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Integration of Meta-Analysis and Modeling of Marine Aquaculture and Biodiversity to Inform Evidence-Based Adaptive Management: A Case Study in the Mediterranean Basin

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ABSTRACT

The impact of marine aquaculture on benthic biodiversity has gained significant attention as a result of the growing need for sustainable food production and the preservation – eventual restoration – of marine ecosystems. This study provides a comprehensive meta-analysis of the impacts of aquaculture on benthic biodiversity in the Mediterranean Sea. This evidence-based synthesis demonstrates that aquaculture facilities have a moderate impact on biodiversity compared to undisturbed areas. The impact of aquaculture is highly context-dependent, varying significantly across different Mediterranean eco-regions, habitat types, and specific environmental conditions. Significant effects were observed in the Eastern Basins, while Central and Western Basins exhibited lower effects. Further, the type of habitat affected the extent of the impact, with soft bottom habitats showing more significant impacts. Interestingly, through a further modeling exercise, the trophic state of farmed species, as well the water temperature emerged as critical factors, with low Chlorophyll-a areas with the highest temperatures exhibiting more severe impacts. These results demonstrate the necessity of tailored, ecosystem-based, and adaptive aquaculture management practices that integrate local environmental conditions when promoting sustainable aquaculture practices. Future research should focus on integrating biodiversity as a response variable to understand and manage the ecological impacts of aquaculture more effectively.

Introduction

Aquaculture and biodiversity are increasingly prominent binomial arguments in global discussions due to their critical roles within the One-Health framework (Stentiford et al. 2020). Both are essential for human well-being, as aquaculture plays a crucial role in the Blue Transformation, and meets the growing global demand for aquatic foods which rely on biodiversity. The Blue Transformation is an approach promoted by the FAO (2022) to make aquatic food systems more sustainable, resilient, and inclusive while ensuring their resilience to climate change. It promotes the sustainable intensification and expansion of aquaculture to meet global demand for aquatic foods based on biodiversity. Aquaculture offers multiple benefits, positioning it as a significant driver in several domains (Garlock et al. 2022): (1) Food Security: with a growing global population, aquaculture provides a means to boost food production and meet the rising demand for fish products, particularly in regions with limited access to animal protein (Belton et al. 2018); (2) Economic Development: aquaculture is closely linked to economic growth, as it generates jobs and income opportunities, especially in coastal and rural communities, thereby contributing to social development (Golden et al. 2021), and (3) Environmental Sustainability (Gephart et al. 2021): when managed sustainably, aquaculture can alleviate pressure on capture fisheries, and aid in the conservation of aquatic ecosystems (e.g., restorative ecology; Mizuta et al.

2023; Overton et al. 2024). The implementation of innovative technologies and concepts, such as recirculating systems, alternative feeds, and restorative aquaculture practices (Alleway et al. 2023; Mangano et al. 2023), has been reported as key-practices reducing the environmental impact of aquaculture while enhancing the value of biodiversity (FAO 2024). Biodiversity, conversely, has been historically perceived as an external commodity, seen primarily in terms of its utilitarian, economic, and trade value (Groombridge 1992; Barbier and Schulz 2001; Fischer et al. 2006). Past research focused primarily on the effects of aquaculture practices on the abiotic environmental components, often neglecting the impacts on local biodiversity, or the direct effects on the seabed habitats (Tsikopoulou et al. 2018, 2021). The prominence gained by biodiversity – thanks to the formalized and operationalized mechanistic links between biodiversity and ecosystem functioning (Isbell et al. 2017) – as a provider of ecosystem services, such as food production (Loreau 2010; Cardinale et al. 2012; Naeem et al. 2016 [1844]; De Bello et al. 2021), was initiated by the Millennium Ecosystem Assessment in 2005. In the context of marine aquaculture, biodiversity of benthic habitats can be perhaps the most reliable and informative indicator of external impacts as a result of its role as the memory of the system, with the intrinsic collective ecological characteristics that integrate long-term ecological changes more effectively than other ecosystem components. The lack of a comprehensive knowledge baseline of the aquaculture effects on benthic habitats is often evident in the variables studied or reviewed over the last two decades, including dissolved oxygen concentrations, nutrient levels, Chlorophyll-a concentrations, fouling composition, phytoplankton composition, water quality, habitat modification, benthic organic loading, disease, and the occurrence of invasive species (Sarà 2007a, 2007b, 2007c; Price et al. 2015; Weitzman 2019; Barrett et al. 2019; Tičina et al. 2020; Zhang et al. 2022; Sakamaki et al. 2022; Bath et al. 2023; Zhu et al. 2023; Zoli et al. 2023).

The main aim this review was to analyze and synthesize existing research on the effects of aquaculture on marine benthic habitat biodiversity, focusing on the Mediterranean Sea as a prominent example and a salient region for the expansion. This aligns with the United Nations Sustainable Development Goals objectives, highlighting an increasingly important role of aquaculture in food security, employment, and economic development, while also reducing pressure on the overexploited wild fish stocks across the basin. In 2021, in the Mediterranean Sea, over 35,000 farms produced approximately 3.3 million tons of aquatic foods, directly employing nearly 350,000 people (FAO 2023). Despite covering only 0.82% of the global ocean surface, the Mediterranean Sea hosts almost 8% of global biodiversity within its complex marine ecosystems (Fanelli et al. 2021). It is particularly susceptible to anthropogenic pressures, with concerns being raised regarding potential ecological consequences of aquaculture operations (FAO 2024). Although previous studies (Kalantzi and Karakassis 2006; Martinez-Garcia et al. 2013) have indicated varying degrees of impacts of aquaculture on benthic biodiversity, here the scientific evidence was collated to create an updated knowledge baseline. Data were subjected to a meta-analysis, aggregating and quantifying findings from numerous studies to provide a more comprehensive and robust understanding of the effects of aquaculture on benthic biodiversity. The meta-analysis methodological approach has been used extensively in environmental and ecosystem assessments of human-caused factors, as it allows integration of overall trends and the identification of factors that may influence the magnitude and direction of human-caused impacts (Sarà 2007a, 2007b, 2007c; Sarà et al. 2018; Mangano and Sarà 2017; Salerno et al. 2021; Mirto et al. 2022; Berlino et al. 2021, 2023). By focusing on several key aspects, including the effects of single-species or multi-species farming, the spatial extent of impacts across distance gradients and the habitat and benthic community level effects, it was possible to disentangle how these effects vary across different sub-basins of the Mediterranean Sea. By extrapolating some regression metrics, it was possible to model the threshold of impacts on benthic biodiversity with the aim to upscale the effects to basin level. The results represent an evidence-based layer to inform sustainable aquaculture practices in the framework of the Blue Transformation and the environmental stewardship in the Mediterranean region and beyond, under a climate resilient management of future practices.

Literature search and data collection

The scientific papers included in our meta-analysis were retrieved performing a literature search using two main literature databases, ISI Web of Knowledge (Web of Science Core Collection package, Clarivate Analytics 2024) and Scopus. Research has been conducted using a complex search string to gather all relevant scientific papers answering the main question of whether marine aquaculture has a role in affecting the biodiversity of benthos habitats (hereafter biodiversity measure outcomes), without applying any

temporal scale restriction, and focusing into the Mediterranean Sea. The search was limited to English language. The designed and applied search string was:

> ("Mediterranean Sea" AND ("farm*" OR "aquaculture" OR "mariculture") AND ("impact*" OR "effect*") AND ("Shannon-Wiener index" OR "Shannon index" OR "species diversity" OR "Margalef index" OR "species richness" OR "Pielou index" OR "evenness" OR "dominance" OR "homogeneity" OR "equitability" OR "abundance" OR "diversity" OR "biomass") AND ("*benth*" OR "*fauna*" OR "seabed" OR "habitat" OR "sediment*"))

By running the selected search strings (final search date 12 September 2024; Table S1; Figure S1) references were collated on a reference manager database (EndNote™, Clarivate 2024), then an automated duplicate searching/removal was performed on the created library. A total of 188 peer-reviewed scientific papers were retrieved and then subject to two runs of screening based on the inclusion criteria and on the presence of the search string main elements (see PRISMA flow diagram in Figure S1, and the screening steps description in Supplementary Materials). It was, *a priori,* decided to select those studies focusing on the effects of fish farming system at sea (with active feeding from the external), by excluding mussel farming activities. In fact, molluscan aquaculture – typically referred as unfed farming system – does not utilize manufactured external source of feeds, like as fishmeal or fish oil which is one of the most recognized and heavily criticized source of aquaculture impacts on the environment (Naylor et al. 2009). Additionally, molluscs provide important ecosystem services (e.g., nutrients assimilation, habitat provision; Smaal et al. 2019; Barrett et al. 2022) by simultaneously showing lowest economics performance and riskiest production levels compared to other forms of aquaculture (Garlock et al. 2022). The final datasets included 33 scientific papers that were considered suitable to perform an effective meta-analysis (Table S3; Figure S1 reporting the adapted PRISMA flow diagram; Moher et al. 2009). Details of the studies included in the meta-analysis (including k = number of case studies) are reported in Table S3.

Calculation of the effect size and analysis

The most common metric used in ecological studies is the Hedges' g statistic (Hedges and Olkin 1985), which is a bias-corrected standardized mean difference between treatments (or impacted) and control groups, divided by the pooled standard deviation (Hedges 1981; Sarà 2007a, 2007b, 2007c; Salerno et al. 2021; Berlino et al. 2021, 2023). Hedges' g weighs cases by their sample size and the inverse of their variance (Borenstein et al. 2021). The Hedges' g value and its variance were calculated for each case study ($k = 457$ total case studies within our dataset) to estimate how biodiversity associated with different bottom habitats can be altered by the presence of aquaculture facilities (i.e., impacted zone) in comparison to an undisturbed area located far from the aquaculture facilities (i.e., control zone). A correction for bias attributed to different sample sizes, as well as pooled standard deviation was applied (see Supplementary Materials). The meta-analyses were conducted using the meta for package for R (Anton et al. 2019). A mixed effects model was generated using the "rma.mv" function which use a Wald-type test to determine statistical significance. A statistical model that included the study identification number (i.e., Id of the study in dataset) and the ecological index measured as random factor to account for heterogeneity (Viechbahuer 2007) and non-independence of results from the same study (Konstantopoulos 2011) was run. The overall effect size of the impact of the aquaculture on biodiversity was estimated. Moreover, to explain potential sources of heterogeneity within the dataset and investigate possible differences in the pooled effect, a subgroup analysis including the following categorical fixed factors as moderators of the mixed-effects model was performed: ecological index, bottom habitat, benthic communities, basin where aquaculture facilities were located, distance from the cages, number of farmed species *per* aquaculture and farmed species. Effect sizes for all the above-mentioned models were considered to be significant if their 95% CI (Confidence Interval) did not overlap with zero and if their p-values were ≤ 0.05. Publication bias, characterized by the preferential publication of studies reporting significant effects over those reporting non-significant effects (Koricheva et al. 2013) has been taken into account (see Supplementary Materials).

Satellite environmental data extraction

One objective of this paper was to correlate the effect size of the meta-analysis with local environmental conditions specific to each study site. This approach increases understanding of the study outcomes and, importantly, improves predictions of aquaculture effects on biodiversity under changing local environmental conditions. To achieve this, the study sites were first characterized by extracting six different environmental

variables based on geographic coordinates provided in each study: temperature (°C), salinity, Chlorophyll-a (mg m^{-3}), phosphate (mmol m^{-3}), nitrate (mmol m^{-3}) and dissolved oxygen (mmol m^{-3}) from the Copernicus Marine Environmental Monitoring System (https://resources.marine.copernicus.eu). The data had a spatial resolution of 6.25×6.25 km and a monthly temporal resolution. Environmental data were yearly averaged using monthly data from the study year, and to account for potential local temporal effects, these data were also averaged with information from the two preceding years.

Principal components analysis (PCA) and polynomial analysis of effect sizes

Scores derived from a PCA were utilized to examine the influence of major environmental variables on effect size. The purpose of the PCA was to condense the number of variables describing the dataset into a smaller set of latent variables, while minimizing information loss. The R packages "vegan" and "stats" were employed to perform the PCA (Jari Oksanenet al. 2020; R Core Team 2020). To explore the relationship between environmental variables and PCA axes, the "envfit" function was used, which fits environmental vectors or factors onto the ordination allowing for identification of the most correlated variables with PCA axes. Afterwards, scores from PCA1 and PCA2 were extracted to perform a polynomial regression including PCA scores as independent variable and effect sizes as dependent variables. The analysis was conducted using the "rma.mv" function of the "metaphor" package showing the identification of the PCA2 scores as explanatory variables for effect size as PCA1 was not significant. The residuals were examined for the absence of any discernible patterns and their normal distribution was verified. To facilitate the spatial interpretation and comparison of model outputs, the Mediterranean Sea was subdivided into three longitudinal sectors, delineated according to prevailing oceanographic and biogeographical characteristics. The Western Mediterranean extended from the Strait of Gibraltar (6°W) to approximately 9.5°E, encompassing the Alboran Sea, the Balearic Basin, and the western coasts of Italy and North Africa; the Central Mediterranean spanned from 9.5°E to 23.5°E, covering the Tyrrhenian, Ionian, and Adriatic Seas, as well as the central portions of the North African and southern European coastlines; and the Eastern Mediterranean region ranged from 23.5°E to 36°E, including the Aegean Sea, the Levantine Basin, and adjacent areas such as Cyprus, the southern coast of Turkey, and the easternmost shores of the basin.

Ecological indices

The meta-analysis utilized a dataset comprising 457 case studies sourced from 33 selected papers (details of studies included, including associated variables and number of case studies, provided in Tables S2–S4; Figure S1. Overall, findings from mixed-effect models applied to the entire dataset suggested that aquaculture facilities in the Mediterranean Sea have a moderate impact on biodiversity measured outcomes compared to undisturbed areas ($g = 0.24 \pm 0.18$; $p < 0.006$; Figure 1). Concerning the response variables it was possible to extract fifteen different outcomes selected as representative of biodiversity measures. These outcomes (see Figure 1) specifically referred to: Abundance; AMBI (AZTI Marine Biotic Index for assessing the quality of soft-bottom benthic macroinvertebrate communities; Borja et al. 2000); BENTIX (developed for the purposes of the European Water Framework Directive 2000/60/EC and for the assessment of the ecological quality status of benthic macroinvertebrates' communities, Simboura and Zenetos 2002); Biomass; BOPA (index based on the ratio amphipod/opportunistic polychaetes; Gesteira and Dauvin 2000); Margalef index; number of species; number of taxa; Pielou evennes; Shannon-Wiener diversity; shoot biomass; shoot density; Simpson diversity; species richness and total bacteria. Subgroup analyses indicated significant effects of aquaculture on the number of taxa, Shannon-Wiener diversity, and shoot density of the seagrass *Posidonia oceanica* ($g = 0.71 \pm 0.64$; $p = 0.04$, *; $g = 0.42 \pm 0.33$; $p = 0.008$, **; $g = 1.54 \pm 0.67$; $p < 0.001$, ***).

Subgroup analysis

Effects depending on location in the Mediterranean Sea

The impacts of aquaculture on biodiversity exhibited variation across Mediterranean eco-regions (i.e., basins; Figure 2). Specifically, Hedges' g values indicated that aquaculture in the Eastern basin significantly affected local biodiversity ($g = 0.43 \pm 0.35$; $p = 0.014$, **), whereas no significant effects were observed in the Central ($g = 0.26 \pm 0.32$, $p = 0.114$, ns) and Western basins ($g = 0.29 \pm 0.34$; $p = 0.085$, ns).

Effects on habitats and benthic communities

Aquaculture facilities considered in the analyses were situated primarily in areas characterized (nearby) by three habitat types: maërl beds, *Posidonia oceanica* meadows, and soft bottom habitats. Subgroup analysis revealed a significant effect for soft bottom
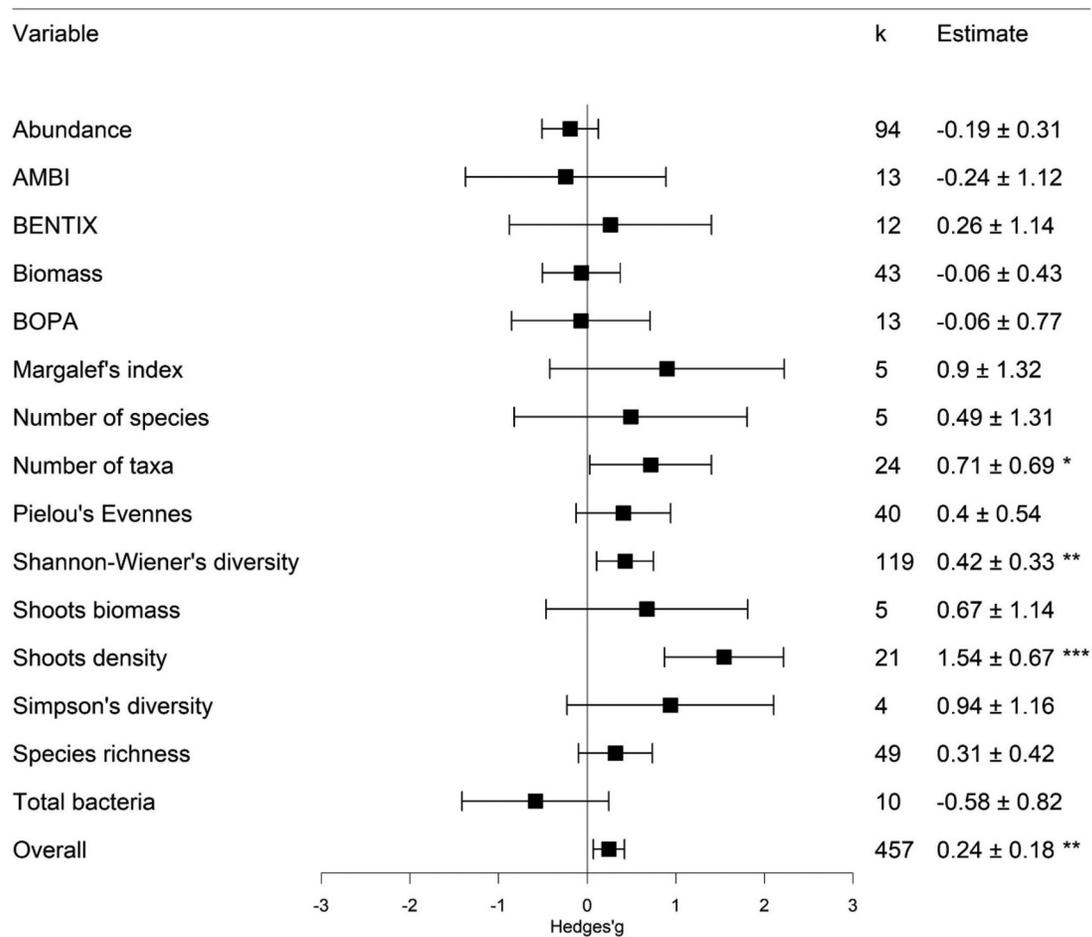
Variable	k	Estimate
Abundance	94	-0.19 ± 0.31
AMBI	13	-0.24 ± 1.12
BENTIX	12	0.26 ± 1.14
Biomass	43	-0.06 ± 0.43
BOPA	13	-0.06 ± 0.77
Margalef's index	5	0.9 ± 1.32
Number of species	5	0.49 ± 1.31
Number of taxa	24	0.71 ± 0.69 *
Pielou's Evennes	40	0.4 ± 0.54
Shannon-Wiener's diversity	119	0.42 ± 0.33 **
Shoots biomass	5	0.67 ± 1.14
Shoots density	21	1.54 ± 0.67 ***
Simpson's diversity	4	0.94 ± 1.16
Species richness	49	0.31 ± 0.42
Total bacteria	10	-0.58 ± 0.82
Overall	457	0.24 ± 0.18 **

Hedges'g

Figure 1. Forest plot of the overall effect-size and ecological index effect-size. Analysis conducted with mixed-effects model, using the rma.mv function of the metaphor package in R, including study Id and biodiversity measure outcomes as random factor. Black boxes represent the Hedges'g (g) value, and the horizontal lines represent the 95% CI for each g value; k = number of study cases. Levels of statistical significance: $p < 0.001$ ***, $p < 0.01$**, $p < 0.05$*. Note: the fifteen biodiversity measures outcomes are: Abundance; AMBI (AZTI's Marine Biotic Index for assessing the quality of soft-bottom benthic macroinvertebrate communities; by Borja et al. 2000); BENTIX (developed for the purposes of the European Water Framework Directive 2000/60/EC and for the assessment of the ecological quality status of benthic macroinvertebrates' communities, by Simboura and Zenetos 2002); Biomass; BOPA (index based on the ratio amphipod/opportunistic polychaetes; by Gomez Gesteira and Dauvin 2000); Margalef's index; Number of species; Number of taxa; Pielou's Evennes; Shannon-Wiener's diversity; Shoot biomass; Shoot density; Simpson's diversity; Species richness; Total bacteria.

habitats ($g = 0.32 \pm 0.30$; $p = 0.03$, *), while non-significant effects have been shown in maërl and *Posidonia* habitats (maërl $g = 0.35 \pm 0.85$; $p = 0.423$, ns; *Posidonia oceanica* seagrass $g = 0.30 \pm 0.38$; $p = 0.114$, ns) (Figure 3); however, macrobenthic infauna, meiofaunal, and bacterial community did not show significant effects ($g = 0.17 \pm 0.22$, $p = 0.114$, ns; $g = 0.57 \pm 0.58$; $p = 0.052$, ns and $g = -0.44 \pm 0.80$, $p = 0.278$, ns) (Figure 4).

Effects of distance from the facilities and farm techniques

The impact of aquaculture on the analyzed biodiversity measures diminished with distance from the cages (Figure 5) with stronger effects closer to the cages, specifically at distances starting from under the cage up to 50 meters away ($g = 0.39 \pm 0.30$; $p = 0.009$, **), with a significant decrease in effects between 50 and 200 meters from the cages ($g = 0.40 \pm 0.41$; $p = 0.004$, *) and a trend toward non-significance beyond 200 up to 500 meters ($g = 0.07 \pm 0.34$; $p = 0.646$, ns).

The effect of farmed species indicated that aquaculture involving multiple species concurrently did not result in a significant effect ($g = 0.21 \pm 0.31$; $p = 0.174$, ns). In contrast, a more pronounced impact was observed when a single species was farmed ($g = 0.54 \pm 0.38$; $p = 0.003$, **; Figure 6).
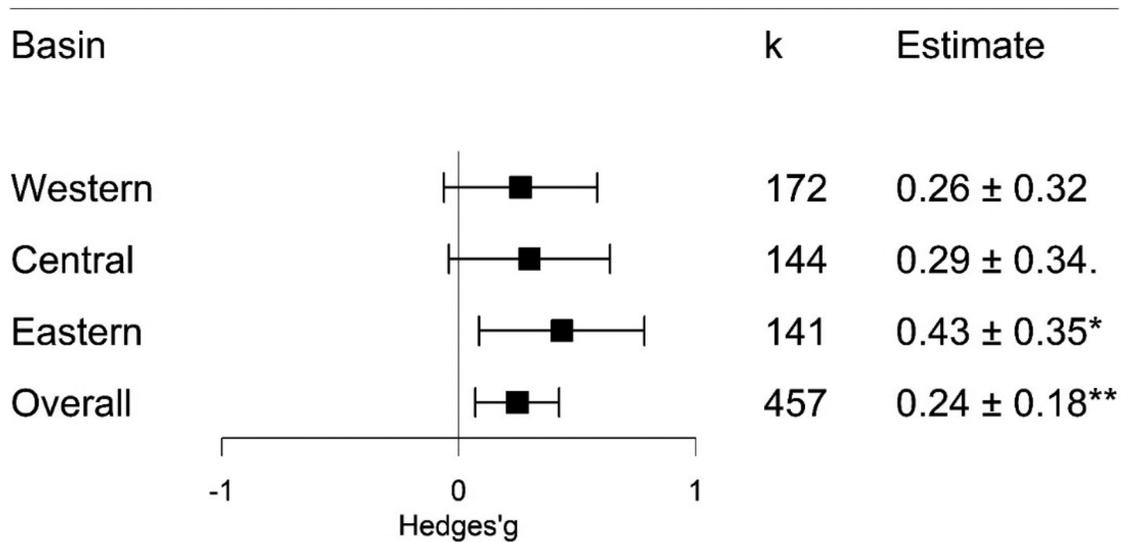
Figure 2. Forest plot of the "Basin" subgroups effect-size. Analysis conducted with mixed-effects model, using the rma.mv function of the metaphor package in R, including study Id and biodiversity measure outcomes as random factor. Black boxes represent the Hedges'g (g) value and the horizontal lines represent the 95% CI for each g value; k = number of study cases. Levels of statistical significance: $p < 0.001***$, $p < 0.01**$, $p < 0.05*$.
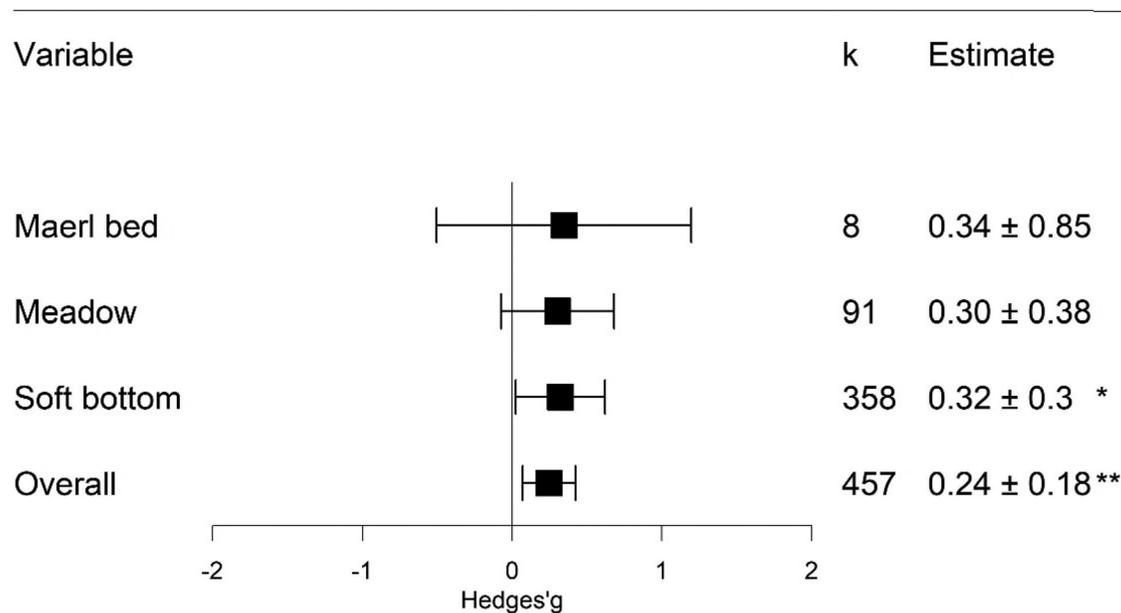

Figure 3. Forest plot of the "Habitat" subgroups effect-size. Analysis conducted with mixed-effects model, using the rma.mv function of the metaphor package in R, including study Id and biodiversity measure outcomes as random factor. Black boxes represent the Hedges'g (g) value and the horizontal lines represent the 95% CI for each g value; k = number of study cases. Levels of statistical significance: $p < 0.001***$, $p < 0.01**$, $p < 0.05*$.

At the species level, analyses revealed significant effects for seabream (*Sparus aurata*) and bluefin tuna (*Thunnus thynnus*) when farmed individually ($g = 0.61 \pm 0.54$; $p = 0.029$, * and $g = 0.61 \pm 0.50$; $p = 0.014$, **), while cultivation of seabass (*Dicentrarchus labrax*), which is also commonly farmed in the Mediterranean Sea, showed non-significant effects. When seabass and seabream were cultivated together (along with other

species), the effects tended to be non-significant (Figure 7).

Correlation of the effect of aquaculture operations with environmental variables

Figure 8a reported on the PCA ordination of multi-variate environmental variables associated with every case study included in the performed meta-analysis
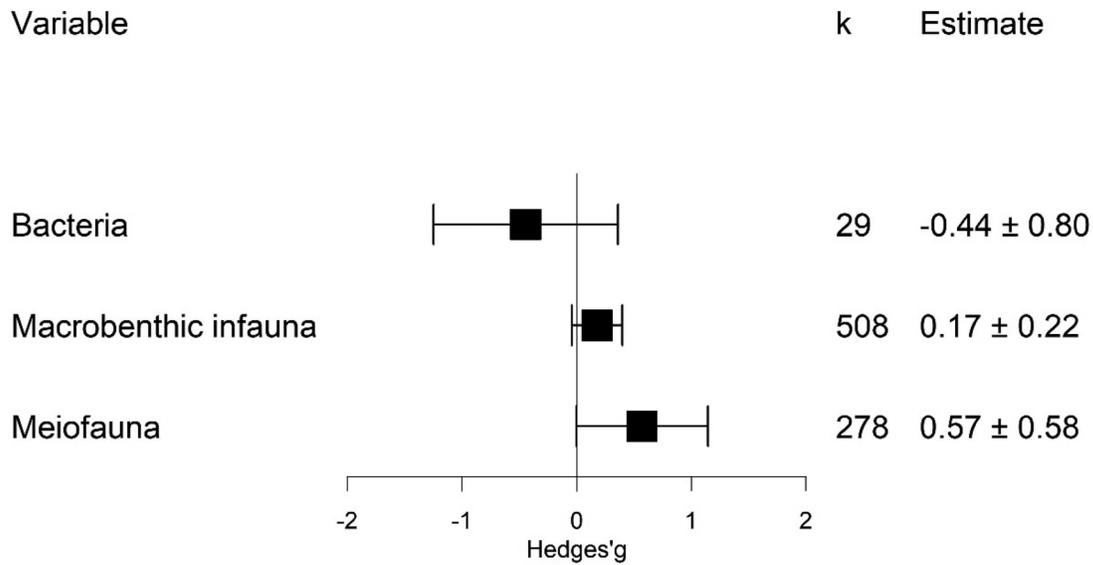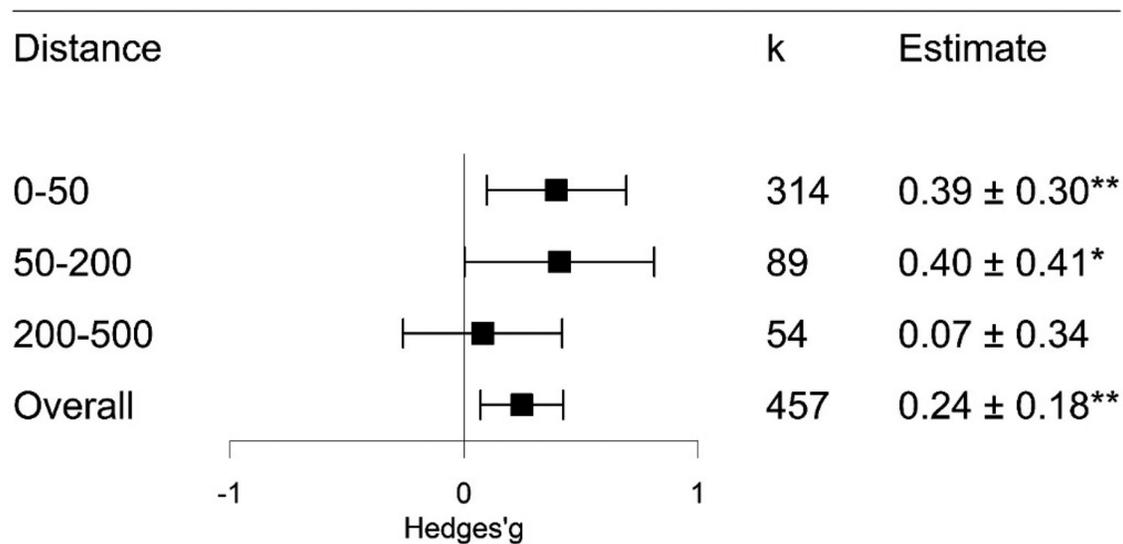
Variable		k	Estimate
Bacteria		29	-0.44 ± 0.80
Macrobenthic infauna		508	0.17 ± 0.22
Meiofauna		278	0.57 ± 0.58

Figure 4. Forest plot of the "Benthic community" subgroups effect-size. Analysis conducted with mixed-effects model, using the rma.mv function of the metaphor package in R, including study Id and biodiversity measure outcomes as random factor. Black boxes represent the Hedges'g (g) value and the horizontal lines represent the 95% CI for each g value; k = number of study cases. Levels of statistical significance: $p < 0.001$***, $p < 0.01$**, $p < 0.05$*.

Distance		k	Estimate
0-50		314	0.39 ± 0.30**
50-200		89	0.40 ± 0.41*
200-500		54	0.07 ± 0.34
Overall		457	0.24 ± 0.18**

Figure 5. Forest plot of the "Class distance" subgroups effect-size. Analysis conducted with mixed-effects model, using the rma.mv function of the metaphor package in R, including study Id and biodiversity measure outcomes as random factor. Black boxes represent the Hedges'g (g) value and the horizontal lines represent the 95% CI for each g value; k = number of study cases. Levels of statistical significance:$p < 0.001$***, $p < 0.01$**, $p < 0.05$*.

effort. The first two axes collectively explained 78% of the total variance (PCA1 42.93%; PCA2 35.58%; Table S5). Temperature and salinity showed strong negative correlations with the PCA1 axis (coefficients of −0.83 and −0.82), whereas phosphate exhibited a significant positive correlation with the PCA1 axis (coefficient of 0.97). Conversely, Chlorophyll- and nitrate were highly negatively correlated with the PCA2 axis (coefficients of −0.97 and −0.80), while

temperature showed a positive correlation with the PCA2 axis (coefficient of 0.55). The polynomial model showed no significant results of the correlation between PCA1 scores and effect size (Table S6a), while the correlation between PCA2 scores and effect size was significant ($p < 0.05$) (Table S6b).

Figure 8b illustrates the polynomial regression using PCA2 scores and measured effect sizes. Given the negative correlation of Chlorophyll-a and the positive
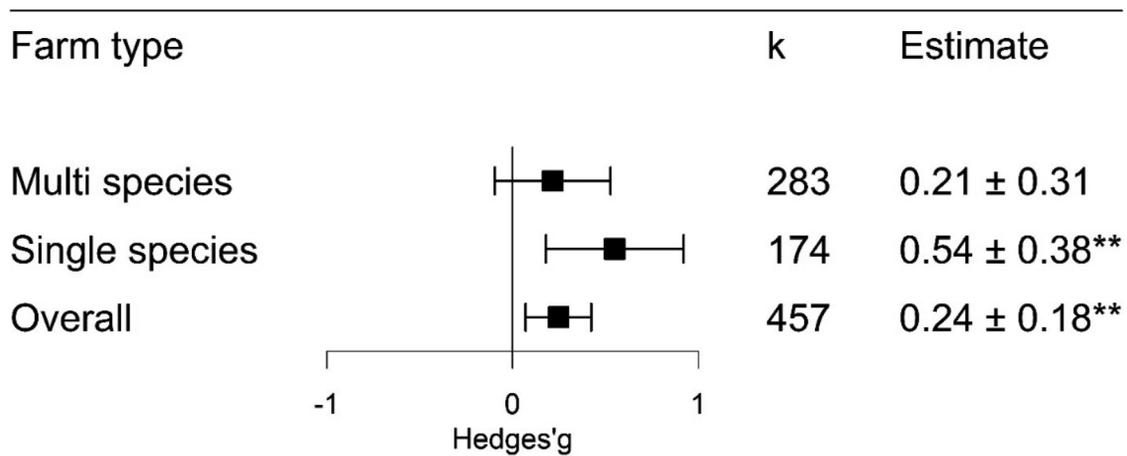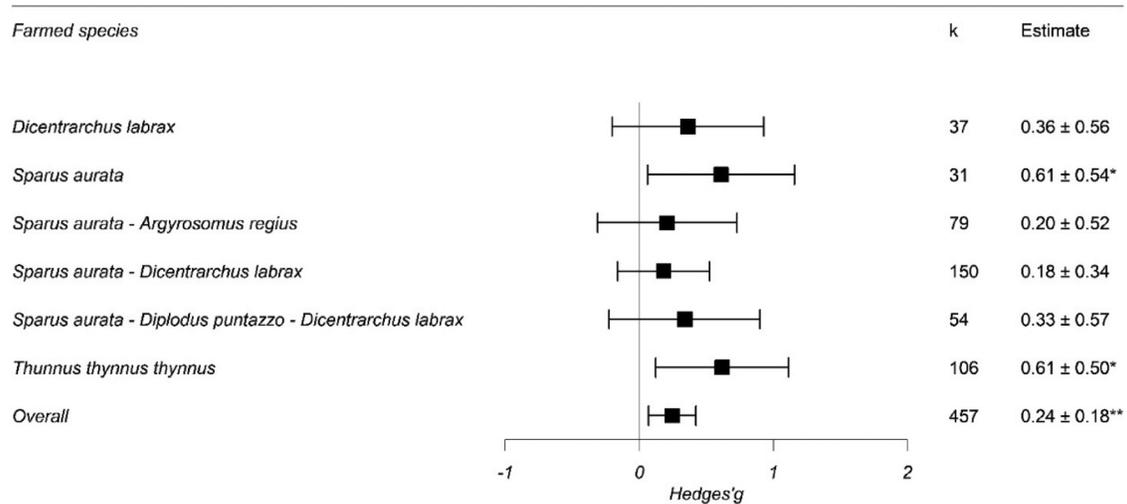
Figure 6. Forest plot of the "Number of farmed species" subgroups effect-size. Analysis conducted with mixed-effects model, using the rma.mv function of the metaphor package in R, including study Id and biodiversity measure outcomes as random factor. Black boxes represent the Hedges'g (g) value and the horizontal lines represent the 95% CI for each g value; k = number of study cases. Levels of statistical significance: $p < 0.001^{***}$, $p < 0.01^{**}$, $p < 0.05^{*}$.

Figure 7. Forest plot of the "Farmed species" subgroups effect-size. Analysis conducted with mixed-effects model, using the rma. mv function of the metaphor package in R, including study Id and biodiversity measure outcomes as random factor. Black boxes represent the Hedges'g (g) value and the horizontal lines represent the 95% CI for each g value; k = number of study cases. Levels of statistical significance: $p < 0.001^{***}$, $p < 0.01^{**}$, $p < 0.05^{*}$.

correlation of temperature with PC2 axis, the results indicate that the negative impact of aquaculture facilities tends to increase in areas with lower average Chlorophyll-a levels (e.g., mean Eastern Mediterranean basin Chlorophyll-a: 0.109 ± 0.009 mg m^{-3}) and higher average temperatures (e.g., mean Eastern Mediterranean basin temperature: 21.414 ± 1.201 °C). Conversely, in areas with higher average Chlorophyll-a concentrations (approaching eutrophic conditions; CHL-a around or more than 0.154 ± 0.009 mg m^{-3}) and lower average temperatures (e.g., mean Western Mediterranean basin temperature: 19.459 ± 1.175 °C), the presence of aquaculture suggested a diminished or non-significant effect on biodiversity.

Given that Chlorophyll-a exhibited the strongest correlation with PCA2, the correlation between PCA2 scores and mean Chlorophyll-a values was calculated, which is a proxy of trophic state of the ecosystem. Using the "predict" function from the R basic package, a threshold value for Chlorophyll-a, above which and below which the effect size shifted from negative (no impact) to positive (significant impact) was identified. Such a values was of 0.14 mg m^{-3}. Subsequently, by using Chlorophyll-a data spatial layer obtained from satellite imagery of the Mediterranean Sea (Figure 9a), a map describing Chlorophyll-a levels, which was scaled to show the expected impact level based on the trophic state of the ecosystem, was created.
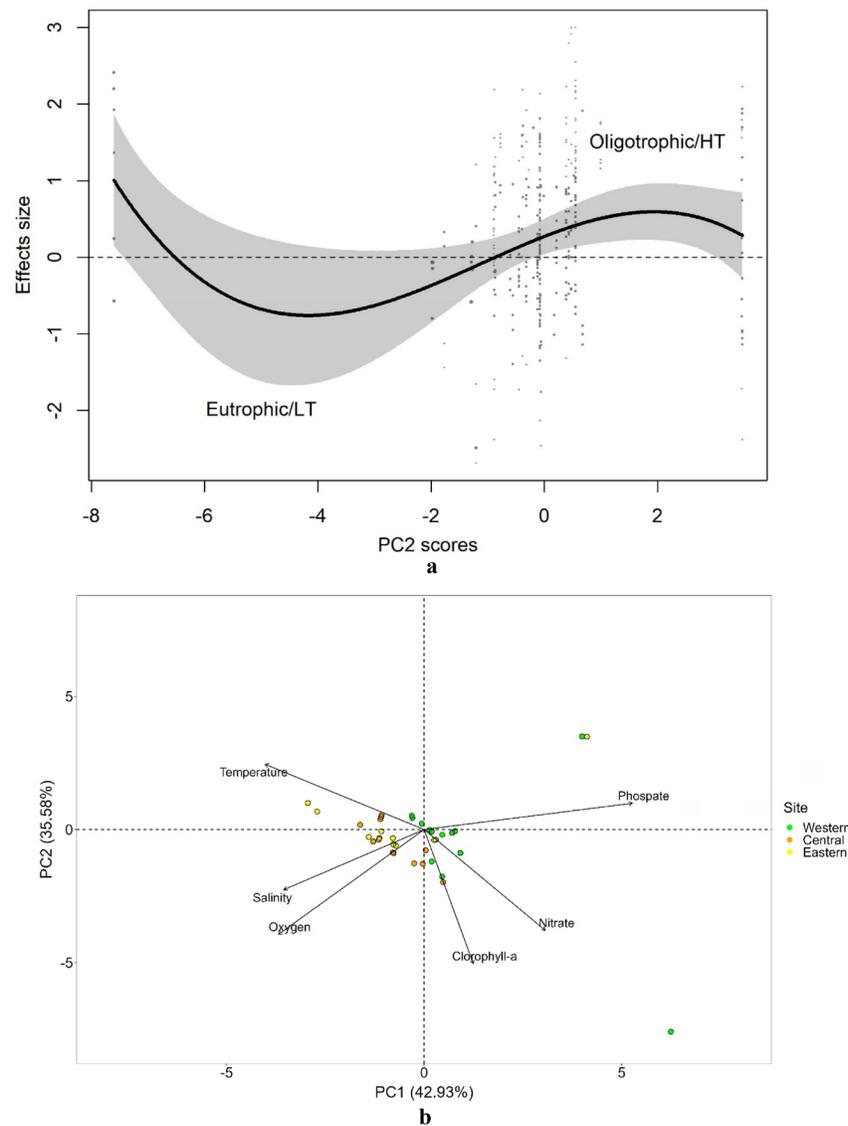
Figure 8. (a) Cubic polynomial regression showing correlation between effect sizes (dependent variable) and PC2 scores (independent variable). Results obtained by fitting a mixed-effect model using the rma.mv function of the metafor package and (b) PCA analysis on environmental variables associated with location of included case studies grouped by position in Mediterranean basin.

The generated map allowed visualization of areas in the Eastern Mediterranean and Central-Southern Tyrrhenian Sea potentially more vulnerable, experiencing a stronger negative effect of aquaculture on biodiversity. As a consequence, these effects appeared to be generally lower in the Central and Western basins (Figure 9b); however, exceptions to this basin-wide pattern were identified, whereby some location situated within high-impact areas – such as the northern Adriatic and the Gulf of Gabes in Tunisia, the Alboran Sea and western Spanish coasts, the Gulf of Lyon in France and the Thracian Sea in northeastern Greece exhibited a less negative impact than surrounding areas. These localized deviations likely reflect environmental heterogeneity at finer spatial scales. In particular, these areas are characterized by higher average Chlorophyll-*a* concentrations (e.g., >0.15 mg m^{-3}) and lower sea surface temperatures (e.g., <20 °C), related to reduced predicted impacts on benthic biodiversity.

Key insights concerning the impact of aquaculture on seabed benthic biodiversity

The comprehensive synthesis produced through this meta-analytic approach revealed several key insights concerning the impact of aquaculture on seabed benthic biodiversity across different eco-regions and habitats of the Mediterranean Sea. The observed moderate overall impact on the biodiversity measure suggests the necessity of examining localized ecological contexts when assessing the footprint of aquaculture on
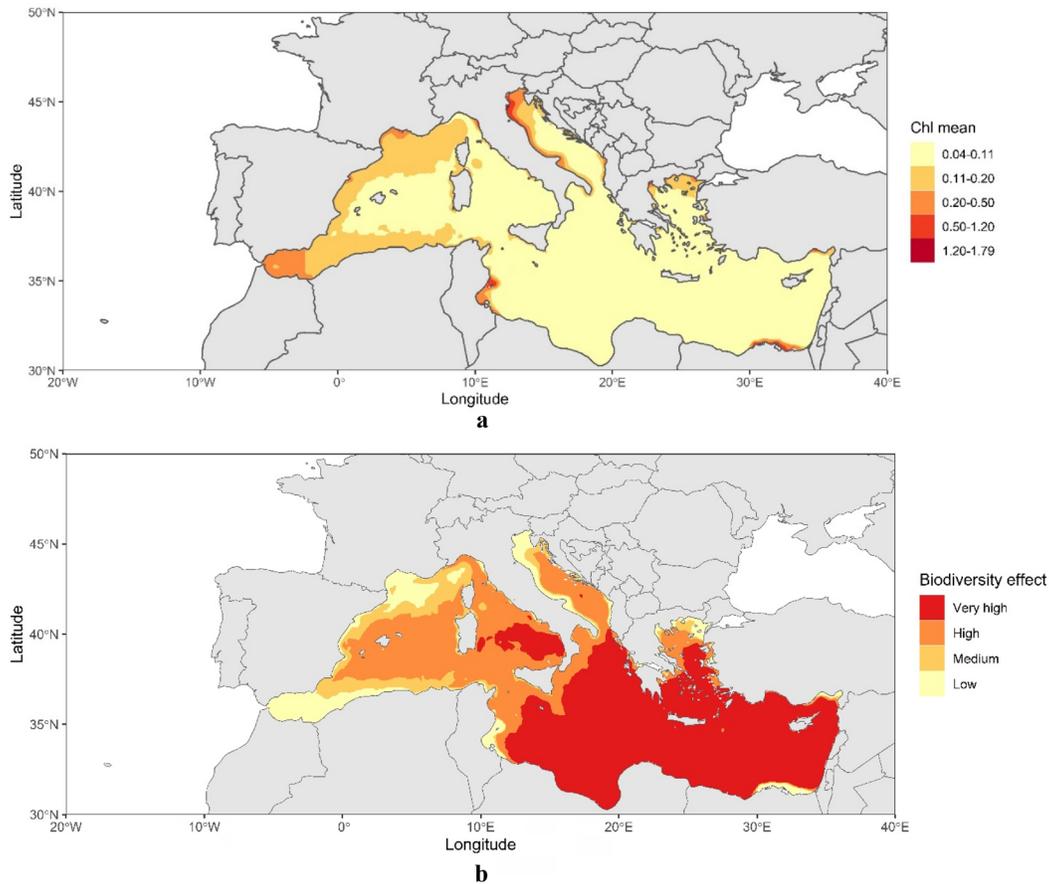
Figure 9. (a) Map of the Mediterranean Sea displaying average chlorophyll-a concentrations (mg m^{-3}) derived from satellite imagery, sourced from Copernicus Marine Environmental Monitoring System – Service data; (b) map illustrating the predicted impact of aquaculture on biodiversity in the Mediterranean Sea, based on correlations with chlorophyll-a concentrations in the Mediterranean Sea.

the environment and specifically on biodiversity. Specifically, the significant effects on taxa number, Shannon-Wiener diversity, and seagrass shoot density indicate that impact response of aquaculture varies significantly based on the specific biodiversity measure outcomes considered. As a function of habitat, ecological biodiversity indices can be more effective in describing the composition and the structure of biodiversity. The present analysis highlighted the use of almost all the most popular measures of alfa- and beta-diversity commonly used to assess the aquaculture effects in the Mediterranean Sea. These included Pielou, Simpson, Margalef and Shannon-Wiener metrics, with this latter remaining the most frequently used and confirmed as the most effective when dealing with benthic biodiversity. While the species richness was not sensitive to detect the effects of aquaculture, the taxa number was significantly effective, along with other structural characteristics (i.e., shoot density) of habitat-forming organisms such as seagrasses. Only recently, the latest United Nation Environment Program – Mediterranean Regional

report on aquaculture (UNEP/MED IG.26/22 2023) has emphasized the importance to monitor the effects of aquaculture on both benthic and pelagic biodiversity composition and structure. This is something strongly recommended in the present assessment, especially in the context of a rapidly growing food production technology such as aquaculture, that still shows a global knowledge gap on one of the three pillars of sustainability framework, the environmental aspect (Garlock et al. 2022). This gap has been here confirmed in the Mediterranean Sea, a region with ancient aquaculture traditions and future perspectives and investments potentials, but where the number of studies dealing with the aquaculture potential effects on the environment, specifically on seabed biodiversity, is limited and dated (the last study was published 7 years ago; Mangion et al. 2018).

The current analysis demonstrated that the results are strongly context (habitat)-dependent. Macro-benthic infaunal communities inhabiting soft bottoms are sensitive to aquaculture, showing a negative effect, even if the definition of such habitats is particularly

challenging in highly dynamic and apparently homogeneous systems such as marine coastal seabed (McArthur et al. 2010). This information is highly relevant for the design of monitoring and conservation programs based on habitat-based approach, especially considering the complexities underlying soft bottom habitats (Checon et al. 2018). The classification of soft bottoms is generally done *a posteriori*, relying on variations in sediment properties (Gray and Elliott 2009) and based only on environmental conditions. Additionally, results here confirmed that the organisms inhabiting the matrix of soft sediments can exhibit complex and various interactions with the environmental characteristics (McArthur et al. 2010) not always easy to disentangle and grasp (see the non-significant results from the benthic community subgroup analysis). Benthic communities (such us the analyzed microbenthic infaunal, meiofaunal and bacterial communities) represent a complex species-environment interaction, crucial for properly delimiting habitats (Diaz et al. 2004) and detecting responses to sources/regimes of different environmental disturbance (Hall and Harding 1997), such as aquaculture, thus deserving more attention regarding the design of future monitoring programs. A complementary method to the habitat-based approach in monitoring and conservation programs is the selection of indicator species, as the ones proposed by the collated and synthesized literature (e.g., AMBI, BENTIX, BOPA). This solution has been promoted as less time-consuming activity by several authors (Aguado-Giménez et al. 2007, 2015; Mangion et al. 2017, 2018), therefore suggesting that this synthesis did not show a clear response pattern against aquaculture impact, but confirming the importance to understand the optimum environmental conditions of each indicator species, to address/facilitate monitoring programs (Anderson 2008; Fonseca and Gallucci 2016). In addition to the attention paid to megabenthic species such as the habitat-forming *Posidonia oceanica* and maërl habitat, this meta-analysis revealed another significant knowledge gap related to the absence of monitoring studies dealing with this dimensional benthic component that can include both sessile and motile epifaunal organisms larger than 1 cm. The responses of megabenthic assemblages (cnidarians, sponges, tunicates, and decapod crustaceans) inhabiting coastal Mediterranean soft bottoms, playing a crucial role in supporting high levels of biodiversity as well as ecosystem function and services, have been ignored to the present The investigated habitats characterized by the presence of the habitat-forming species, maërl beds and *Posidonia oceanica* meadows, did

not show negative effects in response to aquaculture. This may suggest that aquaculture effects on biodiversity vary depending on the resilience of specific habitat to such disturbance. The major structural complexity and ecological functions of seagrass meadows and maërl beds might buffer against anthropogenic disturbances (Isbell et al. 2017). Future research should focus on understanding the mechanisms underpinning this resilience, which could inform the development of aquaculture practices that minimize habitat degradation. Moreover, prioritizing the conservation of more vulnerable habitats could enhance the overall sustainability of aquaculture.

The need to focus major attention on the study of community responses and seabed biodiversity across aquaculture impact gradients is further supported by the results obtained when testing the effect on different eco-regions of the Mediterranean Sea. Aquaculture facilities in the Eastern basins significantly impacted local biodiversity, whereas those in Central and Western basins did not show significant effects. This suggests that regional and local environmental conditions, and possibly the intensity of aquaculture practices in the Eastern basin, exacerbate ecological impacts. Policymakers, managers, and aquaculture-related stakeholders should consider regional environmental conditions and implement stricter regulations and monitoring protocols in areas identified as more vulnerable. Such results are connected to the present regression and spatial modeling effort, which results highlighted the crucial role of low Chlorophyll-*a* levels and higher average temperature in synergistically amplifying the negative effects of aquaculture on the seabed biodiversity as happens in the Eastern Mediterranean Sea. This finding demonstrates that nutrient availability (i.e., trophic state baseline) and thermal conditions (i.e., primary driver of metabolic processes) are critical factors influencing the performance and resilience of benthic ecosystems in response to aquaculture, driving the response of biodiversity to the disturbance due to the organic enrichment by aquaculture. Ecosystem Based Aquaculture Management practices should incorporate environmental monitoring of these variables to both predict and mitigate potential impacts. For instance, in oligotrophic regions, more stringent environmental regulations might be necessary to prevent further strain on already nutrient-poor conditions. Higher resolution in both environmental data and biodiversity measure outcomes from more extensive monitoring programs will allow increasing the resolution of basin observed patterns disentangling more jeopardized sub-basin responses as well

describing how environmental condition can exacerbate these impacts.

The analysis presented here aligns with current findings when examining the effects of aquaculture on the surrounding environment relative to the distance from farm facilities (Sarà et al. 2006; Borja et al. 2009; Froehlich et al. 2018; Del Valle et al. 2022; Katselis et al. 2022; Wu et al. 2023). This pattern, confirmed by the selected biodiversity measure outcomes revealed that the severity of aquaculture impact modulates with distance from focal areas of emission, such a pattern that, may be largely influenced by local hydrodynamic conditions (e.g., marine currents), which can significantly affect the dispersion of waste and pollutants, but that is only rarely provided by the studies from the literature – as typically requiring extensive field research and data modeling effort – then impossible to test at this stage. Specifically, this meta-analysis showed that closer proximities (from under the cages up to 50 m) are particularly vulnerable, confirming the clear presence of a buffer zone with a significantly reduced effect and suggesting a distance from which the effect become negligible. This evidence can clearly be exploited to implement a more effective siting of aquaculture at sea in the Mediterranean Sea, specifically informing a zoning regulations based on buffer zones of measured potential risks to be placed around sensitive habitats to mitigate direct impacts. This finding advocates for more ecosystem-based (see here biodiversity responses) spatial planning solutions into the future of aquaculture productive sector.

Farmed species and their combinations can have a different footprint on seabed biodiversity. Cultivation of single species, such as seabream and bluefin tuna, has a more pronounced negative impact on biodiversity compared to systems where more than one species was cultivated together, with species like seabass having no significant effect when both farming alone or in combination to seabream and meager. Species-specific behaviors and waste outputs may drive these differences. Seabream and bluefin tuna, for instance, may produce more waste or may have different feeding habits that result in a negative effect on seabed biodiversity. These insights highlight the potential of integrated multi-trophic aquaculture (IMTA) and polyculture practices as viable mitigation strategies, as fostering more balanced nutrient cycles, organic matter fluxes and ecological interactions. Nevertheless, this is in contrast to a recent analysis by Garlok et al. (2024), that, dealing with all aspects of sustainability in aquaculture, indicated monoculture as preferable to polyculture across both marine and freshwater systems. Specifically, their analysis revealed that monocultures generally scored higher on the environmental pillar of sustainability, challenging the prevailing view that IMTA and polyculture optimize resource use by utilizing wastes and by-products (Chopin et al. 2012; Knowler et al. 2020). Here it was recommended to include biodiversity measures as a response variable in studies examining the effects of aquaculture on surrounding environment.

Implications for management and policy

This study provides actionable insights to inform a more Ecosystem-Based Aquaculture Management and the relative policy development at Mediterranean Sea level. These include:

- **Implementation of regional regulations:** tailoring regulations to specific eco-regions based on their vulnerability to aquaculture impacts. For example, stricter monitoring and control measures in the Eastern basins could mitigate the higher observed impacts.
- **Implementation of risk-based buffer zones**: establishing mandatory buffer zones around aquaculture sites to protect nearby ecosystems from direct impacts, tailored on local environmental condition and integrating biodiversity-habitat layers.
- **Promotion of polyculture and/or IMTA**: encouraging the adoption of polyculture systems to reduce the negative impacts associated with single-species farming and promote biodiversity mainstreaming in aquaculture.
- **Integration of environmental monitoring and implementing biodiversity mainstreaming**: enhancing environmental monitoring programs, regionally shared protocols and practices, to include key indicators such as benthic communities' biodiversity and functioning measures (covering macro and megafauna and flora), Chlorophyll-*a*, local hydrodynamic conditions, particularly marine currents, and water temperature measures, to be able to collate high resolution datasets enabling proactive management responses.
- **Maintainence of gradient responses study design:** as showed by this synthesis, the number of studies dealing with this monitoring design stopped 5 years ago, mostly alarming with regard to the risk of losing a relatively large portion of the available information concerning the community structure (e.g., abundance, biomass, diversity – often considered

cost/benefit unbalanced) and the chance to compare timeseries.

- **Involvement of stakeholders in monitoring plan realization and design.** Future research should aim to deepen the understanding of the mechanisms driving habitat resilience and vulnerability to aquaculture impacts. Studies specifically designed to track environmental changes over time in different habitats could provide valuable insights. Additionally, experimental studies that manipulate environmental conditions and species compositions in controlled settings could help elucidate causative factors. Investigating mechanisms behind disturbance response is essential, and integrating ecological, social and economic aspects will be crucial for developing holistic strategies for sustainable aquaculture.

- **Promotion of adaptive management to improve long-term management:** developing monitoring cycles with periodic revision, develop performance indicators based on biodiversity responses that can be adapted while learning from the ecosystem responses, adapting management actions and arrangements to enhance effectiveness coping with the fast global and local changes, and support of stakeholder engagement in the management process.

- **Investment in research and innovation**: investing in research to develop sustainable aquaculture monitoring technologies based on the Internet of Things, and precision aquaculture practices that minimize environmental footprints, such as recirculating systems and alternative feeds.

By adopting targeted management strategies and fostering innovation, it is possible to mitigate the negative impacts of aquaculture and promote sustainable practices that support both ecological health and economic benefits through mainstreaming biodiversity. This study offers valuable insights to the debate on sustainable aquaculture and sets the stage for future research and policy development in this critical area.

Authors contributions

M. Cristina Mangano: data curation (literature), methodology, visualization, writing-review and editing, conceptualization, writing original draft. Manuel Berlino: methodology (meta-analysis), data visualization (meta-analysis), writing-review and editing. M. Bosch-Belmar: writing-review and editing, modeling and data curation (environmental). G. Milisenda: modeling (environmental). G. Sarà: conceptualization, methodology, visualization, writing, review and editing, writing original draft, writing-review and editing.

Disclosure statement

Funding

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Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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