



Original Articles

Ecosystem functioning and ecological status in the Venice lagoon, which relationships?

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ABSTRACT

The implementation of management measures for improving the ecological status within an Ecosystem Based Management approach represents one of the main challenges in coastal and transitional water environments. In general terms, ecological status and ecosystem functioning are expected to be positively associated, being good ecological processes a sort of prerequisite for the ecosystem health, but often relationships between ecosystem functioning indicators and the metrics used to define ecological status resulted to be rather puzzling. Moreover, the Biological Quality Elements (BQEs) do not show a consistent response to the changes in the ecosystem. This situation does not allow to recognize where interventions are really needed, hindering the definition of effective management strategies. In the present paper, a spatially explicit food web model of the Venice lagoon (with the resolution of 300 m) is used to simulate changes in the ecological status and related them to different management scenarios. Functional changes in the food web were investigated by comparing values of a set of 12 indicators derived by the ecological network analysis. In general, results highlighted on one hand the need for more discussion about the implementation of the WFD, at least in complex and spatially heterogeneous transitional waters environments, as the Venice lagoon; on the other, results remark the opportunity to support the BQEs monitoring with an ecological modelling approach. These models are certainly not the panacea for addressing questions about the environmental management, as they have inherent uncertainties (on parameters, structure, processes etc.); however, they can prove useful for selecting among different policy choices, since they offer the opportunity to simulate the mean effects, preliminarily verifying the efficacy of the proposed interventions.

1. Introduction

One of the most critical elements within the context of the Ecosystem-Based Management (EBM) implementation is related to the identification of the measures to adopt to improve the ecological conditions. A good example comes from the Water Framework Directive (WFD, 2000/60/EC) implementation. WFD still represents a major challenge at the EU level since the good ecological status was achieved, after several years of adoption, only in 50% of EU surface waters (Voulvoulis et al., 2017). According to the WFD, the environmental quality of transitional waters is assessed on the basis of a set of Biological

Quality Elements (BQEs) that describes the status of different ecological compartments, namely primary producers, benthic organisms, fish assemblages. The overall ecological status of a water body is given by the lowest BQE score, whatever the compartment. In relation to this, the raised question is how to improve a BQE score, and which kind of interventions could be put in place. Big efforts have been devoted to the identification of the BQEs, and related indicators, in order to assess the ecological status of the analyzed water bodies. Nevertheless, few indications have been collected concerning the performance of measures aimed at improving the status (Voulvoulis et al., 2017). This difficulty has been attributed to a reductionist interpretation of the Directive by

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targeting the improvement of the biological quality elements, rather than managing the pressures to improve the ecological status - i.e., targeting the symptoms rather than the causes of aquatic ecosystems degradation (Voulvoulis et al., 2017).

A second issue is related to the difficulty of using observations in disentangling the influence of the past system conditions on its present state. Understanding the disturbance regime experimented by an ecosystem can indeed provide useful insights on the single and cumulative effects of the factors involved. For exploring this issue, simulated scenarios produced by mathematical models could represent a useful resource.

Within the WFD implementation, the Venice lagoon (Northern Adriatic Sea, Italy) was partitioned into 14 operational units, defined as water bodies (ISPRA-ARPAV, 2018). Based on their salinity (the range 20–30 psu has been defined as polyhaline and the 30–40 psu as euryhaline) and the confinement degree (confined refers to the inner parts of the lagoon, delimited by salt marshes, where water exchange is low, whereas not confined refers to more open areas of the lagoon), the water bodies were categorized as “polyhaline confined”, “polyhaline not-confined”, “euryhaline confined” and “euryhaline not-confined” (see ISPRA-ARPAV, 2018). An examination of the BQEs resulting from the second assessment cycle carried out by ISPRA (2017), indicates that the lagoon’s areas closer to the sea, in general exhibit better quality than those located close to the industrial area and the historical cities (Venice and Chioggia) (ISPRA-ARPAV, 2018).

The big challenge is now related, as in many other European transitional-waters basins, to set up sound measures for improving the ecological status of a given water body. At present, indeed, it is quite difficult to delineate interventions aimed at driving the Venice lagoon towards a desired trajectory/direction or defined reference conditions. Recent papers (Vlachopoulou et al., 2014; Voulvoulis et al., 2017; Rova et al., 2019) highlighted the need for a new integrated perspective for overcoming the limitations imposed by the “reductionist interpretation” and supporting cost-effective management plans.

Spatially explicit ecosystem models can contribute to the implementation of an ecosystem-based management approach, enabling one to simulate changes in the ecological status and related them to different management scenarios. A number of modelling frameworks that can represent complex ecosystem dynamics over space and time have been developed: Osmose (Shin and Cury, 2001), Atlantis (Fulton et al., 2011) and Ecopath with Ecosim (Christensen and Pauly, 1992; Walters et al., 1997) are among the most used tools (Pelletier and Mahévas, 2005; Plagányi, 2007).

Ecopath with Ecosim is based on a mass-balanced food-web model (Christensen and Pauly, 1992; Walters et al., 1997) and it includes the spatial component Ecospace (Walters et al., 1999), which aims at reproducing general, but realistic, spatial distribution patterns of species or groups of species by considering trophic interactions at the community level. Ecospace was developed mainly for studying spatial management scenarios, in particular marine protected areas, and their effect on ecosystem dynamics and fishing performance (de Mutsert et al., 2017; Hernvann et al., 2020; Steenbeek et al., 2020).

The present paper presents an application of Ecospace to the Lagoon of Venice aimed at investigating the relationships between ecosystem functioning and the ecological status of its water bodies (sensu WFD).

Specific aims are:

- identifying a new spatially explicit model of the lagoon food web, capable to analyze the main ecological features within each water body;
- exploring relationships between ecological processes and BQEs in the different water bodies;
- analyzing outcomes of a portfolio of management options, in relation to changes in the BQEs.

2. Material and methods

2.1. Study area and ecological status assessment

The Venice lagoon (Fig. 1) is a shallow coastal ecosystem covering an area of about 550 Km², of which nearly 400 km² characterized by open waters, and the remaining part by extensive fish farms (locally called “valli da pesca”) where the water circulation and the fish species movement is controlled. The average depth is about 1 m, but the main navigation channels and the sea inlets are more than 20 m deep. The lagoon connects to the Adriatic Sea by three inlets namely, from north to south, Lido, Malamocco and Chioggia. A system of mobile gates (MoSE), designed and built to protect the historical town from the effects of high tides, was recently completed and it is in the pre-operational phase. This system allows to disconnect the lagoon from the open sea in case of forecasted high tide, maintaining a lower level of water inside the lagoon.

Within the WFD implementation, the assessment of the ecological status was carried out by means of different BQEs. The Macrophyte Quality Index (MaQI, Sfriso et al., 2007; Sfriso et al., 2009), for the primary producers, the Multivariate AZTI’s Marine Biotic Index (M-AMBI, Bald et al., 2005) for the benthic community, and the Habitat Fish Bioindicator Index (HFBI, Catalano et al., 2017) for the nekton assemblage. The classification of each water body, according to the three BQEs is reported in Table 1.

2.2. The food web model

The model was applied to a surface of approximately 388 km² of the lagoon covering 11 of the 14 water bodies shown in Fig. 1: the water bodies including valli da pesca and the Venice downtown were excluded, since these were defined as “highly modified water bodies”, according to the WFD. The domain was represented with a grid of 300 × 300 m cells.

The food web model was built by using the Ecopath with Ecosim 6.5 software package (Christensen et al., 2008). Ecopath first produces a static representation of the energy/matter flows among the food web compartments, which either represent functional groups or single species of high ecological relevance. Based on Ecopath initial conditions a system of differential equations is used in the Ecosim routine to provide a dynamic simulation of the energy/matter flows among the food web nodes (Walters et al., 2000). The Ecospace spatial routine enables implementing the time dynamic module Ecosim in each squared cell used to represent the 2D spatial domain. Ecospace space and time dynamic combines the trophic dynamics with a-priori definition of the spatial distribution of preferred habitats, 2D maps of environmental and anthropogenic drivers influencing selected functional groups mortality, predation and/or productivity in each cell (Christensen et al., 2014).

Building on the base of knowledge established by previous works on the Venice lagoon food web modelling (Pranovi et al., 2003; Libralato and Solidoro, 2009; Brigolin et al., 2011; 2014), the present work introduces significant novelties, which include: i) the spatial implementation; ii) the differentiation among fishing activities; iii) new functional groups; iv) a more detailed representation of the food web (with multi stanzas aspect for some key species). Cohort functions were introduced for 5 single-species compartments (Manila clam, grey mullet, grass goby, gilthead seabream and European seabass), a new compartment was set for *Mnemiopsis leidyi* - an invasive ctenophore, plankton feeder, for fish larvae represent an important food source-, and updated biomass values of all functional groups of primary producers were included. Fishing activities present in Venice lagoon, namely artisanal, mechanical clams harvesting and recreational fishery, have been implemented (Table S2). Ecopath input values refer to the 2004–2008 time-window, which was regarded as the most complete in terms of data availability for the different food web components: data from these years are here used in a time averaged form as the model initial conditions. Overall, the model is composed by 33 functional groups, including

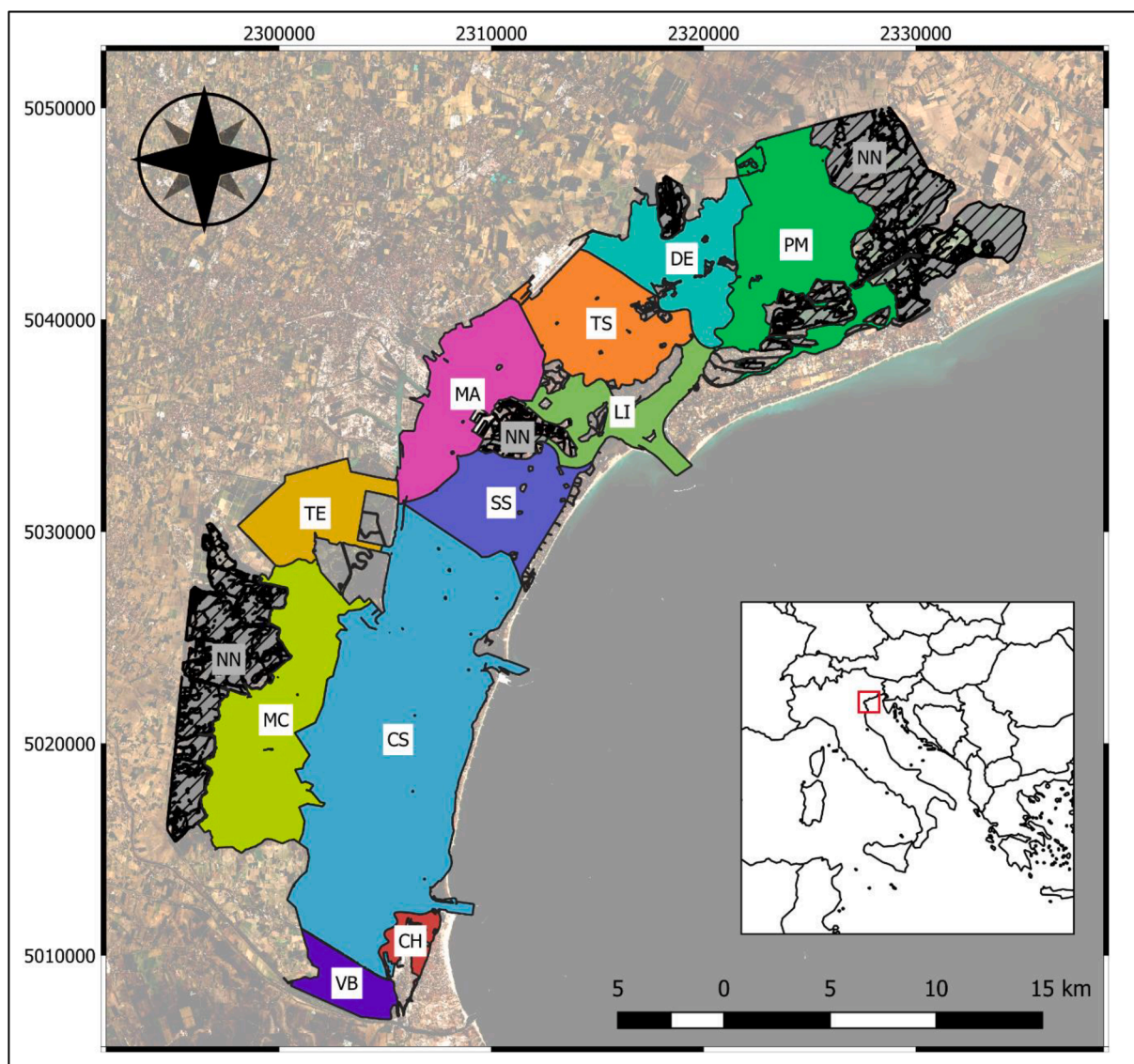


Fig. 1. The Venice lagoon and the 14 water bodies defined according to the Water Framework Directive; in solid color the 11 water bodies considered in the present analysis NN: not considered zones); for acronyms see Table 1.

Table 1
BQEs values for the analyzed water bodies (data from ISPRA-ARPAV, 2018).

NAME	ACRONYM	Km ²	M-AMBI	MaQI	HFBI
Centro Sud	CS	133.5	0.63	0.783	0.58
Chioggia	CH	4.5	0.67	0.483	0.66
Dese	DE	27.6	0.68	0.333	0.66
Lido	LI	18.2	0.64	0.656	0.65
Marghera	MA	32.9	0.67	0.35	0.52
Millecampi Teneri	MC	50.4	0.67	0.35	0.35
Palude Maggiore	PM	49.1	0.65	0.646	0.63
Sacca Sessola	SS	26.8	0.57	0.49	0.47
Teneri	TE	21.1	0.6	0.283	0.47
Tessera	TS	31.5	0.67	0.35	0.64
Val di Brenta	VB	10.0	0.81	0.283	0.69

5 producers, 24 marine consumers, 2 birds and 2 sediment compartments; to better integrate data coming from fishing activities and monitoring campaigns the unit of measure used is wet weight per space (t/km²) (Tables S1 and S2, Fig. S1).

2.3. Environmental/anthropogenic drivers and spatial module parameterization

Although large, the set of available data for the period 2004–2008 are not enough for describing the spatial distribution of all species, that were thus reconstructed for the reference state (mid 2000 s) using habitats and gradients definitions in Ecospace. This module allows defining also “habitats”, i.e., subdivisions of the model domain to which it is possible to assign functional group preferences. Specifically, the habitats were used in this work to define spatial initial conditions by assigning to each habitat an initial proportion of biomass for each functional group, thus affecting its mortality when present in non-preferred habitat (Ahrens et al., 2012). Habitats were also used for spatially constraining fishing activities, in particular clam fishing was assigned to macroalgal beds and Manila clam ones. Four main habitats were identified:

- 1) *seagrass meadows* is the lagoon area mainly occupied by *Zostera marina*, *Cymodocea nodosa* and other seagrasses (with an extension of approximately 75.5 km², equal to 19.5% of the model domain);
- 2) *macroalgal beds* is the area covered mainly by *Ulvaceae* and *Gracilariaceae* (115.1 km², 29.7% of the domain). This habitat comprises also

areas where the environmental conditions are deeply modified by human activities (i.e. channels receiving a high pressure from maritime traffic);

3) *tidal flats* is the submerged area surrounding the almost emerged portion of the domain, exposed to the air during the lowest low tide events; (i.e. sandbanks and saltmarshes for a total of 129.7 km², 33.4% of the domain).

4) *Manila clam banks* (approximately 67.7 km², 17.4%) is the area distinguished by being composed mainly by a bare and flat sediment bottom. A lagoon habitats distribution map (Fig. 2) was produced by using previous data collected from satellite imagery, vector maps made available by the Venice authorities through their official websites, and other territorial authorities. More specifically, information regarding the spatial distribution of clam fishing concessions in the lagoon can be found in the “Plan of use of the areas in concession for clam farming” (Pessa et al., 2013) and spatial data related to the distributions of salt marshes and seagrasses can be found in the “Atlante della Laguna” open data repository (Guerzoni & Tagliapietra, 2006).

Moreover, Ecospace allows to consider spatial gradients of environmental and anthropogenic drivers that are applied to functional groups defined in Ecopath. In the present work, the environmental parameters considered are bathymetry and turbidity, which spatial distribution are shown in Fig. 3. These environmental parameters were linked, by means

of the specific functions shown in Fig. 4, to the tolerance of seagrasses, macroalgae and manila clam functional groups. These functions present different shapes among the three groups, with a suitability value ranging between 0 and 1, and mapped within the interval of values characterizing each environmental parameter (see also De Mutsert et al., 2016). In this specific case, turbidity is thought to express the limitation of several factors, including light and oligotrophy, therefore, extremely low values of this parameter correspond to unfavorable environmental conditions for the rooting of seagrasses and algae. Planktonic primary production spatial distribution was also used as driver for phytoplankton, thus contributing to a dynamic spatial distribution of food web components. In the Ecospace routine, vulnerability, search and dispersion rates and feeding rate can be fine-tuned to adjust the functional groups trend to move among the cells and outside from the elective habitats (Walters et al., 2000). In this work, the default values of most Ecosim and Ecospace parameters have been used (Ahrens et al., 2012; De Mutsert et al., 2017) and spatial dynamics of functional groups and fisheries result solely from habitat definition and spatial gradients imposed, i.e., bathymetry and turbidity (Fig. 3).

2.4. Reference simulation and scenario analysis

On the basis of initial conditions represented in Ecopath, and under

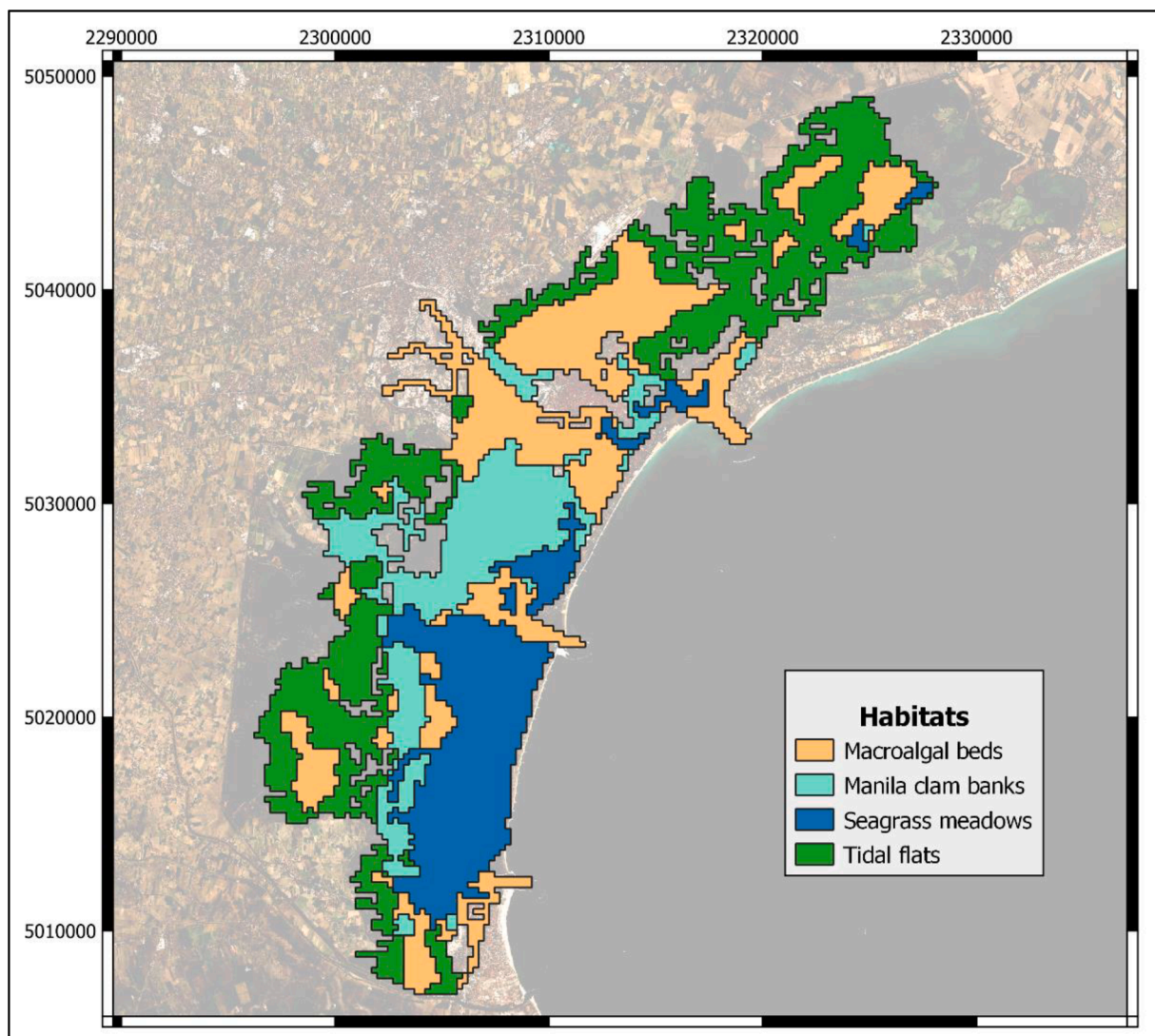


Fig. 2. Map of the Venice lagoon distinguishing the 4 main habitats, with the 300 m*300 m grid used in Ecospace.

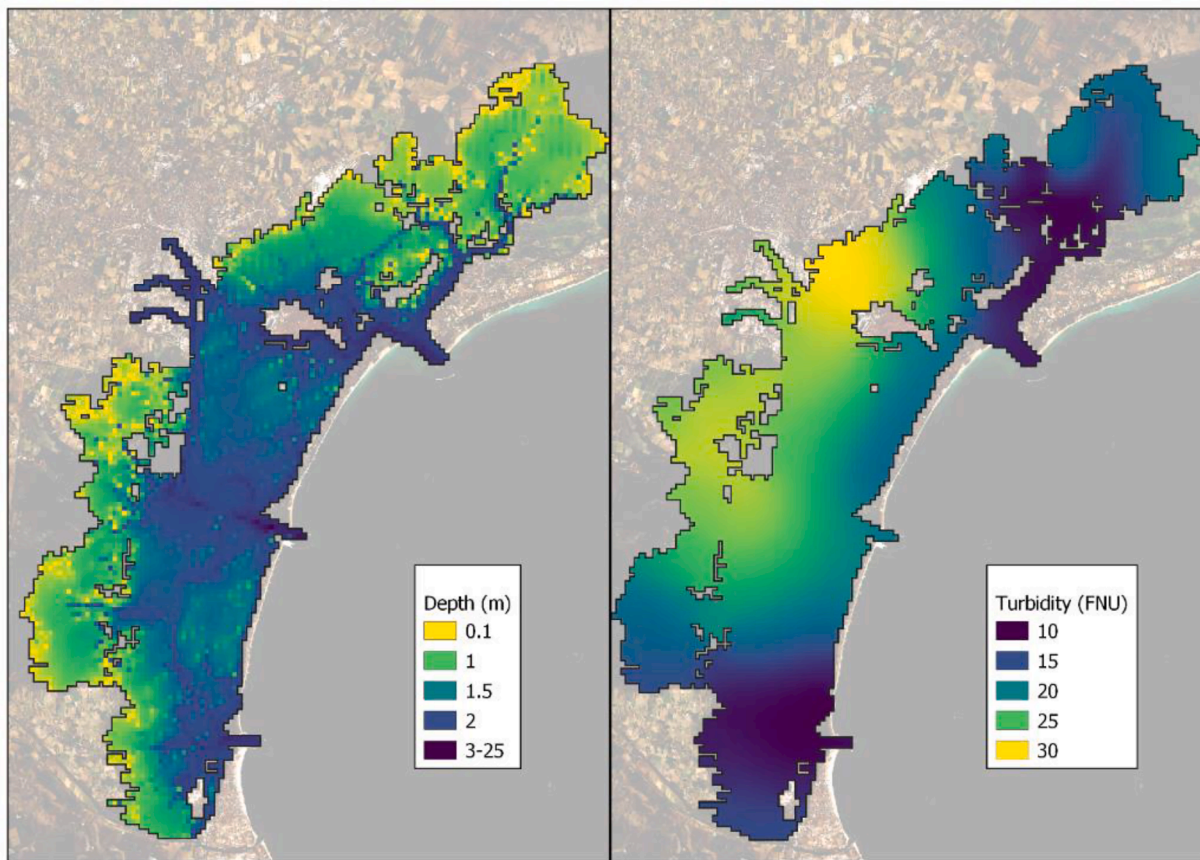


Fig. 3. Maps of depth (left) and turbidity (right); depth data referred to the period 1999–2011 and turbidity data referred to 2004, data available from www.atlantedelalaguna.it.

constant fishing and environmental forcing through time (in Ecosim), the spatialized reference conditions were obtained by running the model with assignments of species to Ecospace habitats and influence of spatial gradients of drivers fixed in time. Spatial data for bathymetry and turbidity were available only for specific time windows, thus an average gradient representative for the years 2000 s was used (Fig. 3) to dynamically drive functional groups distribution in the spatial domain. This initialization step required a long term spin up of 100 years to obtain a 2D steady state representation of the food web for years 2000 s, which was used as a reference condition within this study.

To compare different possible states of the Venice Lagoon under relevant drivers of change, 3 different scenarios were defined:

- The seagrass meadows increase (Fig. 5), a condition that assume the lowering seagrasses vulnerability through their seedling and consequent expansion in highly suitable areas. This scenario is in agreement with the recent observations, mainly in the northern part of the lagoon (Sfriso, et al., 2019);
- The seagrass meadows decrease (Fig. 5), a condition that implicitly mimics the consequences of the increase in the turbidity levels, followed by a reduction of the areas suitable for seagrasses expansion; in this case seagrasses do not disseminate out their elective habitat.
- A 50% decrease in the fishing effort concerning the three fishing activities.

The first two scenarios consider the effect of interventions of ecological restoration (A), and of an increase in turbidity levels (B), while scenario C is a top-down constraint that could be implemented by local regulation authority and is the only scenarios that is an expression of management's decisions. The drivers of change (increase and

decrease of seagrasses, decrease of fishing effort) are imposed over time and their effects, combined with constant spatial gradients for bathymetry and turbidity, are evaluated in terms of steady state spatial distribution obtained from long simulations (100 years). Scenarios, therefore, do not represent a real projection of the state of the system over a transient, but aim at describing the spatial reorganization of resources under modified drivers, which can thus be compared with the reference condition. The reference condition and the three different scenarios were thus compared at steady state.

2.5. Ecosystem functioning indicators and their relationships with BQEs

Ecosystem structure and functioning have been investigated by using 12 indicators (Ecosystem Functioning Indicators) chosen for covering both the biomass structure and the energy flow of the living compartment (Shin and Cury, 2001; Varkitzi et al., 2018; Steenbeek et al., 2020) and assessed at the water bodies scale, by treating Ecospace outputs and averaging values for the grid cells pertaining to the different water bodies. The Ecosystem Functioning Indicators considered in the present study are: the total biomass of the system, the commercial biomass (i.e. the biomass of all commercial species targeted by fishing activities), the fish biomass, the invertebrate biomass, the ratio invertebrate/fish biomass, the total catches by all fishing activities, the fish catches, the mean trophic level of catches, the mean trophic level of the whole community, and the Primary Production Required (PPR) by all fishing activities catches and the Kempton Index.

In order to test the possible relationships between ecosystem functioning and ecological status, a Generalized Linear Model (GLM) analysis was performed between Ecosystem Functioning Indicators and BQEs, at the water body level. The analysis was carried out by means of

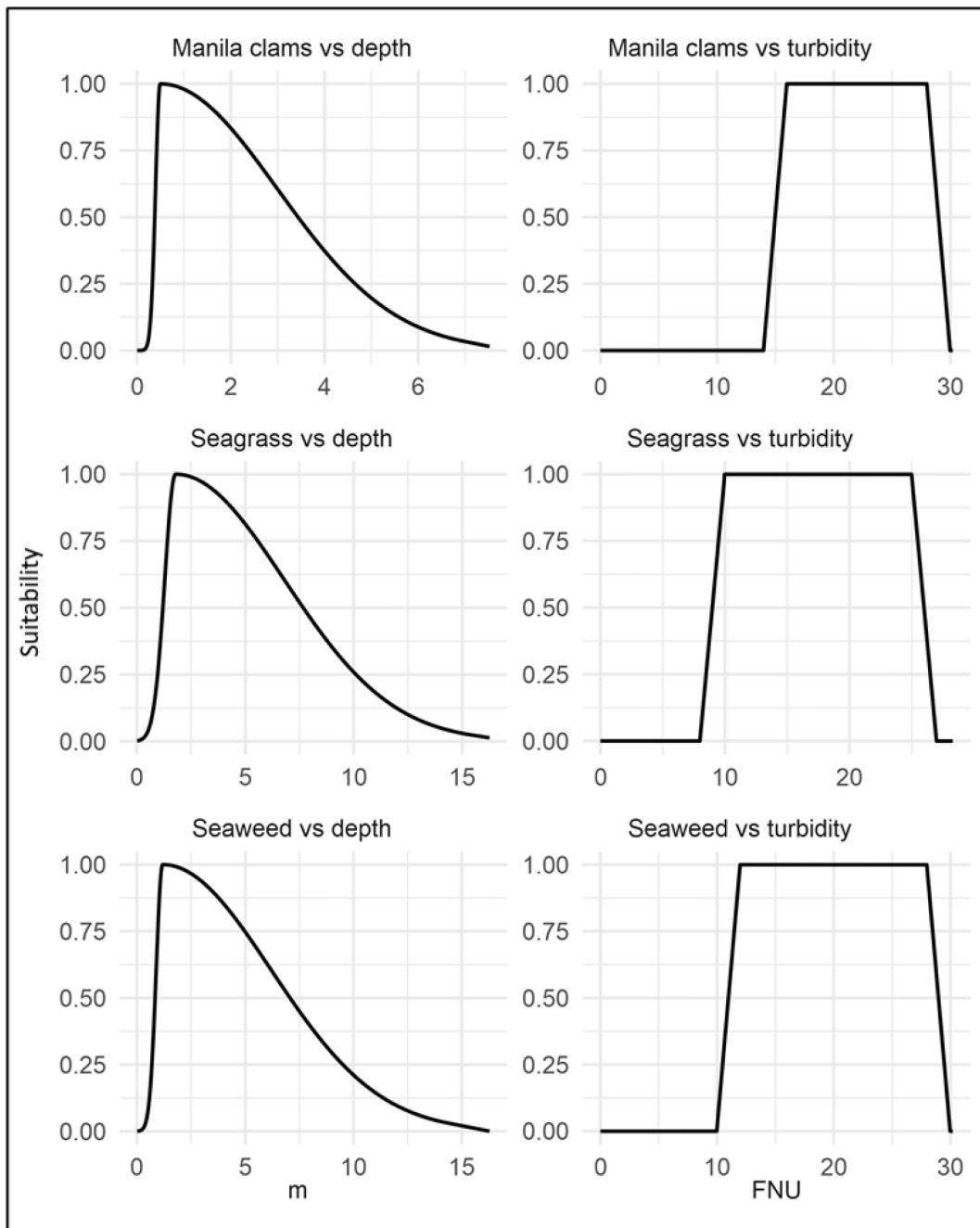


Fig. 4. Forcing functions of factors that regulate the spatial distribution of Manila clam, Seagrass and Seaweed functional groups in the model (respectively, from top to bottom).

Primer 6 and R (R Core Team, 2021), and figures were produced using the package ggplot2 and QGIS (QGIS Development Team, 2021).

The comparison was performed by carrying out a multidimensional reordination by Principal Component Analysis (PCA), on the Ecosystem Functioning Indicators values of the different water bodies. The same procedure was applied independently for the three different scenarios, and the deviations of each scenario with respect to the reference state was mapped on the space of the first two components. The Pearson correlation between BEQs and eigenvalues of principal components (based on the Ecosystem Functioning Indicators) allow to establish a relationship between variation of Ecosystem Functioning Indicators in scenarios and BEQs. A vector plot of the Pearson correlation of BEQs to the PCA axis is thus over-imposed to PCA graphs, where BEQs vector lengths are proportional to the Pearson correlations found.

3. Results

3.1. Water bodies characterization, ecosystem functioning indicators and BQEs

Values of Ecosystem Functioning Indicators for each water body and for the reference condition are reported in the Table 2. Biomass indicators are quite comparable among the water bodies; whereas, fisheries-related indicators show more clear variations. Total catches indicator presents the highest variability, peaking in SS, Mc, Ma, Te and Ts (areas with high density of fishing traps or Manila clam concessions). On the contrary, Chioggia (an anthropized water body) exhibits the lowest values. Also, Li and CS, water bodies characterized by a prevalent seagrasses' coverage, show a low catches level. In Fig. 6, the spatial

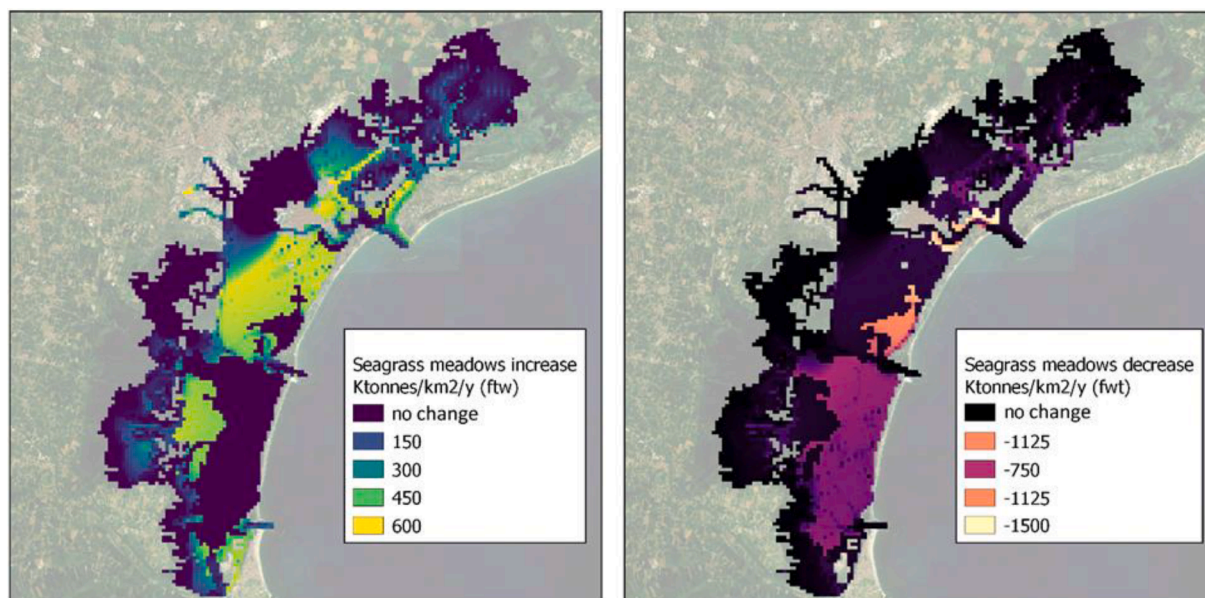


Fig. 5. Seagrass meadows scenarios: the increase (left; warm tones = increase from the reference condition) and the reduction (right; warm tones = reduction from the reference condition).

Table 2

Ecosystem Functioning Indicators estimated for each water basin under the reference conditions, mean and standard error in brackets.

Name	Acronym	tot biom (t/km ²)	comm biom (t/km ²)	fish biom (t/km ²)	inv biom (t/km ²)	inv biom/fish biom	tot catches (t/km ²)	fish catches (t/km ²)	mTL catches	mTL	ppr catches	K
Centro Sud	CS	20,485 (47)	22.4 (0.2)	12.3 (0.01)	235.2 (0.3)	19.1 (0.03)	6.2 (0.08)	2.0 (0.002)	2.5 (0.01)	2.3 (0.001)	19.9 (0.64)	2.89 (0.01)
Chioggia	CH	20,012 (210)	14.7 (0.1)	13.6 (0.06)	240.4 (1.0)	17.7 (0.03)	2.3 (0.01)	2.2 (0.01)	2.8 (0.01)	2.3 (0.002)	15.2 (2.39)	2.54 (0.02)
Dese	DE	18,354 (21)	16.3 (0.3)	12.4 (0.01)	241.1 (0.5)	19.5 (0.04)	3.5 (0.11)	2.0 (0.002)	2.7 (0.01)	2.3 (0.001)	17.5 (0.31)	3.14 (0.02)
Lido	LI	18,365 (65)	17.4 (0.4)	12.6 (0.01)	229.5 (0.6)	18.2 (0.06)	3.8 (0.16)	2.1 (0.002)	2.6 (0.01)	2.3 (0.002)	17.1 (1.06)	2.74 (0.01)
Marghera	MA	19,887 (32)	27.4 (0.2)	13.0 (0.01)	274.8 (0.6)	21.1 (0.03)	8.0 (0.11)	2.1 (0.002)	2.3 (0.01)	2.274 (0.001)	18.1 (0.50)	3.23 (0.01)
Mille Campi	MC	19,712 (20)	28.3 (0.2)	12.4 (0.01)	271.4 (0.4)	21.8 (0.02)	8.7 (0.11)	2.0 (0.002)	2.3 (0.01)	2.3 (0.001)	19.4 (0.30)	3.25 (0.01)
Palude Maggiore	PM	18,239 (10)	19.0 (0.2)	12.0 (0.01)	242.5 (0.4)	20.2 (0.04)	4.8 (0.11)	1.9 (0.001)	2.5 (0.01)	2.3 (0.001)	17.8 (0.15)	3.25 (0.02)
Sacca Sessola	SS	18,071 (48)	28.9 (0.3)	11.9 (0.01)	238.1 (0.6)	19.9 (0.03)	9.2 (0.12)	1.9 (0.002)	2.2 (0.01)	2.3 (0.001)	16.9 (0.70)	2.82 (0.01)
Teneri	TE	21,393 (35)	29.0 (0.7)	13.5 (0.01)	300.5 (0.8)	22.2 (0.05)	8.7 (0.30)	2.2 (0.002)	2.4 (0.02)	2.3 (0.002)	25.5 (0.80)	3.52 (0.02)
Tessera	TS	19,057 (42)	25.8 (0.3)	12.5 (0.01)	257.7 (0.8)	20.6 (0.05)	7.6 (0.12)	2.1 (0.002)	2.3 (0.01)	2.3 (0.001)	18.1 (0.63)	3.00 (0.01)
Val di Brenta	VB	20,525 (18)	15.3 (0.03)	14.0 (0.01)	266.8 (0.4)	19.1 (0.02)	2.3 (0.002)	2.3 (0.002)	2.8 (0.01)	2.3 (0.001)	16.8 (0.21)	2.67 (0.02)

pattern for the Primary Production Required (PPR), a good proxy of the exploitation level in terms of the energetic cost for the entire ecosystem, and the Kempton index, a measure of the diversity at the system level, are reported. The two indicators showed almost specular patterns, with the most exploited areas (located in the Central-Southern part of the lagoon) showing the highest values of PPR and the lowest ones of diversity.

The GLM results analysis showed few statistically significant correlations between Ecosystem Functioning Indicators and BQEs (Fig. 7). In particular,

- MaQi showed a negative relationship with the invertebrate biomass, mainly due to the competition for space, and a positive one with the Kempton index, mainly related to increased biodiversity, due to higher spatial heterogeneity;

- MAMBI showed a negative correlation with the total catches, due to the low diversity of benthos within the Manila clams fishing grounds, and a positive correlation with both the mTL of catches and mTL of community, related to the fact that the areas without Manila clam dominance are more balanced in terms of the benthic community composition;
- Hfbi showed a negative correlation with the commercial biomass and total catches; on contrary it shows a positive correlation with mTL of catches and mTL; this is mainly due to the fact that a more heterogeneous fish community implies more target species for the fishing activities, highlighting the important role played by the fish community in the area and a whole more structured community.

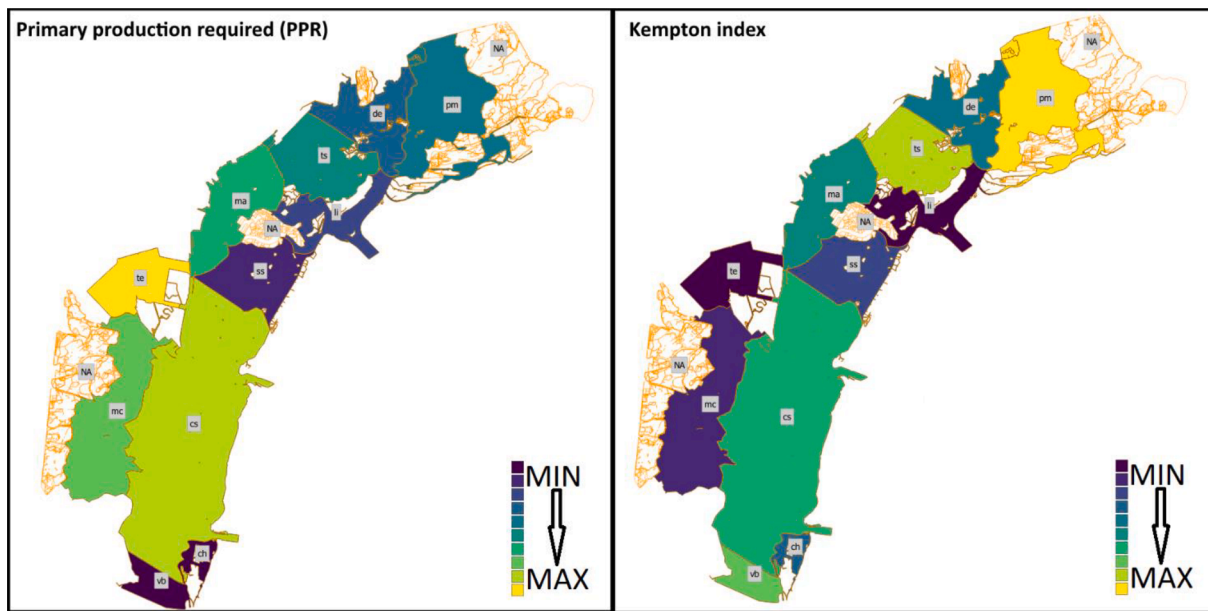


Fig. 6. PPR (left) and Kempton index (right) distribution in the different water basins.

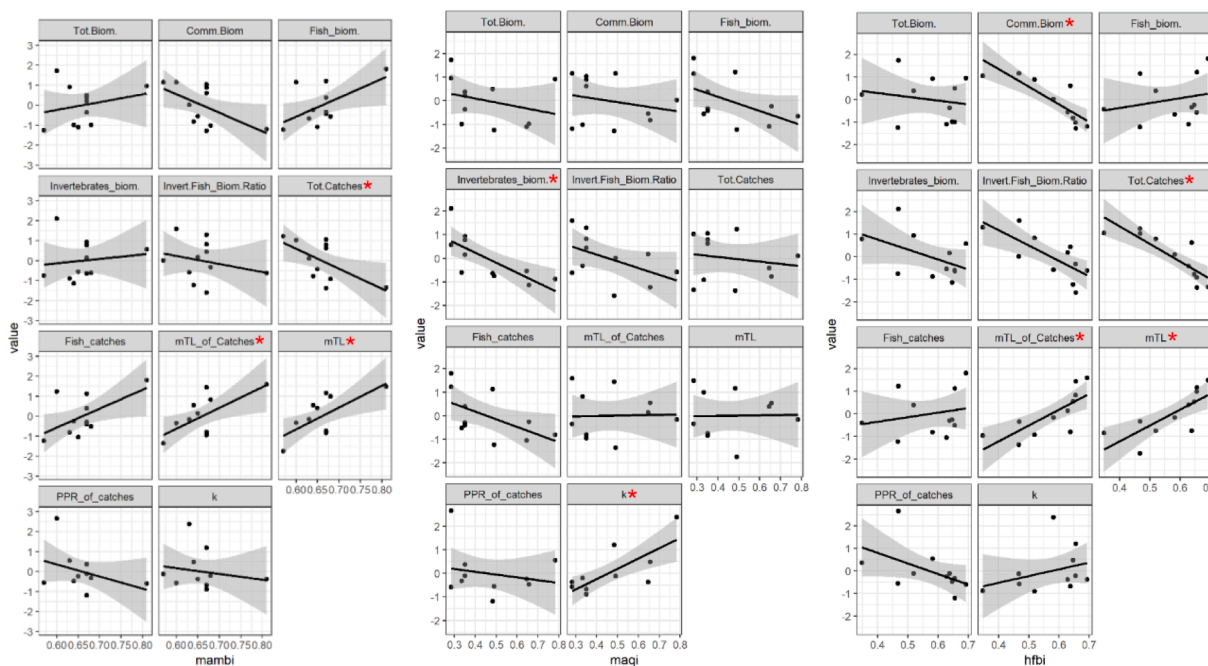
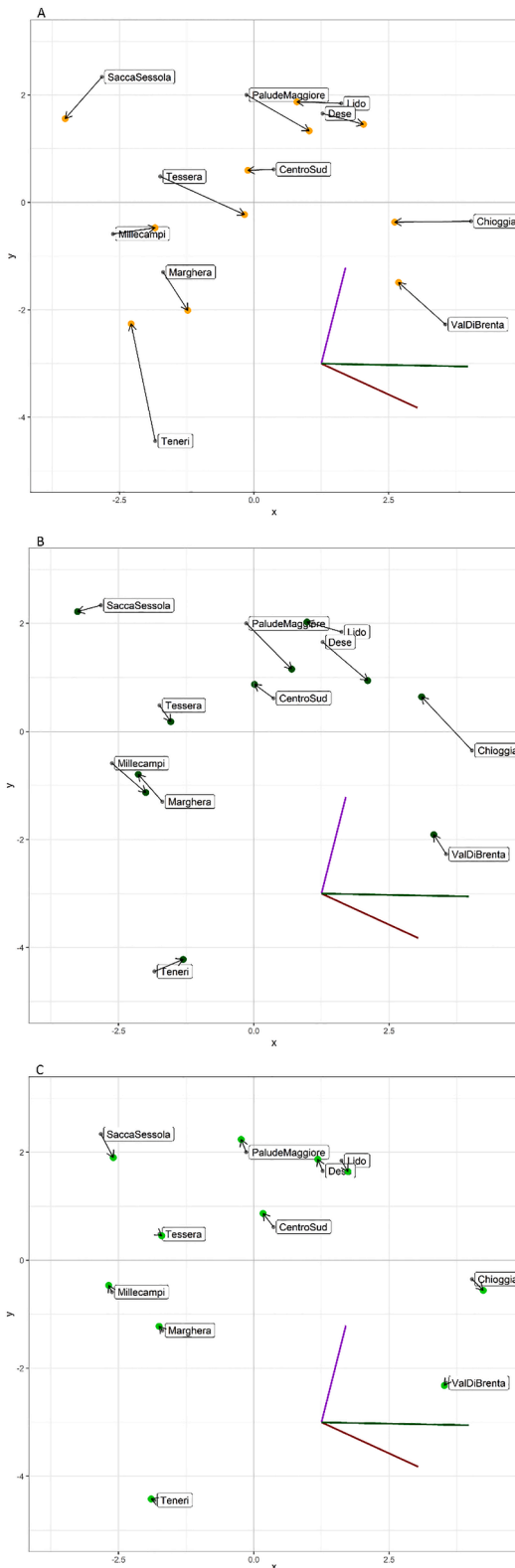


Fig. 7. Relationships between ecosystem functioning indicators and BQE, based on GLM analysis: MAMBI (left); MaQi (centre); HFBI (right); * = p-value < 0.05.

3.2. Scenarios analysis

The results of the comparison between the scenarios and the reference conditions are reported in the Fig. 8-A-C and Table 3. The most ‘impacting’ scenario resulted to be the fishing effort reduction, which may be related to the fact the top–down effects are more efficient in the lagoon environment, whereas the lowest is the seagrass up one, which could be related to the fact that the structuring effects on the habitat are more difficult to be replicated and require more time to produce effects. However, it would be worthy to note that under both the seagrass variation scenarios, almost all the water bodies (with the exception of Teneri and Sacca Sessola, in the Central area) moved on the same trajectory, even if in opposite directions, whereas fishing effort reduction produced a more heterogeneous pattern, in terms of trajectories. Not

always the two seagrass scenarios, produced opposite trajectories, as it would be expected (being one the opposite of the other). On the other hand, the same driver could produce opposite trajectories, also in water bodies clustered, as in Lido in comparison with Palude Maggiore and Dese, under the two seagrass scenarios (whereas the three showed the same trajectory under the fishing effort reduction scenarios). Some water body resulted to be quite stable and on the same trajectory under the different scenarios (e.g., Centro-Sud), maybe in relation to the important role of habitat structuring played by the seagrass meadow in increasing resilience at the basin level (this water body is almost entirely occupied by the meadow). On the contrary the most ‘reactive’ water body under each scenario are Teneri (under the fishing effort reduction), Chioggia (under the Seagrass reduction) and Sacca Sessola (under the seagrass increase); the most ‘reactive’ considering more than one



(caption on next column)

Fig. 8. -A. Water basins trajectory under the 50% fishing effort reduction in the comparison with the reference conditions; black arrows represent the movement of each water body in the space of the first two components of the PCA (83.9% of explained variation) performed on Ecosystem Functioning Indicators values; a vector plot of the Pearson correlation of BEQs to the PCA axis is over-imposed, with the vector length proportional to the Pearson correlation found. B- Water basins trajectory under the seagrass meadows reduction in the comparison with the reference conditions; black arrows represent the movement of each water body in the space of the first two components of the PCA performed on Ecosystem Functioning Indicators values; a vector plot of the Pearson correlation of BEQs to the PCA axis is over-imposed, with the vector length proportional to the Pearson correlation found. C- Water basins trajectory under the seagrass meadows increase in the comparison with the reference conditions; black arrows represent the movement of each water body in the space of the first two components of the PCA performed on Ecosystem Functioning Indicators values; a vector plot of the Pearson correlation of BEQs to the PCA axis is over-imposed, with the vector length proportional to the Pearson correlation found.

scenario are Chioggia and Palude Maggiore (Table 3).

The superimposition of the three BQEs in the PCA plots, highlighted that the three BQEs diverge among them, meaning that, in general a recovering according to one of them would be expected to produce a decrease in another one (see Fig. 8). On the other hand, obtained results showed that in all the water bodies (with the exception of Teneri and Millecampi, under the Seagrass down and Seagrass up scenarios respectively) Mambi is not affected by simulated drivers' changes.

4. Discussion

4.1. Spatially explicit food web models and EBM.

The possibility to characterize spatial gradients in ecosystem functions seems to be a pre-requisite for the implementation of a sound ecosystem management. Undoubtedly, spatial gradients can be resolved at multiple scales, from the micro-habitat to the ecosystem and the landscape-seascape. After the Millennium Ecosystem Assessment, the ecosystem has been identified as the management unit, however, current directives, such as the WFD in the specific of the Venice lagoon examined in this work, called for a sub-division of the ecosystem in different water bodies. The operational choice adopted here was thus to use the model for estimating indicators of food web functioning at the water bodies scale. Nonetheless, in order to capture the complexity derived by habitat heterogeneity and environmental gradients, it was necessary to consider a higher spatial resolution within the model (finer grid scale). A first attempt at spatializing food web models in the Venice lagoon was made by Brigolin et al. (2014), by balancing 3 zero-dimensional steady-state inverse models - one per lagoon macro-habitat (defined on the basis of a confinement gradient). Functional changes in food web ecology were investigated by comparing values of a set of 12 indicators derived by the ecological network analysis (Allesina and Bondavalli, 2004). From the methodological standpoint, the present work introduces two novelties with respect to the former approach: i) to represent the food web in two dimensions, with the resolution of 300 m; ii) to synthesize the information provided by food web functioning indicators, by using an ordination technique, the PCA, allowing the possibility to compare scenarios based on their distance with respect to the current state in the space of the first two components. This seems to be a resource supporting environmental evaluation, since the strategic environmental assessment (SEA), which is carried out for evaluating the environmental sustainability of plans and programs requires: a) the comparison of management scenarios with the reference conditions, b) the analysis carried out independently for each different effect, needs finally to be aggregated in order to provide an overall picture of the environmental effects of management measures at the whole system scale.

Table 3

Intensity of effects recorded under the three scenarios, in comparison with the reference conditions for each water body and relationship with each BQE vector; + = increasing condition for that.

Name	Acronym	Fishing Effort reduction	Seagrass meadow reduction	Seagrass meadow increase	Fishing effort reduction	Seagrass meadow reduction	Seagrass meadow increase
CentroSud	CS	0.48	0.44	0.32	maqi +	maqi +	none
Chioggia	CH	1.42	1.36	0.29	hbfi +	maqi +	none
Dese	DE	0.79	1.10	0.23	maqi +	hbfi +	hbfi +
Lido	LI	0.83	0.67	0.23	hbfi +	maqi +	none
Marghera	MA	0.85	0.67	0.10	maqi +	maqi +	hbfi +
Millecampi	MC	0.79	0.83	0.14	maqi +	hbfi +	mambi +
PaludeMaggiore	PM	1.34	1.19	0.25	maqi +	hbfi +	hbfi +
SaccaSessola	SS	1.04	0.45	0.49	hbfi +	none	none
Teneri	TE	2.23	0.57	0.07	none	mambi+	maqi +
Tessera	TS	1.72	0.37	0.05	hbfi +	hbfi +	hbfi +
ValDiBrenta	VB	1.17	0.43	0.06	none	maqi +	maqi +
Mean distance		1.15	0.73	0.20			

Based on the elements of novelty described, the Ecospace model developed within this work seems to provide an interesting resource to support EBM. The use of Ecospace was already suggested for management purposes, e.g., within the framework of ecosystem-based fisheries management efforts in Europe (ICES, 2012b). A key requirement for the future applicability of the present model in a management context is the verification of its capability of reproducing the system behavior. The work presented here show, anyway, that simplified steady state spatial results are giving already important information on ecosystem reorganization in space due to change in the absolute value of driving forces. The simulations do not account for changes in sea level rise, since bathymetric changes would have made even more complex to disentangle the role of seagrasses and fisheries in the spatial distribution of resources.

The Northern area of the lagoon is most diverse, with the highest diversity values (Kempton index), confirming the important role played by the presence of the sea-land salinity gradient in the structure and functioning of the transitional waters environments; whereas confined water bodies, located in the Central-Southern area, showed the lowest diversity. The opposite pattern has been observed in terms of human exploitation of the renewable resources (namely fishing activities), in terms of primary production required (PPR), with the most relevant areas located both in the most confined areas and in the seagrass meadows located in the Central-Southern part of the lagoon. The water bodies more impacted by the Venice town, as Lido and Sacca Sessola, showed at the same time lower diversity and lower exploitation. According to the combined picture provided by the PCA, water bodies seem to segregate on the basis of a combination between geographical (North vs South) and confinement degree. The Northern area confirmed to be that with the highest similarity among the water bodies, being the three water bodies (Lido, Palude Maggiore and Dese) closer each other (Fig. 8); indeed, this represents the last area in the lagoon maintaining the sea – land gradient (e.g. in terms of salinity); the most confined water bodies are located on the left part of the plot, even if quite spread along the second component (y-axis). Millecampi and Marghera, geographically distant and subjected to different disturbance regimes, resulted however almost clustered together, whereas the Southern part of the lagoon (Chioggia and Val di Brenta) resulted to be quite separated from the other ones.

Each water body is characterized by a different ecological equilibrium and reacts in a different way under the same driver variation – e.g. Lido in comparison with Palude Maggiore and Dese, under the two seagrass variation scenarios. On one side, different scenarios could affect in different way each water body, in some cases forcing a similar shift in all the water bodies (seagrass ones), in others showing contrasting directions of the shifts also in contiguous water bodies; moreover, the ‘effects intensity’ showed large differences among the three scenarios.

4.2. Ecological status and ecosystem functioning

In general terms, ecological status and ecosystem functioning are expected to be positively associated, being good ecological processes a sort of prerequisite for the ecosystem health. Obtained results show rather puzzling relationships between ecosystem functioning indicators and the metrics used to define ecological status in the Venice lagoon. Each BQE, indeed, showed statistically significant relationships with some Ecosystem Functioning Indicators, reflecting the hard work done by researchers for validating BQE, but also the lack of many relationships. This could be as a sign that the structural proxies used by the WFD do not exactly match with the functioning ones, and/or that the analysis at the compartment level performed in the WFD focused of different issues in relation to the functioning one. The metrics used to assess the biological quality elements are structural indicators based on the composition – at the taxa or functional group level - of the biological community (Borja et al., 2013; Vlachopoulou et al., 2014); whereas the ecosystem functioning indicators estimated by Ecospace are more comprehensive in terms of ecological processes, being referred to the entire trophic web of each water body, particularly with reference to the energy flows and energy required to sustain the biomass production. Moreover, it is worthy to note that many authors (Elliott and Quintino, 2007; Borja et al., 2013; Reyjol et al., 2014) highlighted that the assessment of biological quality elements in transitional environments can be particularly challenging: different metrics can produce contrasting results due to the unclear response to natural and anthropogenic stressors, and due the difficult identification of reference conditions. With respect to management, all this rises for a possibly relevant question about the real capability to verify under which scenarios each water body could respond according to a given EQB.

In the Venice lagoon, for instance, the M–AMBI and MAQI metrics show rather contrasting classifications across the water bodies, and furthermore, if a comparison between the first (2010–2012) and the second (2013–2015) monitoring cycles is made, the two metrics do not show a consistent response to the changes in the system (there are water bodies in which both metrics improve, others in which one improves and the other get worse, and vice-versa) (ISPRA-ARPAV, 2016). This behavior, combined with the “one-out-out-all” approach in the definition of the overall ecological status (which has been heavily criticized by several authors (Borja et al., 2013; Borja and Rodriguez, 2010; Hering et al., 2010) has resulted in a generally “flattened” classification, in which all water bodies are classified either as poor or moderate status (ISPRA-ARPAV, 2016). This situation does not allow to recognize where interventions are really needed. Overall, this situation hinders the definition of effective management strategies, leaving the WFD implementation at a standstill. Within this context, the adoption of an explicit spatial modeling approach could play an important role in fostering the WFD implementation, through the application of a systemic thinking that puts more emphasis also on ecosystem functioning, going beyond

the reductionist focus on “structural” biological quality elements. These have in fact been identified as essential advancements needed for a more effective implementation of the WFD (Vlachopoulou et al., 2014; Voulvoulis et al., 2017).

5. Conclusions

In general, obtained results on one side highlighted the need for more discussion about the implementation of the WFD, at least in complex and spatially heterogeneous transitional waters environments, as the Venice lagoon. For instance, it could be necessary to revise the adopted spatial units, i.e. the water bodies. On the other side, the opportunity to support the BQEs monitoring with an ecological modelling approach. These models are certainly not the panacea for addressing questions about the environmental management, as they have inherent uncertainties (on parameters, structure, processes etc.); however, they can prove useful for selecting among different policy choices, since they offer the opportunity to simulate the mean effects, preliminarily verifying the efficacy of the proposed interventions.

In this work, for instance, a first attempt of model corroboration was attempted, in which the operational choice was not to focus on the capability of reproducing observed trends in ecosystem functioning but, rather on how our model outputs match with the general ecological knowledge on the Venice lagoon. Moving in this direction, it could be possible to build up operational models useful for helping in the decision-making process.

CRedit authorship contribution statement

M. Anelli Monti: Writing – original draft, Data curation, Formal analysis, Methodology, Conceptualization, Investigation. **D. Brigolin:** Formal analysis, Writing – review & editing. **P. Franzoi:** Writing – review & editing. **S. Libralato:** Formal analysis, Writing – review & editing. **R. Pastres:** Writing – review & editing. **C. Solidoro:** Writing – review & editing. **M. Zucchetto:** Formal analysis, Writing – review & editing. **F. Pranovi:** Writing – review & editing, Supervision, Validation, Visualization, Conceptualization.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.108461>.

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