

Linking food web functioning and habitat diversity for an ecosystem based management: A Mediterranean lagoon case-study

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Abstract:

We propose a modelling approach relating the functioning of a transitional ecosystem with the spatial extension of its habitats. A test case is presented for the lagoon of Venice, discussing the results in the context of the application of current EU directives. The effects on food web functioning due to changes related to manageable and unmanageable drivers were investigated. The modelling procedure involved the use of steady-state food web models and network analysis, respectively applied to estimate the fluxes of energy associated with trophic interactions, and to compute indices of food web functioning. On the long term (hundred years) temporal scale, the model indicated that the expected loss of salt marshes will produce further changes at the system level, with a lagoon showing a decrease in the energy processing efficiency. On the short term scale, simulation results indicated that fishery management accompanied by seagrass restoration measures would produce a slight transition towards a more healthy system, with higher energy cycling, and maintaining a good balance between processing efficiency and resilience. Scenarios presented suggest that the effectiveness of short term management strategies can be better evaluated when contextualized in the long term trends of evolution of a system. We also remark the need for further studying the relationship between habitat diversity and indicators of food web functioning.

Keywords:

Habitat diversity; Food web functioning; Food web; Trophodynamic indicators; Water Framework Directive; Venice lagoon

1. Introduction

The investigation of the relationships between two major features of ecosystem structure, namely the community diversity and the spatial distribution of habitats, has become increasingly prominent during the last decade (Duffy, 2006; Raffaelli, 2006). In particular, spatial heterogeneity, once often neglected by ecologists in order to simplify conceptual models, at present is recognized as one of the main drivers affecting many ecological processes in terrestrial and aquatic environments (Yeager et al., 2011), and plays an important role in determining food web functioning (Rooney et al., 2008). These issues are not only of theoretical interest for community ecologists, but also of remarkable relevance for practitioners within the context of environmental management, since goods and services availability depends on ecosystem health and proper functioning (McLeod et al., 2005). As regards the implementation of the UNEP-MAP EcAp, "Ecological Approach" (UNEP/MAP/PAP, 2008), one of the main issues is the central role played by ecosystems, which are perceived as the 'management unit', as also suggested by the Marine Strategy Framework Directive 2008/56/EC (MSFD; European Community, 2008). The latter policy framework recognises the importance of achieving a Good Environmental Status (GES) of the EU's marine waters, in order to protect the natural resources upon which economic activities and society depend. As suggested by Rossberg et al. (2012), an increasing attention has to be devoted to the food web analysis in the context of the GES assessment, focussing on the key processes and relating them to the structure of the system both in terms of communities and habitat spatial distribution.

A major limitation in relation to the effective possibility to explore causal relationships between ecosystem structures and their functioning is the lacking of experiments (Ims, 2005), as the broad spatial scales at which many landscape/ecosystem processes occur make manipulation and replication either very difficult or impossible. The adoption of modelling approaches could help facilitating this understanding process (McCann and Rooney, 2009).

Food web models allow one to estimate energy flows within ecosystems, and to investigate their relationships with the system structure (Cury et al., 2003). Indices, based on thermodynamic concepts, information theory and trophic level descriptions, are calculated from the models (Müller, 1997). Even though spatially explicit results are nowadays provided by different food-web models, such as Ecospace (Walters et al., 1999), and Atlantis (Fulton et al., 2005, 2007), existing applications are mostly focused on the description of spatial gradients of biomasses for higher trophic level species, and in particular for those of commercial relevance (e.g. Steenbeek et al., 2013). To our knowledge, a gap exists in exploring the possible effects of spatial heterogeneity on the food web functioning at the scale of the entire ecosystem.

This work aims at explicitly relating the functioning of a transitional ecosystem with the spatial extension of its habitats. The approach is used to assess the effects on food web functioning due to changes related to manageable and unmanageable drivers. Results are discussed in the context of the application of current EU directives. Due to the high uncertainty involved in the dynamic representation of the community matrix, the temporal dimension was considered only at the ecosystem scale, i.e. as changes in habitat size, and assuming that the structure and functioning of each habitat remained at the steady-state. The model was tested in the

lagoon of Venice, where a comprehensive archive of data is available.

Operatively, the paper focuses on shifts in indicators of food web functioning induced by changes in habitat size, in relation to:

- i) long term changes, namely the increase of marine influence due to synergistic effects of erosion and sea level rise;
- ii) the implementation of an effective management of the mechanical clam harvesting - one of the main drivers affecting the Venice lagoon ecosystem in the last decades (Pranovi et al., 2006, 2008; Solidoro et al., 2010).

2. Material and methods

2.1. Food web models

The proposed approach aims at describing the food web functioning of spatial contiguous units (habitats), characterised by different community structures, and estimating the effects due to variation in their size. The modelling procedure includes the following steps:

- i) habitats are identified;
- ii) a different food-web is identified for each habitat;
- iii) energy flows within each food-web and energy exchanges among habitats are estimated by means of steady-state food web models;
- iv) an unique set of fluxes for the whole ecosystem is estimated, as a linear combination of the fluxes characterizing each habitat.

Energy fluxes were estimated using the so called “inverse method” first presented in Vézina and Platt (1988) and recently applied to the Venice lagoon ecosystem in Brigolin et al. (2011). Assuming that no biomass variation occurs during the time frame in which field data are sampled, the energy balance equation for the general i -th consumer at steady state reads as:

$$Q_i - R_i - D_i - F_i - P_i - M_i - EX_i = \varepsilon_i, \quad (1)$$

where: Q_i = consumption, R_i = respiration, D_i = egestion, F_i = fishing mortality, P_i = predation, M_i = other mortality, EX_i = net migration, and ε_i represents a residual term.

Predator-prey interactions were considered to be linear and top-down controlled by the biomass of the predator (Hosak and Eldridge, 2009). Metabolic gains and losses were parameterized based on specific metabolic rates (see references in Appendix A, Table A1). The extended formulation of each term of the budget is reported in Tables A2 and A3. In mathematical terms, the application of Eq. (1) to each of the “ m ” compartment of the food web leads to a system of “ m ” linear difference equations, which can be written as:

$$\mathbf{A} \cdot \mathbf{x} = \boldsymbol{\varepsilon} \quad , \quad (2)$$

in which, \mathbf{x} ($n \times 1$) represents the vector of “ n ” unknown flows among the compartments, \mathbf{A} ($m \times n$), a matrix which summarizes continuity equations and represents the vector of residuals, which are assumed to be randomly and independently distributed with uniform variance. Following the notation by Van de Meersche et al. (2009), the “inverse problem”, i.e. the estimation of energy fluxes, was therefore defined as:

$$\begin{cases} Ax = \varepsilon \\ Ex = f \\ Gx \geq h \end{cases} \quad (3)$$

The first row is, in fact, Equation (2), while the second and the third rows respectively set equality and inequality constraints, with E ($d \times n$), f ($d \times 1$) and G ($c \times n$), h ($c \times 1$). In general, the linear system of equations used to represent the food web is underdetermined, since the number of flows n largely exceeds the number m of independent mass-balance equations. The space of possible solutions is then reduced by introducing the set of constraints, see Table A4, which takes into account both site-specific information available (primary production estimates, landings data and feeding preferences, etc...), and general eco-physiological principles (assimilation efficiency, growth efficiency, and ecotrophic efficiency) (Savenkoff et al., 2004). Energy exchanges between habitats are also taken into account, and quantified by allowing an export of organic detritus from the more productive habitats towards the heterotrophic ones. This is done by balancing first the model at the more productive habitats, where an export of energy from the system is allowed. Once estimated, this energy is imposed as an input in the model as equality constraint at the heterotrophic habitats. Only detritus exchanges within the ecosystem were considered in the model, with no exchanges at the system boundaries (e.g. burial in deep sediments). Net energy export from the system was also considered in the form of catches.

In order to find out a unique solution within the space of mathematically equivalent solutions defined by system (3), the IM applied in this work uses an objective method of constrained optimization, based on the minimum-norm principle. This method was initially adapted from physical sciences by Vézina and Platt (1988) for the reconstruction of planktonic food webs. Details on the solution algorithm are reported in Vézina and Platt (1988).

A unique set of fluxes for the whole ecosystem are estimated, as a linear combination of the $x_{i,j}$ fluxes, where j indicates each different habitat:

$$\bar{x}_i = \sum_{j=1}^n x_{i,j} \cdot b_j \quad (4)$$

where the i -th flux x_i , represents a weighted average of the contributions by n habitats, and the b_j coefficients express the relative coverage of each habitat with respect to the entire ecosystem surface. Ecosystem

indicators are computed on the set of x_i fluxes.

2.2. Indicators of food web functioning

The set of selected indicators concerned two different categories of descriptors/criteria of environmental status, namely food web and fishery, and integrates simple combination of energy fluxes with more complex measures based on information theory. The ratio between total Primary Production, PP, and Total Respiration, TR, is intended to provide a measure of the overall auto/eterotrophism of the system. The first one was calculated as the sum of net primary productions of all the autotrophs, while the latter, which quantifies the total respiration, is obtained by cumulating the contributions of the whole community. According to Ulanowicz (2004), the Total System Throughput (TST), equal to the sum of all flows, is an indicator of ecosystem activity, while ascendancy (A) provides an integrated measure on the system performance in processing energy. Ecosystems propend to increase in ascendancy at the expense of the complementary overhead (F) which, in turn, expresses system capacity to adapt to new perturbations (Ulanowicz, 2004; Goerner et al., 2009). "A" and "F" were estimated from the inverse model output through a network analysis performed by means of the WAND software (Allesina and Bondavalli, 2004). FINN's CI and mean path length provide a measure of the energy cycling properties of the system, i.e. how many times further than the straight throughflow path length an average system inflow will travel because of cycling (Finn, 1976). Production of apex predators (TL4) was taken as an indicator of the state of top-predator species, as suggested within the context of the Descriptor 4 (marine food web) of the MSFD (Rombouts et al., 2013). Finally, with respect to fishing activity, the sum of catches and the ratio catches/PP were taken as indicators of the level of pressure on renewable resources.

2.3. Study area and identification of habitats

The approach outlined in the previous section was applied to Venice lagoon, a shallow water body covering an area of nearly 500 km² (around 400 km² of open water surface), with an average depth of approximately 1 m, and only the 5% of the lagoon deeper than 5 m (some navigable channels deeper than 15 m). The lagoon is connected to the Northern Adriatic Sea through three inlets (500-1000 m wide and 15-50 m deep), with a yearly averaged exchange of 8000 m³ s⁻¹ (Gacic et al., 2005). Water renewal is on the order of a few days for the area closest to the inlets and up to 30 d for the inner part (Cucco and Umgiesser, 2006). The lagoon is subjected to the implementation of different management measures and various planning actions, such as the Water Framework Directive 2000/60/EC (WFD; European Community, 2000) and local plans. Notwithstanding the high anthropogenic impact, it still shows a good resilience, sustaining plentiful of goods and services (Solidoro et al., 2010). During the last decades, the main drivers affecting the structure and functioning of the food web have been identified in: 1) changes in morphology and hydrodynamic conditions; 2) excessive nutrient loads; 3) mechanical harvesting of Manila clam. Many types of habitats, sub-tidal and intertidal, are present, such as seagrass meadows, tidal flats (both muddy and sandy), and salt marshes, each one playing a different ecological role (Franco et al., 2006; Tagliapietra et al., 2009). The open surface of the lagoon has been tessellated into a number of discrete territorial units using natural discontinuities (canals, watersheds)

(Tagliapietra et al., 2011). Upon this spatial discretization of the Lagoon, three main macrohabitats (hereafter

also MHs) were identified on the basis of morphological features, hydrodynamics and coverage (Fig. 1). These MHs come in succession from land seaward, along a composite gradient which includes salinity and water renewal. In the inner part of the lagoon, we distinguish a confined area (MH1), characterized by a high residence time and the presence of tidal flats surrounded by salt-marshes, which represent the structuring element of the macrohabitat itself. The remaining portion of the lagoon was subdivided into two macro-habitats, based on the presence/absence of seagrass meadows. This allowed us to distinguish between a bare-bottom macrohabitat (MH2), seasonally colonized by macroalgae, located in an intermediate position within the sea-land gradient, acting as a sort of transition area between the two others, and a seagrass-dominated macrohabitat (MH3), located in proximity of the inlets, characterized by the presence of well-structured seagrass meadows, mainly *Cymodocea nodosa* and *Zostera marina*.

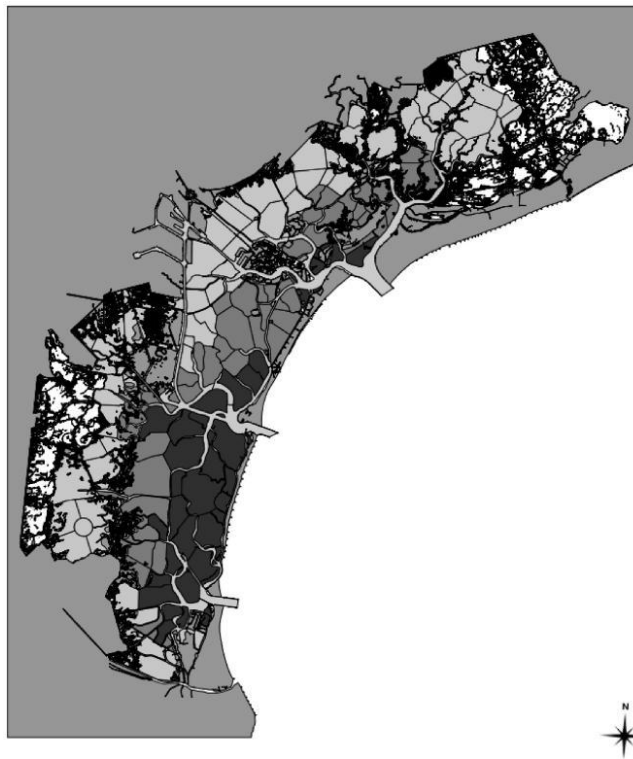


Fig. 1. Study area: the lagoon of Venice. The map shows the division in habitats adopted within this work: MH1; MH2; MH3.

As stated above, on the basis of the available literature (Libralato et al., 2002; Franco et al., 2006; Tagliapietra et al., 2009), we assumed that the ecological processes in the 3 macrohabitats give rise to different food web structures. The number of potential trophic interactions in aquatic food webs is far too high to provide its exact mathematical representation. Therefore, following an approach commonly adopted in system ecology (Belgrano et al., 2005), species were grouped based on their trophic guild. In the present case, the grouping procedure presents a further advantage, since it allows to represent communities belonging to different macrohabitats as networks characterised by the same topology. Table 1 introduces the 24 compartments composing MH1, MH2 and MH3 food webs, and lists the most important species included in each compartment. As can be seen, the only single-species compartment in the network is the Manila clam -

Ruditapes philippinarum, which represents one the most important economic ‘resources’ provided by the lagoon ecosystem, as well as one of the most difficult to manage. Manila clam biomasses show a remarkable spatial variability though present in all the three macro-habitats (Vincenzi et al., 2011).

Table 1. Aggregation of the community into compartments, and definition of network topology. Were possible, the most important MH/MHs (in terms of biomass) for the species were identified.

Compartment	Code	Groups included
Microphytobenthos	Mpb	<i>Amphora sp.</i> , <i>Cocconeis sp.</i> , <i>Navicula sp.</i> , <i>Nitzschia sp.</i> , <i>Thalassiosira sp.</i>
Seagrasses	Sg	<i>Zostera marina</i> (MH3), <i>Nanozostera noltii</i> (MH3), <i>Cymodocea nodosa</i> (MH3)
Macroalgae	Ma	<i>Vaucheria submarina</i> , <i>Ulva rigida</i> , Chlorophyceae, Rhodophyceae
Epiphytes	Ep	
Phytoplankton	Phy	
Bacterioplankton and microzooplankton	Ba	
Mesozooplankton	Zoo	Copepoda, Cladocera
Benthic bacteria and microzoobenthos	Mi	
Meiobenthos	Me	Protozoa, Nematoda, Copepoda
Macrobenthos detritivorous	Md	Polychaeta pro parte., Amphipoda pp., Isopoda
Macrobenthic herbivores	Mh	Amphipoda pp., Gastropoda pp.
Macrobenthos filter-feeders	Mff	Bivalvia (except <i>Ruditapes philippinarum</i>)
Manila clam	Rp	<i>Ruditapes philippinarum</i> (MH2)
Macrobenthos mixed-feeders	Mmf	Anthozoa, Decapoda pp.
Macrobenthos carnivorous	Mc	Decapoda pp., Gastropoda pp., Polychaeta pp.
Suprabenthos	Sb	<i>Crangon crangon</i>
Hyperbenthivores-Zooplanktivores fishes	HZ	Mugilidae juveniles (<i>Liza</i> spp. MH1-MH2), <i>Atherina boyeri</i> , <i>Dicentrarchus labrax</i> juveniles (MH1)
Microbenthivores	Mib	Syngnathidae (MH3), <i>Knipowitschia panizzae</i> (MH1-MH2), <i>Pomatoschistus</i> spp (MH1-MH2),
Zosterisessor ophiocephalus juveniles (MH1-MH3), Sparus aurata juveniles (MH1)		

Macrobenthivores	Mab	<i>Zosterisessor ophiocephalus</i> (MH1-MH3), <i>Solea solea</i> , <i>Sepia officinalis</i> (MH3-MH2), Plathichthys flesus (MH1), Sparus aurata (MH3)
Detritivores	Dtv	Mugilidae (Liza spp. MH1)
Hyperbenthivores-piscivores	Hp	<i>Dicentrarchus labrax</i>
Birds	Bi	<i>Chroicocephalus ridibundus</i> , <i>Larus melanocephalus</i> , <i>Larus michahellis</i> , <i>Sterna hirundo</i> , <i>Sterna sandvicensis</i> , <i>Sterna albifrons</i> , <i>Podiceps cristatus</i> , <i>Podiceps nigricollis</i> , <i>Calidris alpina</i> (MH1), <i>Tringa totanus</i> (MH1)
Organic detritus	DET	Dissolved and particulate detrital organic matter present in the water column. Fast degradable detrital organic matter deposited on the upper layer of the sediment and dissolved in interstitial waters

The biomass densities of the 23 compartments for the 3 food-webs were estimated on the basis of a comprehensive archive of ecological data, collected between 2001 and 2005 and reported in Table A1 (supporting material). Data for 12 over 23 compartments were sampled in 2003, from May to October. For primary producers and macrozoobenthos, available data were assigned to each macrohabitat based on the geographic positions of sampling stations, and median values and ranges were computed for each aggregated set of data. Most of fish biomasses were estimated on the basis of commercial landings, which were sub-divided among the three macrohabitats, on the basis of the spatial distribution of the fishing effort (in terms of number of fishing gear per unit of area) (Pranovi et al., 2013b). Parameters specifying metabolic rates were set based on in situ measurements (Mpb, Sg, Ma, Phy), statistical models (Md, Mh, Mff, Mmf, Mc) and literature references (Sb, Hz, Mib, Mab, Dtv, Hp, Pb, Wa) (see Table A1 in the supporting material).

Each food-web model consisted in 23 energy balance equations which had to be solved for 164 unknown flows (Tables A2-A4). As expected, the system was strongly underdetermined, since the number of flows largely exceeded the number of independent mass balance relations. In order to reduce the space of solutions, a set of 28 equality and 491 inequality constraints was added. Equality constraints were used for specifying fishery landings, the net-primary production and, in the case of MH2, the import of organic detritus. As described in Table A4, organic detritus in the overall lagoon was considered to be at steady-state (Brigolin et al., 2011). Exchanges of organic detritus among different macro-habitats were quantified by allowing an export of detritus from MH1 and MH3, which are considered as the most productive systems (Sfriso and Facca, 2007; Franco et al., 2006). The sum of detritus exported by MH1 and MH3 was imposed as an import for MH2. According to Pranovi et al. (2003) MH2 is largely sustained by the resuspension of benthic production. An

increase in microphytobentos productivity as a consequence of sediment resuspension, burial activity or

different hydrodynamic regimes has been also described in other lagoons and coastal areas (Pérez Ruzafa et al., 1991, 2007; Lohrer et al., 2004; Jantzen et al., 2013). In the present work we assumed that MH2 also benefits from an energy import in the form of labile detritus, resuspended in the contiguous MH_s, along with the finest sediment fraction, by the action of tidal currents and winds (see e.g. Sfriso et al., 2005). Based on the shape of MH2 (see Fig. 1), located in a well flushed portion of the lagoon (Cucco and Umgiesser, 2006) and completely bordered by MH1 and MH3, no limitations of detritus transport in space were assumed.

Inequality constraints were used for setting the ranges of consumption, ecotrophic and absorption efficiencies and imposing the positiveness of flows. All diet preferences were introduced in the model as inequality constraints. For each proportion of prey *i* consumed by the group *j*, lower and upper limits were set ($DCMIN_{ij} = DC_{ij} - SD$, $DCMAX_{ij} = DC_{ij} + SD$), where DC_{ij} represents the average estimated diet. In the case of macrobenthos diet constraints were based on expert opinion. Diet compositions for most fish and birds were based on samples from the Venice lagoon and species-specific knowledge from Mediterranean wetlands (Ass Faunisti Veneti, 2004; Franzoi et al., 2005).

2.4. Simulations set up

The model was used for assessing the consequences on the lagoon food web of:

- long-term changes in the bathymetry, which could be due to sea level rise and erosion synergistic effects, producing important macrohabitat modifications and shifting (S2100);
- short-term changes, due to the implementation of measures for enforcing a sustainable exploitation of the stock of Manila clam through a progressive reduction of fishery and transition towards aquaculture production in leased areas, thus allowing recolonization of seagrasses in areas at present heavily impacted by clam fishery (S2020).

Food web functioning trend was evaluated on the basis of a historical reconstruction of macrohabitat extension, and a future scenario of change in their size, respectively named R_{1900} and S_{2100} , see Table 2. The R_{1900} considers the state of the lagoon at the beginning of the 20th century, before salt marshes started decreasing due to land reclamation for industrial activities, housing, airport construction and changes in the hydrodynamic conditions due to the opening of new channels, wave erosion and alteration of sediment budget (Sarretta et al., 2010). In this case, moreover, the Manila clam and its mechanical harvesting were absent, since they started in '90s (Boatto and Pellizzato, 2005). All this, combined with the fact that turbidity was maintained at values remarkably lower compared to the current ones, creates a favourable situation for the survival of seagrass meadows also in the area currently occupied by MH2 (Sfriso and Facca, 2007). The future scenario of change, S_{2100} , focuses on the sea level rise induced by climate change, which is expected to cause the loss of a relevant fraction of the area at present occupied by salt marshes: based on the projections reported in different works (see e.g. Day et al., 1999) we tentatively set a 50% reduction of the size of salt-marshes by 2100. The presence of salt marshes represents the key morphological feature structuring MH1 and, we assumed that the disappearance of salt marshes would irreversibly compromise the macrohabitat

functionality. As a baseline assumption, we hypothesised that the space lost by MH1 would be replaced by MH2 and MH3, proportionally to their extension in 2003. An upper limit to the extension of MH2 had to be set, in order to avoid a deficit of organic detritus at the scale of the whole lagoon: this was implemented by imposing MH2 detritus import $1/4$ MH1 μ MH3 detritus exports.

Table 2. Areas occupied by the three macrohabitats in 2000 (see Fig. 1) and in the different scenarios explored.

Macrohabitat	Area [km ²]			
	2000	2020	2100	1900
MH ₁	191.8	191.8	95.9	220
MH ₂	100.3	51.1	158.8	0
MH ₃	64.1	113.3	101.5	136.2
tot. open lagoon	356.2			

In relation to the short term scenarios, it has to be considered that the Manila clam exploitation represented one of the most important drivers affecting the lagoon ecosystem during last decades (Pranovi et al., 2013a). This species, indeed, was introduced for aquaculture purposes in 1983 (Cesari and Pellizzato, 1985) and quickly spread to the whole lagoon, deeply changing macrobenthic community structure (Pranovi et al., 2008) and feeding an exploitation activity, which peaked in 1999 with a production of about 40,000 tonnes (Boatto and Pellizzato, 2005). This fishing activity was carried out, within a context of an open access regime, by using highly impacting gears, even if they were banned in the lagoon (Pranovi et al., 2004). All management efforts implemented during the time to reduce the fishing pressure regularly failed, due to its high profitability. At present, the only management option is related to the transition towards a proper clam aquaculture. In the scenario at 2020, S_{2020} , Manila clam harvesting is strictly limited to leased areas, identified by local authorities. Under this scenario we hypothesised a re-colonization of MH2 by seagrass meadows, favoured by the local decreased disturbance, e.g. in terms of sediment resuspension (Sfriso et al., 2005). In fact, the effect of turbidity induced by the mechanical bottom dredging would probably affect above all the small portion of the lagoon devoted to clam aquaculture.

3. Results

An extended set of model outputs is reported in Appendix B, Tables B1, B2, B3: energy flows associated with consumption, respiration, egestion, natural and fishing mortality, are detailed for the 23 compartments of the three macrohabitats studied, along with assimilation efficiencies, growth and ecotrophic efficiencies, and trophic levels. Consumption fluxes obtained by closing the energy balance are reported in Tables B4, B5, B6. Indicators of functioning of the 3 separated macrohabitats for 2000s are reported and commented in Table B7. In accordance with the specific objectives of this work, the following paragraphs will focus on model predictions

concerning the scenarios described above.

3.1. Long term (hundred years) changes

Indicators for the spatial macrohabitat distributions R_{1900} and S_{2100} are compared in Table 3 to the current situation, C_{2000} . As can be seen, the primary production grows under both the considered scenarios at almost the same level, but the respiration process remains dominant in the S_{2100} , whereas in the R_{1900} , production largely exceeded respiration processes. The overall system activity, measured by TST, resulted significantly higher in the S_{2100} compared to the other two configurations. In R_{1900} the system shows a high accumulation of organic detritus, whereas in the other two cases no accumulation is recorded. In relation to this it is worth to note that in the S_{2100} scenarios the global production of the MH2 was limited by the detritus availability in the lagoon environment. In terms of maturity, the R_{1900} showed the better situation as reflected by the Ascendency value, and no appreciable difference is predicted between the present and the future state. Also, related to system functioning, the top predators production (PTL4) shows the lowest value in the present configuration. As concerns the energy cycling in the system, the lowest values for both Finn's CI and mean path length are recorded in the future scenarios, whereas the highest values are showed by the past one. Finally, a slight increase in the fishery production is observed in the future scenario.

Table 3. Model results under long-term scenarios of change.

	R1900	C2000	S2100
Total PP [kj m ² d ¹]	172.3	148.5	171.0
Tot. PP/tot. resp. [-]	2.72	1.0	1.01
Total System Throughput [kj m ² d ¹]	610.2	752.8	869.6
Organic detritus surplus	108.5	0	0
Ascendency (A) [% Capacity]	0.51	0.44	0.44
Overhead (F) [% Capacity]	0.49	0.56	0.56
P TL4 (Hp p Pb)	0.045	0.040	0.043
[kj m ⁻² d ¹]			
Finn's CI [%TST]	2.8	2.2	1.4
Finn's mean path length [-]	3.54	3.49	3.42
Catches [kj m ² d ¹]	0.33	1.04	1.12
Catches/NPP [-]	0.002	0.007	0.007

3.2. Short term changes

The primary, and expected, effect related to the management strategy implementation for the Manila clam exploitation is the significant reduction in total catches, see Table 4. In parallel, the total primary production increases of about 10%, with a reduction of the overall system respiration, and a lower ecosystem activity, as indicated by the 8% decrease of TST. Moreover, a tendency towards an increase in system maturity is recorded, as highlighted by the slight increase in Ascendency and P TL₄ indicators. Finally, the model predicted a slight increase in terms of cycling efficiency, as shown by Finn's Cycling index values.

Table 4. Model results under short-term management interventions.

	C2000	S2020
Total net primary production (PP) [kj m ⁻² d ⁻¹]	148.5	164.5
Tot. PP/tot. Resp. (PP/R) [-]	1	1.55
Organic detritus surplus	0	57.7
Total System Throughput (TST) [kj m ⁻² d ⁻¹]	752.8	695.7
Ascendency (A) [% Capacity]	0.44	0.45
Overhead (F) [% Capacity]	0.56	0.55
P TL ₄ (HppPb) [kj m ⁻² d ⁻¹]	0.04	0.043
Finn's CI [%TST]	2.2	2.4
Finn's mean path length [-]	3.49	3.50
Catches [kj m ⁻² d ⁻¹]	1.04	0.68
Catches/NPP [-]	0.0070	0.0041

4. Discussion

4.1. Suitable food web indicators in the context of current directives

The WFD is the policy framework enforced in the Venice lagoon. This requires that the classification of each water body “shall be represented by the lower of its values (classes) for the biological and physico-chemical monitoring results for the relevant quality elements” (European Union, 2000, Annex V, section 1.4.2 (i)). This procedure, also known as the “one-out-all-out” rule (Clarke, 2012), has been selected to reduce the likelihood that a water body is classified as good status, when in reality it is below good status (Hering et al., 2010). However, this rule has been largely criticized by different authors (Borja and Heinrich, 2005; Sandin, 2005; Sondergaard et al., 2005; Tueros et al., 2009), in particular considering that the results are not representative of the functioning of the ecosystem (Borja et al., 2012). EU environmental policies have evolved taking into account this limitation, and in the MFSD there is a clear effort in moving towards an Ecosystem Based approach, by separating the ecosystem into a set of process-related (functional) objectives, then recombining them to ensure the integrity of the ecosystem at a regional scale (Borja et al., 2011). Within this context, even

though performed in a water body interested by the WFD, the simple exercise presented in this work has an applied interest. In fact, deriving indicators of food web functioning taking into account spatial habitats diversity can be seen as a useful science based approach to integrate a recognized WFD limitation.

An important challenge related to the implementation of the MSFD, is referred to the selection of indicators for assessing the ecological status. Indeed, whilst criteria and indicators suggested aim to be informative on food web functioning, they are, at their current state of development, possibly insufficient to assess whether marine environments really are at GES. MSFD Descriptor 4 refers to the food web analysis, although, as underlined by Rombouts et al. (2013), the attention is mainly focused on the structure (with a clearer focus on macrohabitat/species composition, rather than on energy and matter flows) and less on the processes (just the TL4 secondary production). The implementation of indicators able to catch different features of energy flow in the food web therefore represents an important challenge. According to Kones et al. (2009) indicators derived by network analysis are quantities much better constrained with respect to the single food webs fluxes on which they are calculated, and can therefore be seen as more robust measures to describe the functioning of a food web. In this context, one key idea behind the present work, is that indicators directly measurable in the field could be complemented with more integrative ones, such as those resulting from ecological network analysis (Ulanowicz, 2004). In the application presented we choose to complement PTL4 with classical system growth and development indices (Ascendency-Overhead), and pathway analysis (Finn's cycling indices). A general feature of our results is that, as a consequence of a small expansion of the set of indicators, one obtains a more articulated picture of changes in food web functioning. Remarkably, the estimation of indicators carried out embeds the characteristics of the food webs of the three macrohabitats, thus integrating the evaluation across space and across the different food web compartments.

4.2. Management of the Venice lagoon ecosystem

Within the context of the WFD implementation, the Venice lagoon was divided in 11 different water bodies (WBs), on the basis of different criteria, such as salinity (polyaline vs oligoaline) and confinement (Autorità di Bacino, 2010). These areas are treated as management units for which the good ecological status should be achieved and different management strategies implemented. In an ecosystem based management perspective, the challenge remains, therefore, how to combine together these different WBs considering, for example, possible synergistic effects due to the connectivity among different patches. The present paper analyzes how changes in the macrohabitat size, could affect the functioning at the whole system level.

In terms of spatial configuration, even if a different number of sub-units were taken into account in the WFD implementation and in the present study, both discretize the land seaward gradient (Autorità di Bacino, 2010). Seagrass meadows, which characterise in particular the MH3, can be considered structuring elements (Hovel et al., 2002), and are recognized by the EU Directives as a key issue in terms of management objectives, to be preserved, and, if possible, extended in terms of presence (COST ACTION ES0906). The comparison between R_{1900} and C_{2000} confirmed that changes in the relative size of macrohabitats, combined with the Manila clam invasion, have deeply modified the ecological functioning of the lagoon food web, reducing energy processing

efficiency, measured by A , at the expenses of its resilience, given by b . This result, based on the interpretation of complex systemic indicators b and A , is also confirmed by a simpler measure of the food web functioning, which is the fraction of energy reaching the higher trophic levels (P_{TL4}). The comparison between C_{2000} and S_{2100} highlights the important role played in the lagoon ecosystem by MH1 and MH3. Both salt marshes and seagrass meadows can be considered as structuring elements of their macrohabitat. In particular, based on a preliminary comparison among the three distinct macrohabitats (reported and commented in Appendix B), the highest efficiency in energy processing was recorded at MH1, the salt marshes (higher ascendancy and higher values of Finn's indices). In this context, the progressive loss of salt marshes, expected as consequence of the sea level rise and erosion processes, will produce further changes at the system level, with a lagoon showing a decrease in the cycling efficiency (Finn's indices): Finn's CI is 21% lower in S_{2100} with respect to C_{2000} , and 50% lower with respect to R_{1900} . Nonetheless, in S_{2100} , a larger fraction of the production is available for higher trophic level species ($PTL4$) and fisheries (catches indicators). To this regard it is worth remarking that the higher values of catches should not be regarded as an indication of absolute positive change for fishery. In fact, as currently formulated, the model is limited in resolving the expected negative impact on fishery induced by the loss nursery areas located in the salt marshes, MH1.

4.3. Management of MH2

The WFD requires Member States to distinguish between 'natural' and 'heavily modified water bodies' (HMWBs). The latter are allowed to have an acceptably lower ecological status as the result of hydromorphological pressures, which cannot be removed because of the high social or economic cost (Hering et al., 2010). The quality target for HMWBs is 'good ecological potential' (GEP), defined as the ecological quality expected under the conditions of the implementation of all possible measures (Borja and Elliott, 2007). Even though not including any HMWB (Autorità di Bacino, 2010), the structure and morphology of MH2, particularly in the central sub-basin, has been largely shaped by human activities, in order to provide certain functions or uses. The MH2 is composed mainly by bare bottom habitats, seasonally colonized by macro-algae (Sfriso et al., 2003), located in an intermediate position within the sea-land gradient, between the seagrass meadows and the inner salt marshes. The most important modifications have been induced by the excavation of the dei Petroli channel (connecting the Malamocco inlet with the industrial area of Porto Marghera) and the subsequent increase of the erosion processes (Ravera, 2000).

Moreover, this area represents the elective habitat for the Manila clam in the lagoon, and consequently the exploitation activity tends to concentrate here, increasing the negative effects and significantly contributing to its degradation (Pranovi et al., 2008). Restoring the morphology of such water bodies to good ecological status, as required by the WFD, may have a significant impact on these uses and social or economic costs. In the context of the present situation, management options about the Manila clam exploitation are limited to the allocation of clams fishery in small portions of the lagoon dedicated to a sort of aquaculture activity (G.R.A.L., 2009; Province of Venice (2009)). The short term management scenario examined in this work assumed that the implementation of this restricted access to the Manila clam resource would be accompanied by measures

aimed at favouring the re-colonization by seagrass meadows (see e.g. Renton et al., 2011). Simulation results demonstrated that this would produce a slight transition towards a more mature status at the ecosystem level, as highlighted by the different indicators. In particular, the 10% increase in PTL4 indicates a better efficiency in energy flowing towards the highest part of the food web, accompanied by an improved energy cycling, as indicated by Finn's indices. This could be interpreted as an analogue of the GEP measured at the level of the whole ecosystem, thus indicating a way towards the achievement of a better status of the lagoon, under the constraint of a high level of modifications induced by human uses in MH2. It is worth nothing here that the effectiveness of such short term management strategies could be better evaluated when contextualized in the long term trends of the system. Results considered in the present work did not consider explicitly the combined effects of short and long term scenarios. To this end, the simulation set up presented should be modified, by including a proper set of assumptions on the transient dynamics of habitat size.

5. Concluding remarks

According to different ecosystem management frameworks, policies should move from a remediation perspective, which works on compensative and restoration measures related to already impacted situations, towards a precautionary approach, in which decisions and strategies anticipate negative possible events. The present application underlined the importance of adopting modelling tools and indicators of functioning capable to compare possible effects due to different macrohabitat configurations within the same ecosystem. On the long term temporal scale, model results indicated that the expected loss of salt marshes will produce further changes at the system level, with a lagoon showing a decrease in the energy cycling efficiency. On the short term scale, simulation results indicated that fishery management accompanied by seagrass restoration measures would produce a slight transition towards a more efficient food web, in terms of energy processing. In this context, a science-supported planning could help protecting a variety of key habitats, especially those produced by structure-forming organisms, and maintaining adequate populations of apex predators. Scenarios presented suggest that the effectiveness of short term management strategies could be better evaluated when contextualized in the long term trends of evolution of a system. We remark the need for further studying the relationship between habitat diversity and indicators of food web functioning.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.marenvres.2014.02.006>.

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