7.61	−1.81
Italy	2026–2030	4.5	1.65	5.14	7.60	−1.85	8.5	1.64	5.10	7.58	−1.83
Italy	2036–2040	4.5	1.63	5.07	7.47	−1.84	8.5	1.62	5.04	7.52	−1.83
Italy	2046–2050	4.5	1.57	4.89	7.05	−1.78	8.5	1.55	4.84	7.18	−1.76
Lebanon	2006–2010	4.5	1.63	5.02	7.33	−1.75	8.5	1.61	5.03	7.51	−1.60
Lebanon	2016–2020	4.5	1.81	5.59	8.54	−1.74	8.5	1.77	5.55	8.55	−1.85
Lebanon	2026–2030	4.5	1.61	5.05	7.56	−1.64	8.5	1.62	5.00	7.37	−1.69
Lebanon	2036–2040	4.5	1.72	5.47	8.39	−1.82	8.5	1.81	5.62	8.67	−1.77
Lebanon	2046–2050	4.5	1.50	4.74	7.07	−1.41	8.5	1.53	4.80	7.15	−1.75
Libya	2006–2010	4.5	1.64	5.12	7.63	−1.69	8.5	1.62	5.06	7.54	−1.66
Libya	2016–2020	4.5	1.63	5.08	7.58	−1.72	8.5	1.61	5.04	7.55	−1.71
Libya	2026–2030	4.5	1.62	5.06	7.60	−1.73	8.5	1.60	5.01	7.50	−1.72
Libya	2036–2040	4.5	1.58	4.95	7.42	−1.74	8.5	1.59	4.96	7.43	−1.68
Libya	2046–2050	4.5	1.59	4.96	7.45	−1.71	8.5	1.58	4.92	7.42	−1.71
Malta	2006–2010	4.5	1.67	5.24	7.66	−1.56	8.5	1.67	5.27	7.69	−1.62
Malta	2016–2020	4.5	1.63	5.12	7.77	−1.52	8.5	1.68	5.24	7.74	−1.42
Malta	2026–2030	4.5	1.68	5.31	7.93	−1.69	8.5	1.69	5.24	7.92	−1.59
Malta	2036–2040	4.5	1.63	5.15	7.80	−1.54	8.5	1.66	5.21	7.93	−1.45
Malta	2046–2050	4.5	1.72	5.35	8.00	−1.84	8.5	1.71	5.37	8.16	−1.64
Montenegro	2006–2010	4.5	1.74	5.57	8.79	−1.96	8.5	1.80	5.55	8.76	−1.75
Montenegro	2016–2020	4.5	1.71	5.39	8.18	−1.89	8.5	1.71	5.37	8.26	−1.69
Montenegro	2026–2030	4.5	1.85	5.69	9.00	−1.89	8.5	1.77	5.67	8.80	−1.78
Montenegro	2036–2040	4.5	1.72	5.41	8.31	−1.60	8.5	1.70	5.27	8.14	−1.62
Montenegro	2046–2050	4.5	1.83	5.72	9.04	−1.91	8.5	1.89	5.75	9.11	−2.04
Morocco	2006–2010	4.5	1.61	5.10	7.57	−1.57	8.5	1.58	5.03	7.29	−1.50
Morocco	2016–2020	4.5	1.57	5.00	7.52	−1.56	8.5	1.56	5.01	7.44	−1.61
Morocco	2026–2030	4.5	1.59	5.06	7.64	−1.55	8.5	1.62	5.06	7.68	−1.74
Morocco	2036–2040	4.5	1.62	5.00	7.46	−1.64	8.5	1.60	5.04	7.49	−1.60
Morocco	2046–2050	4.5	1.64	5.10	7.60	−1.65	8.5	1.63	5.13	7.65	−1.66
Slovenia	2006–2010	4.5	1.90	5.91	9.15	−2.11	8.5	1.89	5.92	9.13	−2.10
Slovenia	2016–2020	4.5	1.90	6.03	9.44	−2.35	8.5	1.76	5.52	8.69	−1.99
Slovenia	2026–2030	4.5	1.67	5.40	8.44	−2.02	8.5	1.86	5.89	9.16	−2.04

(continued on next page)

Table 4 (continued)

Country	Time	RCP	TL	TW	EGGS	TTCS	RCP	TL	TW	EGGS	TTCS
Slovenia	2036–2040	4.5	1.67	5.18	8.01	-2.02	8.5	1.44	4.56	6.92	-1.26
Slovenia	2046–2050	4.5	1.44	4.56	7.32	-1.98	8.5	1.05	3.18	5.01	-1.71
Spain	2006–2010	4.5	1.68	5.27	7.89	-1.83	8.5	1.69	5.26	7.92	-1.84
Spain	2016–2020	4.5	1.72	5.35	8.10	-1.92	8.5	1.72	5.37	8.08	-1.88
Spain	2026–2030	4.5	1.71	5.31	7.94	-1.87	8.5	1.70	5.27	7.94	-1.87
Spain	2036–2040	4.5	1.72	5.35	7.94	-1.93	8.5	1.71	5.36	8.10	-1.95
Spain	2046–2050	4.5	1.66	5.18	7.38	-1.84	8.5	1.62	5.06	7.66	-1.85
Syria	2006–2010	4.5	1.89	5.75	8.83	-2.14	8.5	1.83	5.71	8.76	-2.18
Syria	2016–2020	4.5	1.63	5.14	7.81	-1.85	8.5	1.65	5.22	7.88	-2.08
Syria	2026–2030	4.5	1.87	5.79	8.85	-2.14	8.5	1.82	5.66	8.69	-2.24
Syria	2036–2040	4.5	1.66	5.14	7.50	-1.87	8.5	1.66	5.22	7.66	-2.05
Syria	2046–2050	4.5	1.85	5.78	8.94	-2.41	8.5	1.82	5.75	8.87	-2.53
Tunisia	2006–2010	4.5	1.63	5.10	7.62	-1.71	8.5	1.63	5.10	7.53	-1.70
Tunisia	2016–2020	4.5	1.63	5.10	7.68	-1.72	8.5	1.64	5.13	7.64	-1.74
Tunisia	2026–2030	4.5	1.63	5.12	7.64	-1.74	8.5	1.64	5.12	7.86	-1.74
Tunisia	2036–2040	4.5	1.64	5.12	7.65	-1.79	8.5	1.64	5.12	7.64	-1.74
Tunisia	2046–2050	4.5	1.63	5.09	7.65	-1.75	8.5	1.63	5.10	7.64	-1.78
Turkey	2006–2010	4.5	1.62	5.11	7.64	-1.81	8.5	1.63	5.13	7.64	-1.83
Turkey	2016–2020	4.5	1.59	4.99	7.33	-1.79	8.5	1.61	5.01	7.43	-1.82
Turkey	2026–2030	4.5	1.63	5.14	7.66	-1.77	8.5	1.63	5.13	7.68	-1.90
Turkey	2036–2040	4.5	1.60	5.02	7.42	-1.84	8.5	1.59	5.01	7.35	-1.83
Turkey	2046–2050	4.5	1.61	5.08	7.59	-1.79	8.5	1.62	5.10	7.61	-1.92

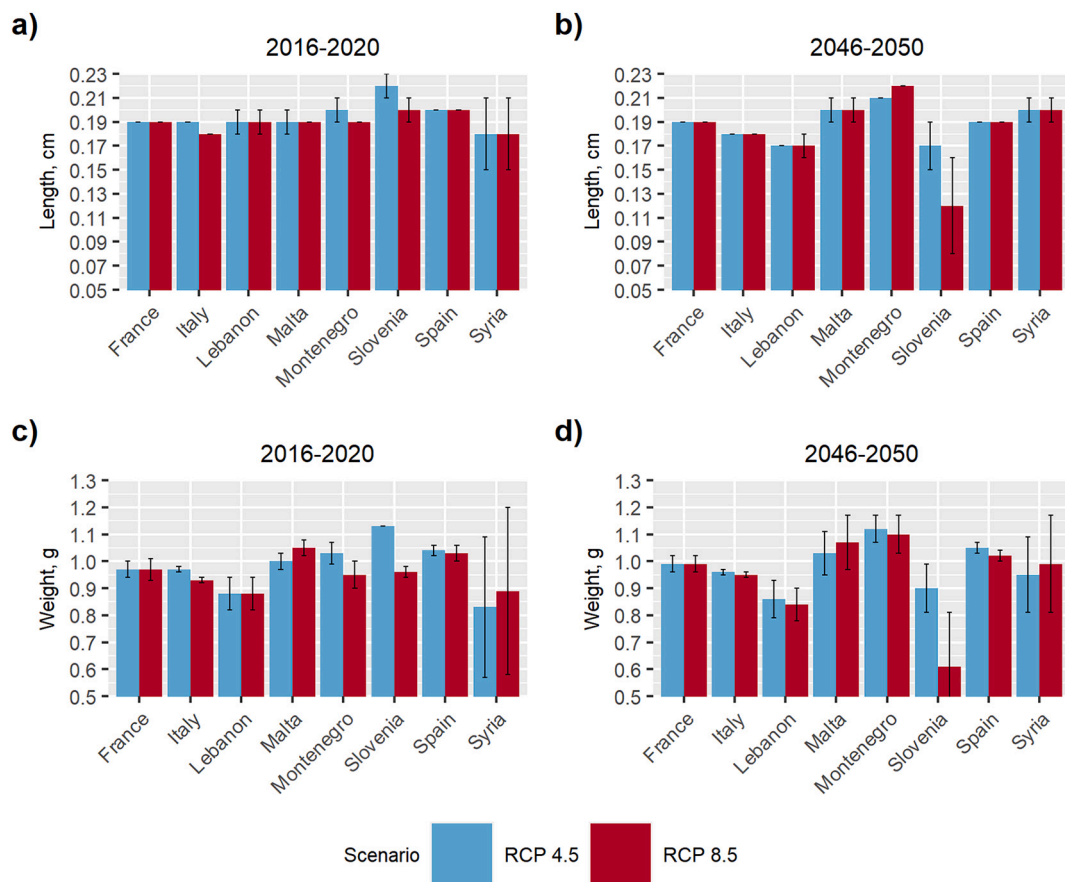


Fig. 4. Average differences (PEN - CTRL) in terms of a), b) Total Length (Length, cm), c), d) Total Wet Weight (Weight, g) relative to both RCP 4.5 and 8.5 scenarios and two selected periods (2016–2020 present, and 2046–2050 last period considered in this study). The figure is relative to the five most influenced countries plus the three main EU28 producer (Spain, Italy and France).

CRedit authorship contribution statement

A. Giacoletti: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. **M. Bosch-Belmar:** Conceptualization, Writing – original draft, Writing – review & editing. **M.C. Mangano:**

Conceptualization, Writing – review & editing. **M.F. Tantillo:** Visualization, Writing – review & editing. **G. Sara:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing, Resources. **G. Milisenda:** Conceptualization, Data curation, Funding acquisition, Project administration, Resources, Software, Supervision, Writing – review & editing, Formal analysis.

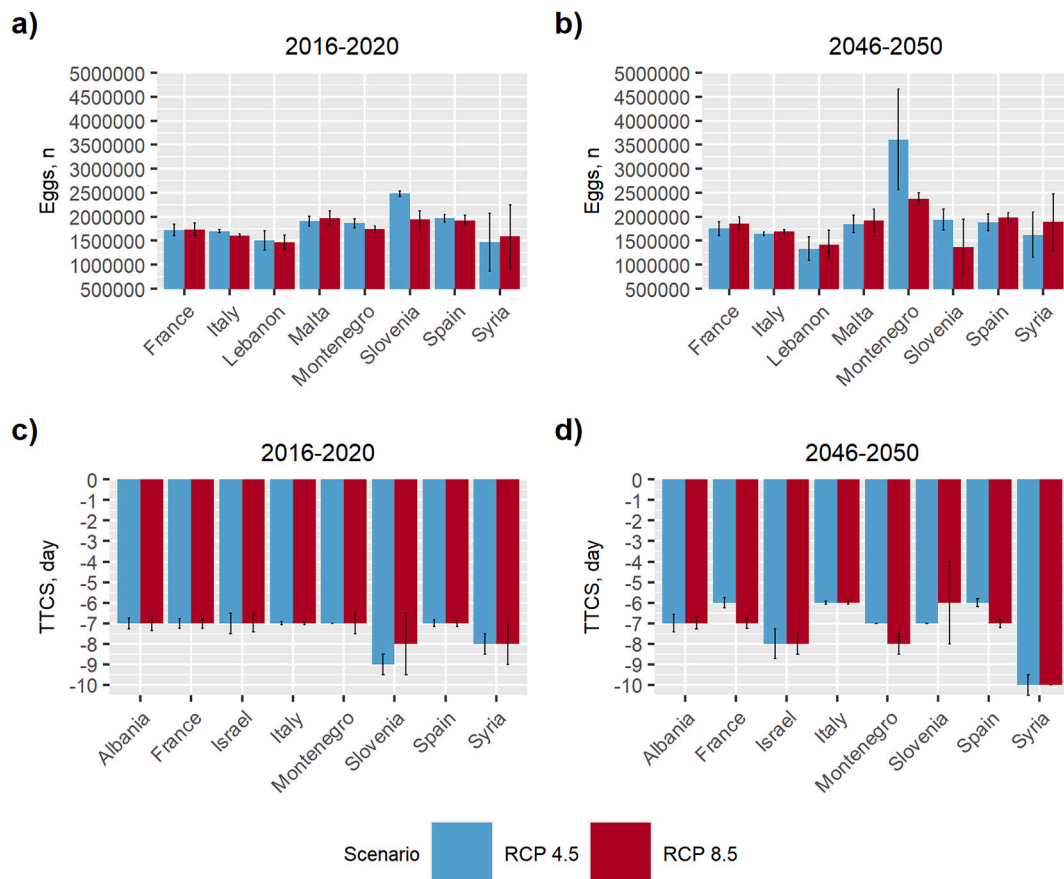


Fig. 5. Average differences (PEN - CTRL) in terms of a), b) Cumulative Eggs (Egg, n) and c), d) Time to Reach the Commercial size (TTCS, day) relative to both RCP 4.5 and 8.5 scenarios and two selected periods (2016–2020 present, and 2046–2050 last period considered in this study). The figure is relative to the five most influenced countries plus the three main EU28 producer (Spain, Italy and France).

Table 5

Effects of *Pennaria* in terms of difference from Control for Total Length (TL, cm), Wet Weight (TW, g), Cumulative Eggs (EGGS, n) and Time To Commercial Size (TTCS, day) among Mediterranean countries in the two considered time periods.

Effects of PEN at a country scale					
Time	RCP	TL (cm)	TW (g)	EGGS (million eggs)	TTCS (day)
2016–2020	4.5	+0.18 to +0.22	+0.83 to 1.13	+1.4 to +2.5	-6 to -9
	8.5	+0.17 to +0.2	+0.85 to 1.13	+1.4 to +2.1	-5 to -8
2046–2050	4.5	+0.16 to +0.21	+0.85 to +1.13	+1.3 to +3.6	-5 to -10
	8.5	+0.12 to +0.22	+0.61 to 1.16	+1.3 to +2.3	-6 to -10

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 including data for model parametrisation are available on Supplementary information (text and tables). Raw data files are available from the corresponding author on reasonable request.

Acknowledgements

This study was funded by the Italian Minister of the University and Research (MIUR) through the project PRIN MARHES (cod. 2017MHHWBN), and by the FEAMP Campania 2014-2020 project (EMFF - European Maritime and Fisheries Fund).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2024.116167>.

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