



Why coastal lagoons are so productive? Physical bases of fishing productivity in coastal lagoons

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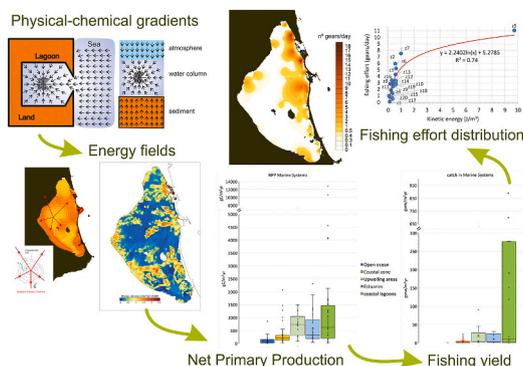
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HIGHLIGHTS

- Coastal lagoons are among the most productive ecosystems in the world.
- Coastal lagoons are exploited by humans, marine birds, fishes and invertebrates.
- Trophic variables can explain <43 % of the fishing yields.
- Lagoons are energy fields determined by multiple physical-chemical gradients.
- Coastal lagoons productivity is mainly promoted by physical and chemical gradients.

GRAPHICAL ABSTRACT



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ABSTRACT

Coastal lagoons are among the most productive marine ecosystems in the world. Annual primary production varies from 50 to > 500 g C m⁻² year⁻¹, being of the same order of magnitude as that of the upwelling areas. Many lagoons lie within the range of eutrophic (300–500 g C m⁻² year⁻¹) or hypereutrophic (> 500 g C m⁻² year⁻¹) conditions. The high productivity of coastal lagoons makes them subject of exploitation by many marine fishes and invertebrates, that use them as nursery areas and feeding grounds during their early life cycle phases, and most lagoons support important fisheries or maintain aquaculture exploitations. The high levels of their biological production can be explained by some of their common features as shallowness and the strong influence of terrestrial systems. Shallowness favors that the photic zone extends to the lagoon bottom and that wind can promote the resuspension of nutrients and organisms. The interaction with land also introduces significant amounts of nutrients. However, trophic variables can explain < 43 % of the fishing yields, and further than the trophic status of the lagoons, several works showed that the biological productivity of coastal lagoons can be explained by their geomorphological features such as the positive influence of shoreline development and the

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negative influence of depth. Using the Mar Menor lagoon as a case study, we propose that although nutrient inputs and light can be limiting factors for photosynthetic based productivity, increasing fishing yield up to a certain limit, the productivity of lagoons is mainly promoted by more general forces associated to physical and chemical gradients.

1. Introduction

Coastal lagoons are among the most productive marine ecosystems in the world (Alongi, 1998) (Fig. 1). They have one of the highest fishing yields (Nixon, 1982; Kapetsky and Lasserre, 1984) and provide a significant number of socio-economic benefits for humans (Farber and Costanza, 1987; Costanza et al., 1989; Spurgeon, 1998). This is not negligible, considering that they represent 13 % of the world's coastline (Barnes, 1980).

Annual primary production ranges from $50 \text{ g C m}^{-2} \text{ year}^{-1}$ to over $500 \text{ g C m}^{-2} \text{ year}^{-1}$ (Knoppers, 1994; Kennish, 2015), comparable to upwelling areas (Knoppers, 1994). Many lagoons experience eutrophic ($300\text{--}500 \text{ g C m}^{-2} \text{ year}^{-1}$) or hypereutrophic ($> 500 \text{ g C m}^{-2} \text{ year}^{-1}$) conditions (Nixon, 1995; Kennish, 2015), with instances like Egypt's Maryut lagoon exceeding $1800 \text{ g C m}^{-2} \text{ year}^{-1}$ (Knoppers, 1994).

In fact, most of the ecosystem services and marketable socio-economic benefits provided by coastal lagoons derive from this biological productivity (Newton et al., 2018; Pérez-Ruzafa et al., 2019a). This is also exploited by many birds, making coastal lagoons some of the important sites for migratory birds being protected by international agreements like the RAMSAR Convention on Wetlands.

These habitats act as nursery areas and feeding grounds for opportunistic marine estuarine fishes that use them for developing during the early phases of their life cycle (Yañez-Arancibia and Nugent, 1977; Clark, 1998). These species colonize the lagoons as juveniles and go back to the sea as adults for reproduction. Taking advantage of this, many lagoons support important fisheries and some of them maintain intensive and extensive aquaculture exploitations that provide incomes based

on the quality and price of their natural products. Excluding aquaculture, the total annual yield for the 356 lagoons with available data recorded in Pérez-Ruzafa and Marcos (2012) reached $694,195.9 \text{ t year}^{-1}$, with a mean of $137.4 (\pm 21.6 \text{ SE}) \text{ kg ha}^{-1} \text{ year}^{-1}$. Considering only the 169 Mediterranean coastal lagoons included in that study, the total catch exceeds $191,534.3 \text{ t year}^{-1}$. As a result, fishing in coastal lagoons accounts for 10 % of fish production and 30 % of demersal fish in the Mediterranean area (Quignard, 1984). Often, at local scale, the economic yield derived from lagoon fisheries equals or surpasses that obtained in the adjacent coastal areas (Amanieu, 1973; Mehanna, 2007).

Despite the high variability in geomorphological features, salinity, trophic status and species composition (Pérez-Ruzafa et al., 2007, 2019a; Newton et al., 2014), coastal lagoons share some common properties like shallowness, restricted connectivity with the open sea and the presence of multiple boundaries and transitions, between land, lagoon waters and sea, sediments, water column and atmosphere. Many lagoons have also freshwater inputs. All this leads to the existence of strong physical-chemical gradients. Furthermore, the photic zone frequently extends to the lagoon bottom in most areas, and these ecosystems usually receive substantial amounts of nutrients from the surrounding catchments, which stimulate primary production (Kennish, 2015). The question is, which of these features are enough to explain the high lagoon biological productivity compared to other coastal areas?

1.1. Factors determining fishing yield in coastal lagoons

Previous works showed that the biological productivity of these ecosystems can be explained to some extent by their geomorphological

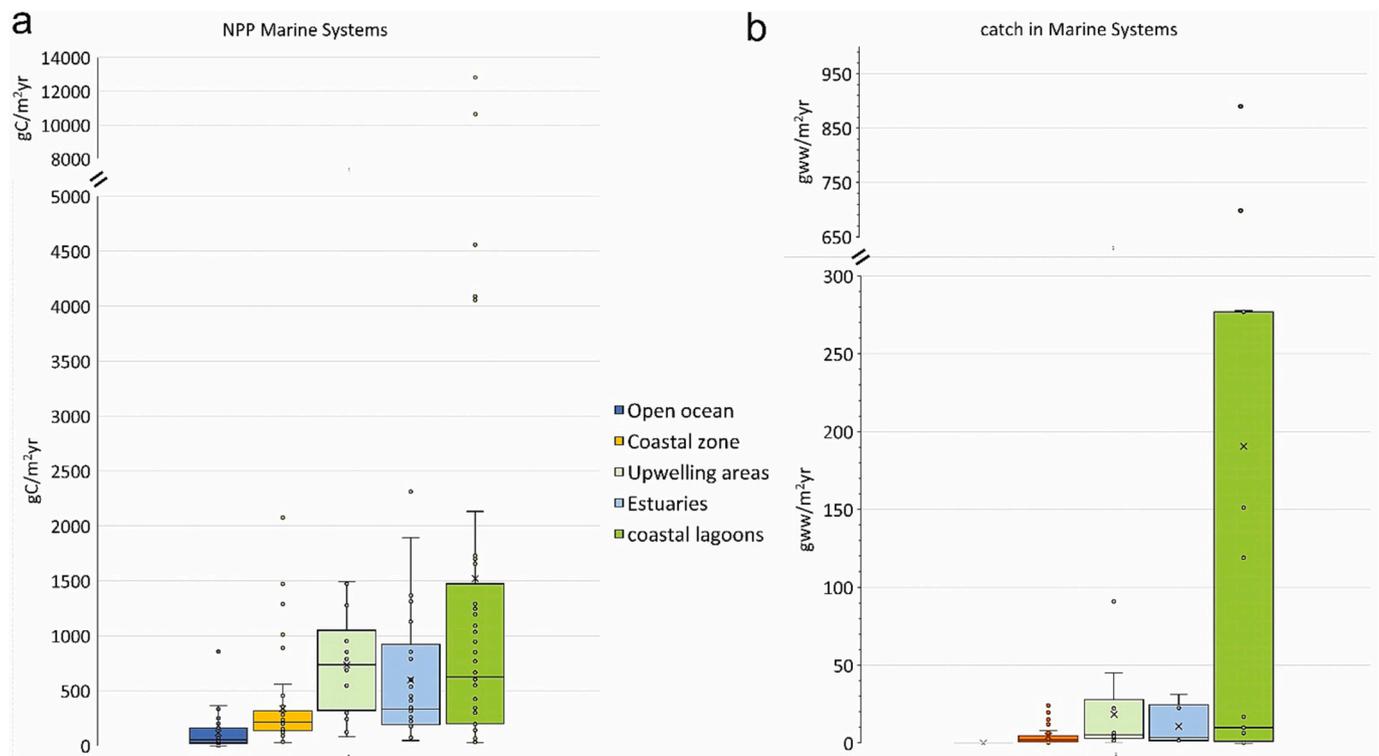


Fig. 1. Net Primary Productivity (NPP) (a) and fishing catch (b) in marine ecosystems according to bibliographic data and published Ecopath models. (See supplementary table A.1 for ecosystems data and references).

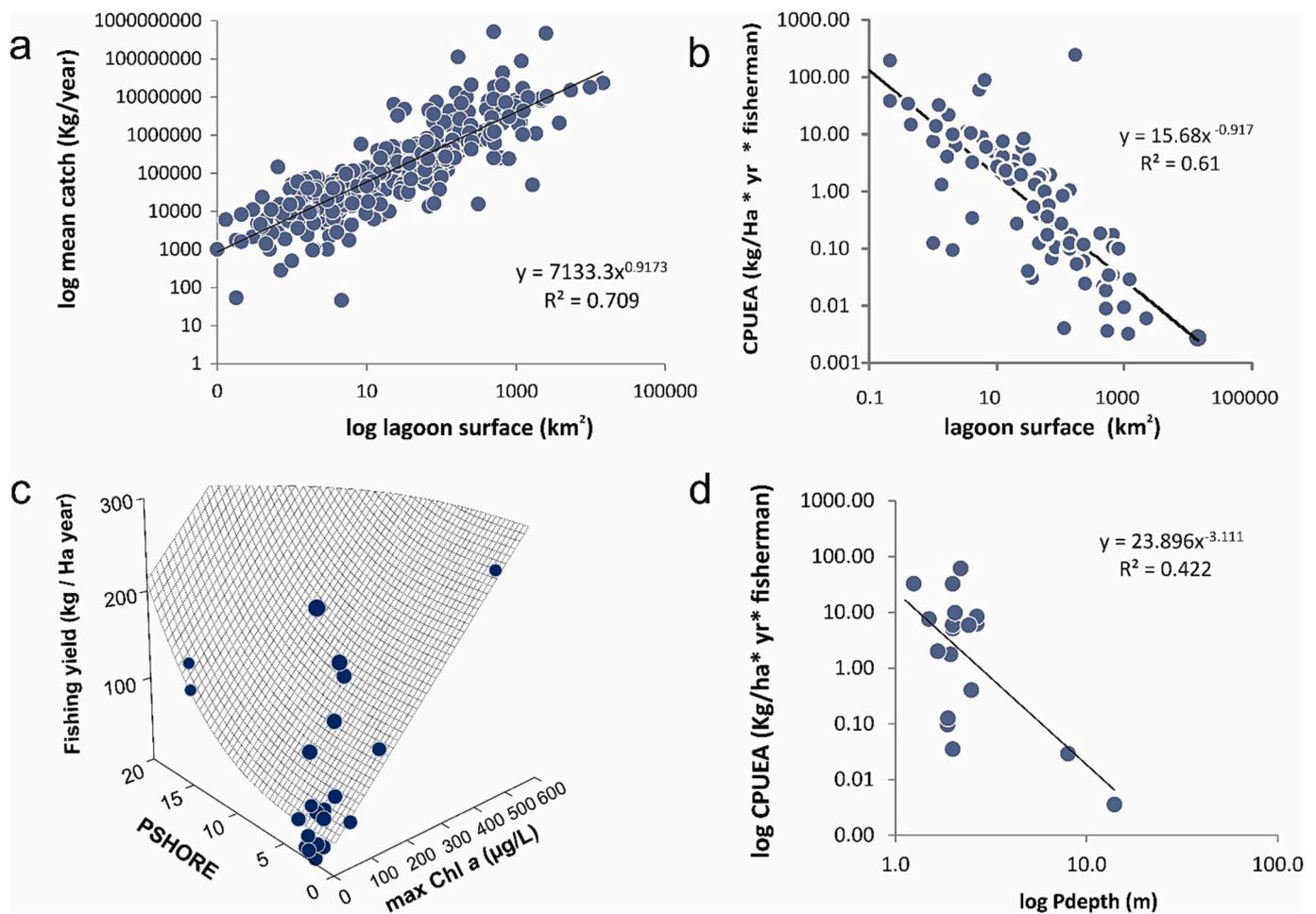


Fig. 2. Relationship between the fishing yield in coastal lagoons and its geomorphological and trophic features. (a) Relationship between mean catch and lagoon surface, (b) Catches per unit effort vs. lagoon surface, (c) Best regression model (GLM) after forward selection of variables explaining the relationship between the fishing yield in a coastal lagoon and their geomorphologic and hydrographical characteristics. The selected variables for the model were PSH or shore development ($p < 0.01$) and maximum chlorophyll concentration in the lagoon water column ($p < 0.05$). Pshore, or Shore development parameter, is the ratio of the length of shoreline or the lagoon perimeter, to the circumference of the circle whose area is equivalent to that of the lagoon (Chubarenko et al., 2005). A large lagoon shoreline development favors nutrient input from runoff. This justifies that the fishing yield increases exponentially with PSHORE (Fig. 2c). Shallowness is also important (Fig. 2d), and due to it, lagoon bottoms are usually well irradiated, currents and hydrodynamics are closely conditioned by bottom topography and wind affects the entire water column, promoting the resuspension of materials, nutrients and small organisms from the sediment surface layer. As coastal, transitional systems between land and sea, it could be expected that this productivity would be explained mainly by the inputs of nutrients coming from land systems and from cultural eutrophication. Being this partially true, in practice it is found that this productivity is, in many cases, relatively independent of the trophic status of each lagoon (Pérez-Ruzafa et al., 2007) and show low variations in the same lagoon under oligotrophic or eutrophic conditions (Marcos et al., 2015). However, despite the relative importance of all these parameters, GLM regression models, considering all together, cannot explain > 40–60 % of the

variance in the fishery productivity data (Joyeux and Ward, 1998; Pérez-Ruzafa et al., 2007; Pérez-Ruzafa and Marcos, 2012). This problem also occurs across disparate marine ecosystems, where it is common to find differences between net primary production and fishery production. In this case, different hypotheses have been sought to explain it (Ryther, 1969; Stock et al., 2017).

1.2. *The importance of physical-chemical gradients*

From a merely physical perspective, coastal lagoon ecosystems are characterized by the presence of boundaries involving strong physical and ecological gradients (UNESCO, 1981), which makes them very dynamic systems (Pérez-Ruzafa et al., 2019a).

1.2. The importance of physical-chemical gradients

Here we propose that although nutrient inputs and light can be the main limiting factors for photosynthetic based biological productivity and therefore enhance productivity of algae and increase the fishing yield up to a certain limit, the productivity of lagoons is strongly promoted by more general physical forces associated to physical and chemical gradients. Gradients involve energy and matter fluxes, and these fluxes are used by the living systems in order to build themselves (Kauffman, 2002).

In coastal lagoons, physical, chemical and biological processes take place along relatively short distances, which increases the intensity of the gradients and could explain the high fishing productivity (Pérez-Ruzafa et al., 2007; Pérez-Ruzafa and Marcos, 2012).

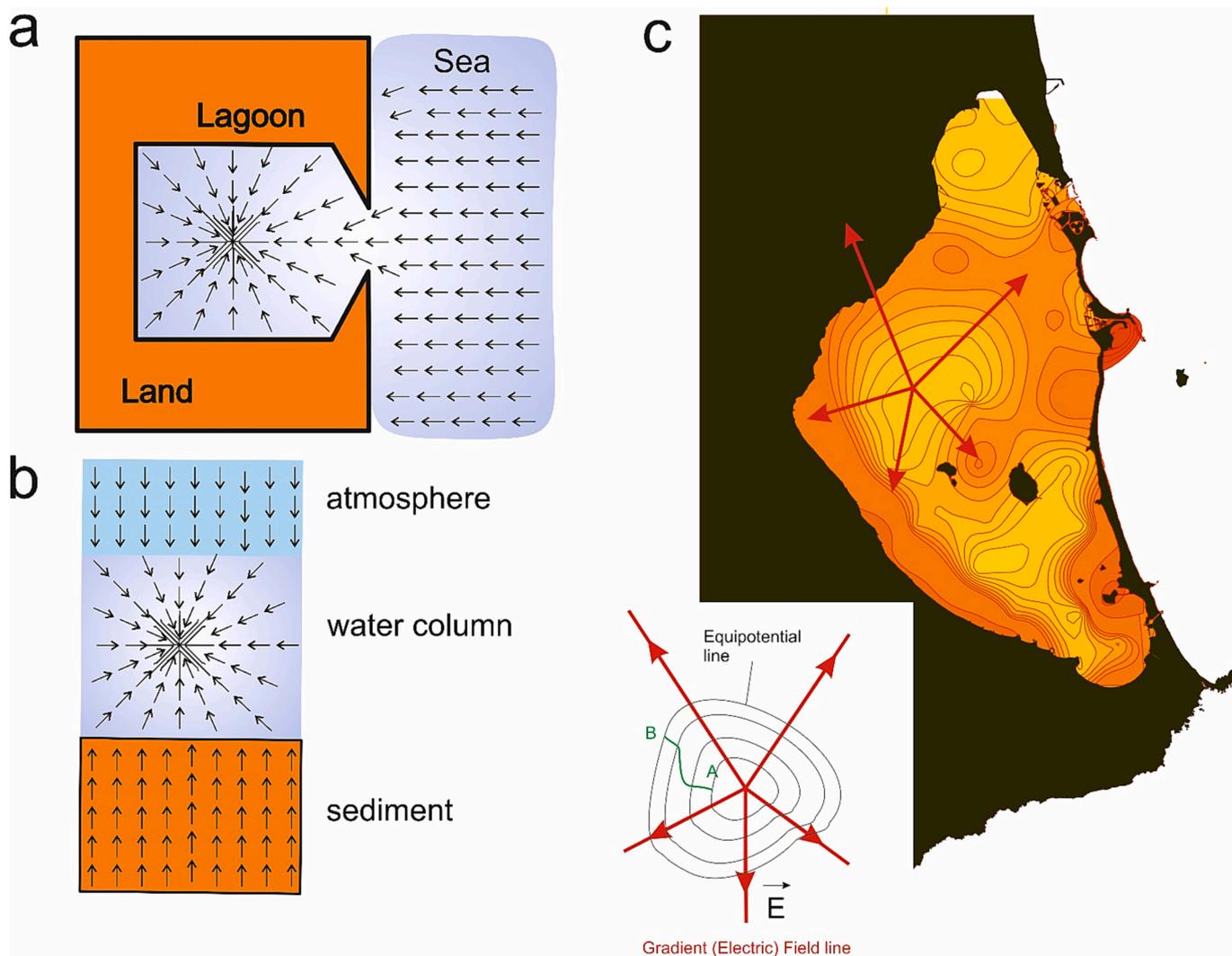


Fig. 3. Main boundaries for physical and biological gradients in coastal lagoons. a) horizontal view, b) vertical section, c) lagoons as an electro-magnetic field constituted by multiple 3D, physical-chemical gradients (adapted from Pérez-Ruzafa, 2015).

Table 1
Main meso and large-scale (>10¹ cm) interfaces in coastal lagoons.

Involved layers	Interface	Involved processes
Bottom sediments – water column	Solid-liquid	Different chemical potential that facilitates chemical reactions, gasses and chemical flows, in addition to the gradient of gravitational potential, causes the deposit of materials on the bottom and the consequent gradient in its concentration. Resuspension of organic matter, sediments and organisms forced by waves and currents
Water –atmosphere	Gas-liquid	Evaporation, gases diffusion, wind stress, temperature and solar radiation gradients
Land-Water (Coast line)	Solid-liquid	The differences in chemical potential, concentrations and temperature involved
Lagoon-sea	Liquid-liquid	Where heat flows occur due to advective movements forced by gradients, such as atmospheric pressure, sea level, temperature, salinity. It also involves passive and active biological interchanges forced by biological productivity, carrying capacity and preference in environmental conditions
River-lagoon	Liquid-liquid	Advective transport forced by gravity involving nutrient flow, water, momentum, and temperature gradients around it

Table 2
Thermodynamic forces and flows (adapted from Kondepudi and Prigogine, 2002).

Gradient	Energy/Flows	Relation	Transport coefficient
V, potential	Electromagnetic/Ion current	$\frac{1}{A} \frac{dq}{dt} = -\sigma \nabla$	σ
Temperature	Caloric/Heat	$\frac{1}{A} \frac{dQ}{dt} = -k \nabla T$	k
Concentration	Phisico-Chemical diffusion/Matter	$\frac{1}{A} \frac{dn_i}{dt} = -D \nabla c_i$	D
Pressure	Kinetic/Water mass velocity	$\frac{1}{A} \frac{dv}{dt} = -\eta \nabla p$	η

The importance of gradient intensity on coastal lagoons productivity is suggested, as showed above, by the fact that the analyses of hydrological, trophic, and geomorphological factors that can explain fishing yields in these ecosystems show that fishing yield and fishing yield per surface unit increase when shore complexity increases and depth and lagoon surface decreases (Fig. 3) (Joyeux and Ward, 1998; Pérez-Ruzafa

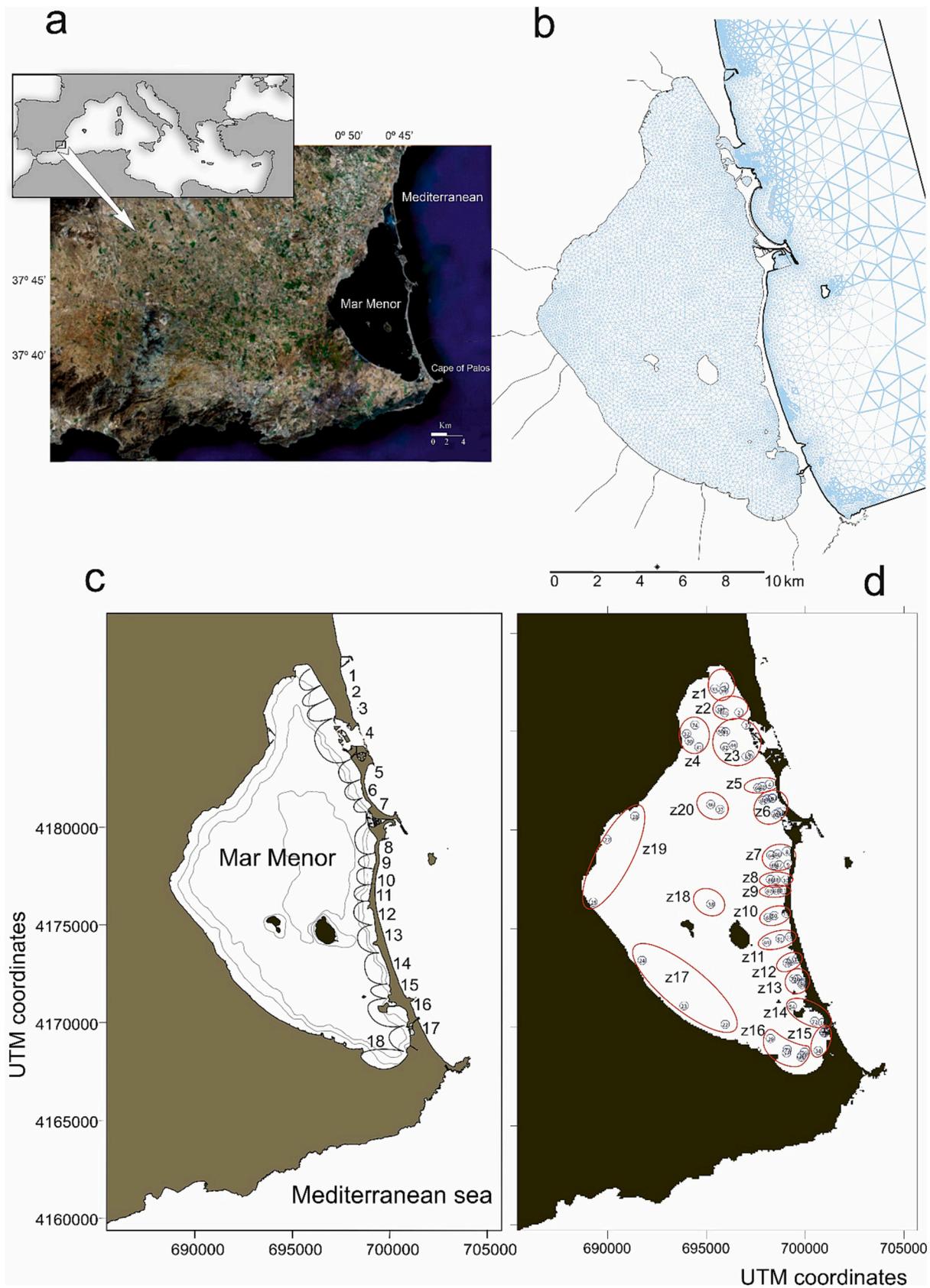


Fig. 4. a) Geographical location of the Mar Menor, b) grid used for the hydrodynamic model, c) distribution of the 18 pieces of companies defined in the decree regulating fishing in the Mar Menor, and d) 74 locations where fishing effort data has been compiled (blue polygons) grouped into 20 zones for the analyses (red ellipses).

Table 3

PERMANOVA table of results for analysing the spatial differences in average kinetic energy using the factors Zone, Season and month (nested in season). Significant values in bold.

Source	df	SS	MS	Pseudo-F	P (perm)
Zone	19	112.34	59.127	610.55	0.001
Season	3	0.57657	0.19219	0.71611	0.559
Month(season)	8	21.471	0.26838	0.59114	0.773
Zone x season	57	10.076	0.017678	18.254	0.006
Zone x month (season)	152	1.472	0.0096843	0.021331	1
Res	648	294.2	0.45401		
Total	887	412.7			

et al., 2007; Pérez-Ruzafa and Marcos, 2012).

1.3. Main gradients in coastal lagoons

In coastal lagoons, the main boundaries through which these gradients appear are the coastline separating terrestrial systems from the lagoon, the inlets for the transition between the lagoon and open sea water masses, the water-air interface on the upper part and the sediment-water column interface in the bottom (Fig. 3a, b, Table 1). Some other boundaries with fresh water fluxes, through temporal or permanent watercourses, can appear depending on the lagoon (UNESCO, 1981; Pérez-Ruzafa et al., 2007, 2011).

The gradient of a function U can be calculated by:

$$F = -\nabla U = -i \frac{\partial U}{\partial x} - j \frac{\partial U}{\partial y} - k \frac{\partial U}{\partial z} \quad (1)$$

where i, j, k are the standard unit vectors in the directions of the x, y and z coordinates, respectively, or the corresponding proportionality constants (or transport coefficients).

Therefore, any coastal lagoon could be represented as an energy field determined by multiple physical-chemical gradients (Fig. 3c). The intensity of a gradient depends on both, the range of variation in a given parameter at the extremes of the gradient, and the distance between both values. In coastal lagoons both aspects are working to increase the intensity of the gradients, as differences in environmental parameter and substance concentrations are high while distances are very short.

The process of transformation of physical and chemical gradients into energy fluxes that living systems can use to proliferate is still a research challenge (Kleidon, 2012) and, in this sense, coastal lagoons could be regarded as a suitable case study (Pérez-Ruzafa, 2015).

2. Conceptual approach

2.1. Thermodynamics

From the thermodynamic point of view, a lagoon is an open system that, in broad strokes, can be considered in a steady state since its state variables (temperature, pressure, volume and density of matter) do not change dramatically over time. In this framework, the state variables can depend on the location. It is expected that neither the total entropy of the lagoon nor the intrinsic entropy should undergo strong temporary changes, so we can consider (Kondepudi and Prigogine, 2002):

$$\Delta_i S^L \approx 0 = \Delta_i S^L + \Delta_e S^L \quad (2)$$

where the entropy of the lagoon can change due to irreversible processes, $\Delta_i S^L > 0$, that occur inside and the exchange of matter or energy with the outside $\Delta_e S^L$. Irreversible processes can be written based on flows J_i and their conjugate forces X_i :

$$\Delta_i S^L = \sum J_i X_i \geq 0 \quad (3)$$

It turns out that each of the products is positive. Table 2 shows some thermodynamic forces and flows that may occur in an ecosystem (adapted from Kondepudi and Prigogine, 2002), where the thermodynamic forces drive the thermodynamic flows. For example, a gradient in salt concentration is the thermodynamic force that produces irreversible flows of matter, being the diffusion coefficient D , the related transport coefficient.

When the lagoon is steady state, because of Eq. (2) and $\Delta_i S^L > 0$, the contribution to the entropy due to the exchange of matter and energy with the outside must be negative:

$$\Delta_e S^L < 0 \quad (4)$$

This means an ongoing net flow of energy and/or material with the outside. The lagoon can exchange entropy with the air, the surrounding terrain through the coastline, the bottom and the outer sea through the canals. In this context, the living organisms that inhabit the lagoon would form a separate system that can also exchange entropy. Each of the living organisms would be an open system that, as a characteristic of biological systems, is characterized by having an entropy S^B that decreases over time:

$$\Delta S^B \leq 0 \Rightarrow \Delta_i S^B + \Delta_e S^B \leq 0 \quad (5)$$

As irreversible processes in every system are positive, $\Delta_i S^B > 0$, therefore $\Delta_e S^B \leq 0$ and $-\Delta_e S^B \geq \Delta_i S^B$.

The organisms reduce their entropy by achieving a net outflow of entropy that occurs at the cost of importing low entropy energy (PAR) and matter (CO₂, nutrients) in the case of autotrophs, or complex organic matter in the case of heterotrophs, from the environment and exporting more simple substances of higher entropy and heat.

To do this, they require that the surrounding environment be able to provide them with energy in form of food, as well as to eliminate waste substances. The existence of gradients around it facilitates both aspects, therefore the organisms that live in gradients capable of providing adequate conditions that keep them out of the thermodynamic equilibrium can develop more easily and the ecosystems that contain these gradients will be more productive.

2.2. Electric field analogy in a coastal lagoon

The proposed approach is like the formulation of electrostatic fields (Fig. 5), where the electric force is proportional to the electric field, E , which can be described by the gradient of the electrostatic potential function, V :

$$E = -\nabla V = -i \frac{\partial V}{\partial x} - j \frac{\partial V}{\partial y} - k \frac{\partial V}{\partial z} \quad (6)$$

The electric charges are the sources of the electrostatic field, and both are related by the Gauss's Law:

$$\nabla \cdot E = \frac{\rho}{\epsilon_0} \quad (7)$$

where ρ is the charge density and ϵ_0 is the vacuum permittivity.

Therefore, the potential is related to the charge density by the Poisson's equation:

$$\nabla \cdot \nabla V = \nabla^2 V = -\frac{\rho}{\epsilon_0} \quad (8)$$

Electric charge is the physical property of the matter that causes the electrostatic force, also known as Coulomb force, which is part of one of the four fundamental forces, the electromagnetic force. All the electric fields store energy; therefore, it is possible to assign a density of energy to the electric field:

$$\eta_E = \frac{\text{energy}}{\text{volume}} = \frac{1}{2} \epsilon_0 E^2 = \frac{1}{2} \epsilon_0 (\nabla V)^2 \quad (9)$$

We see that the energy density of the electric field is proportional to

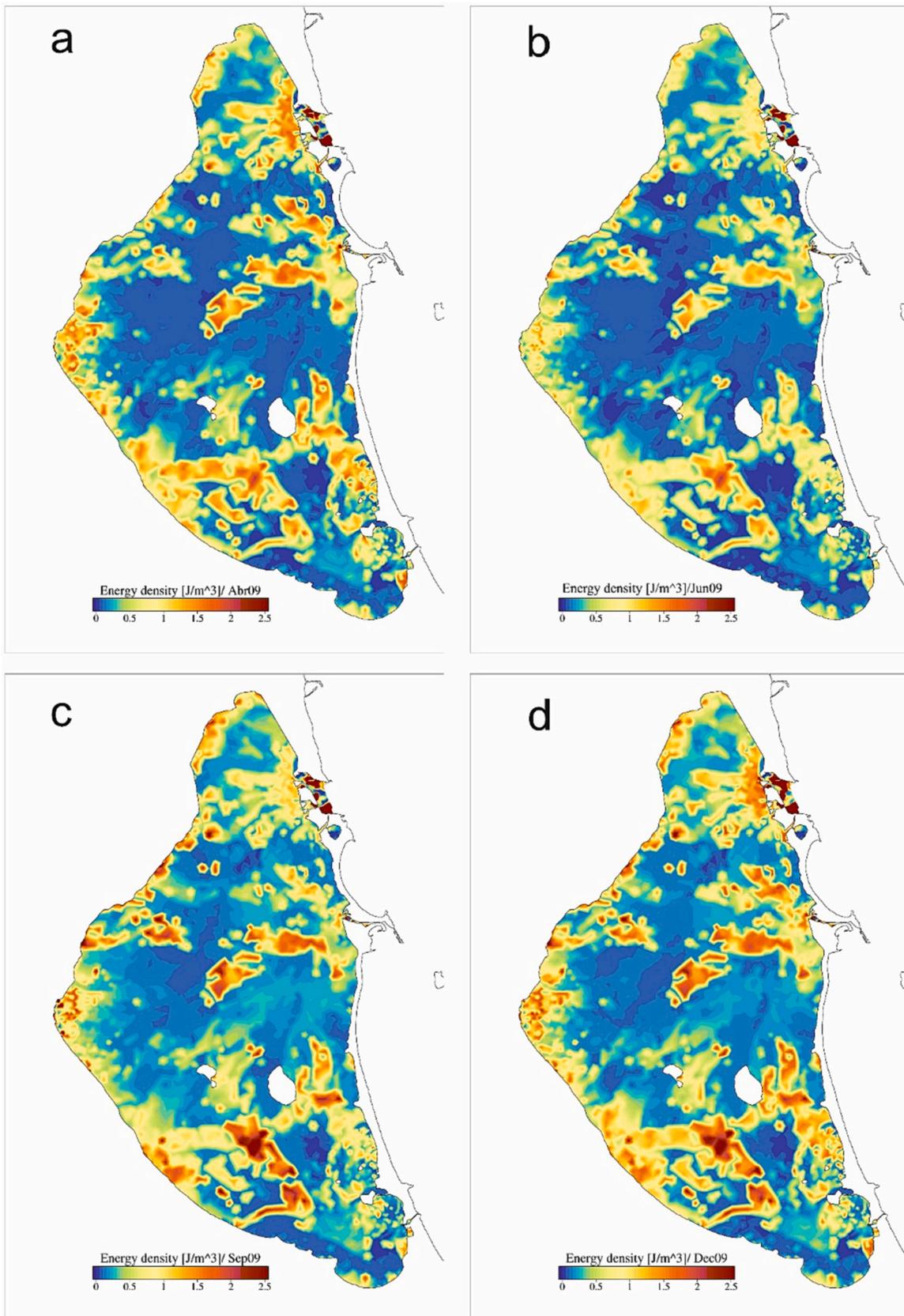


Fig. 5. Distribution of monthly mean kinetic energy density ($J m^{-3}$) associated with marine currents in the Mar Menor coastal lagoon in 2009. a) April, b) June, c) September, d) December.

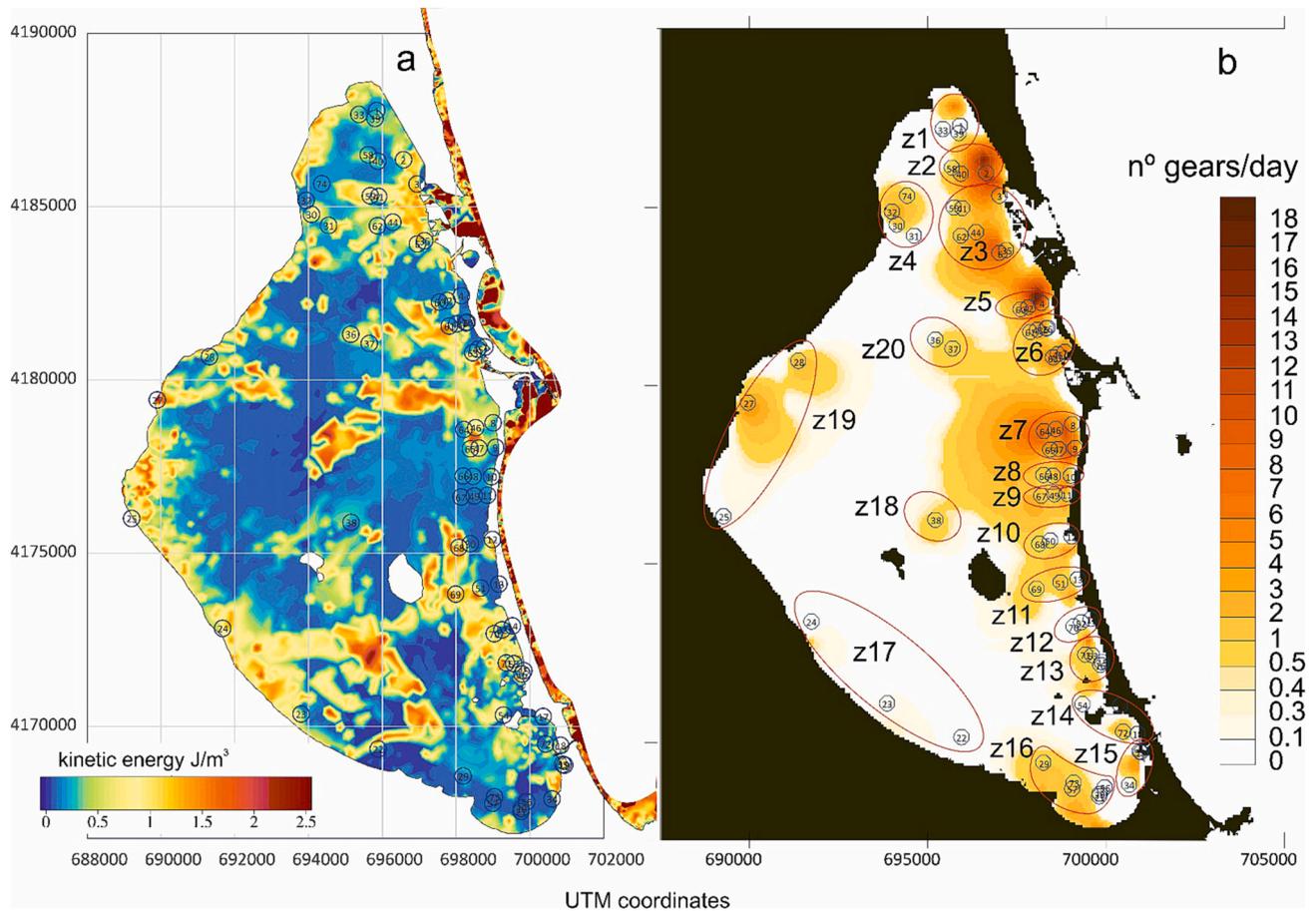


Fig. 6. a) Mean annual distribution of kinetic energy for the Mar Menor lagoon and location of the fishing locations, b) fishing effort distribution (average amount of gears/day in a year). The 74 fishing locations (blue polygons) grouped in 20 zones (red ellipses) used for regression and Permanova analyses are shown.

the square of the potential gradient. The total energy stored by the electric field in a volume can be obtained by integration:

$$Energy = \frac{1}{2} \epsilon_0 \int (\nabla V)^2 dr^3 \quad (10)$$

2.3. Living in the boundaries: The importance of gradients

Whenever we have a gradient of something, for example temperature, salinity, light, concentration, density or velocity, fluxes of heat, salt, particles, or momentum are caused. In a similar way, if there is a potential gradient there can be a flow of charge. In the latter case, the presence of an electrostatic potential has an associated electric potential energy and, like all potential energies, can produce reversible work. Systems with gradients in concentration, temperature, or speed, have a potential energy for useful work production if there are restrictions to the flow and due to the heat dragged to the environment.

The presence of a gradient can be interpreted as a potential energy because gradient have the potential to produce transport (from high to low potential in order to reach equilibrium). This transport produces movement of particles and/or heat that can be used by organisms to harvest energy.

Each gradient can generate different kind of forces and processes (mechanical-movement of water masses, diffusion, thermal fluxes, chemicals, etc.) expressed at different scales. The total energy would be the sum of the energy stored by all existing gradients.

A parallelism can be found between the energy stored by the electric field and the kinetic energy produced by water currents and advection processes, in which masses of water are displaced through a hydrostatic pressure field.

$$E = \frac{1}{2} mv^2 \quad (11)$$

Therefore, the total energy in a lagoon would be estimated as an addition of the energy associated with all the gradients. For example, if electric potential, temperature, concentration, and pressure gradients are present (Table 2), the energy would be a function of the type:

$$Energy = \frac{1}{2} \epsilon_0 \int (\nabla V)^2 dr^3 + \int f(\nabla T) dr^3 + \sum_i \int f(\nabla c_i) dr^3 + \int f(\nabla v) dr^3 \dots \quad (12)$$

where, for simplicity, we have considered only cases in which a gradient contributes only to its corresponding flow. The existence of coupled fluxes is very common, e.g., a temperature gradient produces a flow of heat and matter and a hydrostatic pressure gradient produces water masses movements and currents.

3. Methodological approach

3.1. Estimating kinetic energy in a hydrostatic pressure field

Currents in a water basin at large geographic scale are the result of multiple variables fields including atmospheric pressure, that acts directly or through wind forces, salinity and temperature, that determine density fields, and sea level topography, that joint with density fields and atmospheric pressure, determines the total pressure or the gravitational field.

To estimate kinetic energy, a 3D hydrodynamic model based on the finite element method (SHYFEM) has been used to simulate the

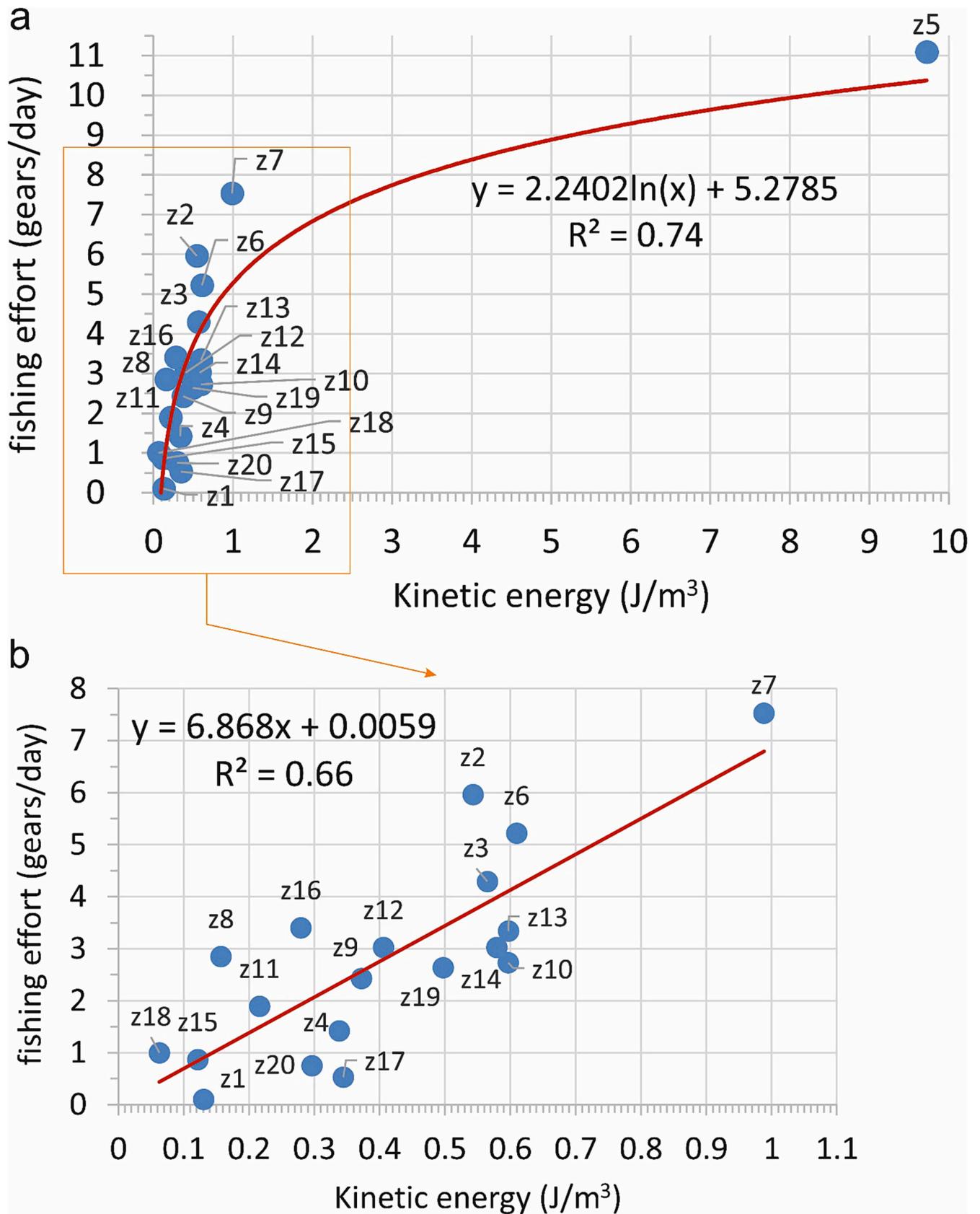


Fig. 7. Regression model relating fishing effort and kinetic energy in the Mar Menor lagoon. a) including all zones studied, b) detail considering the areas with $K < 1 J/m^3$.

circulation and mass transport of the water masses driven by realistic meteorological forcing (Umgiesser et al., 2004).

This model has been already applied and validated successfully in previous studies on the Mar Menor basin and on other lagoons, to reproduce the tidal and wind induced water circulation and lagrangian transport of larvae (De Pascalis et al., 2012; Ghezzi et al., 2015; García-Oliva et al., 2018, 2019; Pérez-Ruzafa et al., 2019b). 3D current modules and total kinetic energy were calculated for each element in a grid containing 8865 elements.

The kinetic energy in a volume of fluid can be defined by Eq. 13 (Gill, 1982):

$$K = \iiint \frac{1}{2} \rho u^2 dx dy dz \quad (13)$$

where ρ is the fluid density and u is the flow velocity.

Taking this formula into account, the kinetic energy of a certain element of the lagoon model for a given time can be calculated as:

$$K_e = \frac{1}{2} \rho_t u_t^2 h_t A_e \quad (14)$$

where h_t is the water depth, A_e is the horizontal area of the element, and the subscript t refers to the moment in time.

The kinetic energy resource over a region can be represented by aggregating the previous values from every element within the region and averaging over a certain period (Eq. 15):

$$K_{S-n} = \frac{1}{n} \sum_{per=0}^{per} \sum_S \left[\frac{1}{2} \rho_t u_t^2 h_t A_e \right] dt \quad (15)$$

where S is the region over which the kinetic energy is averaged, n is the number of observations in the region S , and per is the period of time (days, etc.).

According to Lewis et al. (2015), the spatial distribution of the kinetic energy resource over an area can be successfully described through this method.

In order to identify the magnitude of changes of the kinetic energy over time, the peak energy can be computed at each location as the maximum value happening during a specific period. Peak values do not necessarily mean that the energy at a location will remain at high values most of the time. Therefore, a calculation of the time interval during which the energy is above a threshold would provide a complementary analysis about the temporal variations of the energy.

3.2. Kinetic energy density

The Eq. (15) described in the previous section give some insights about the spatial and temporal variation of the kinetic energy over a region. However, adopting the energy density formulation seems more suitable for calculating the energy gradient between different locations without overestimating the energy resource. For instance, if two elements with the same density, velocity and depth are considered and the horizontal area of the first element is larger than the one in the second element, the energy in the first element would be also higher.

The energy density can be defined as the kinetic energy per unit volume (Eq. 16):

$$K_d = \frac{K_e}{Vol} = \frac{\frac{1}{2} \rho_t u_t^2 h_t A_e}{h_t A_e} = \frac{1}{2} \rho_t u_t^2 \quad (16)$$

3.3. Estimating fishing effort distribution and data analyses

The distribution of fishing effort is often used as an indicator of fishing yields, i.e. to demonstrate the efficiency of biomass export in marine reserves (Murawski et al., 2005; Hilborn et al., 2006; Goni et al., 2008; Pérez-Ruzafa et al., 2008; Stelzenmüller et al., 2008; Vandepierre et al., 2011). In the Mar Menor (Fig. 4a) there are preferred fishing

zones, called “Pieces of companies”, which are distributed in 18 areas defined in the Decree of Regulation of fishing on the Mar Menor (Fig. 4c). These areas are raffled weekly between fishermen. Additionally, professional fishermen can set their fishing nets in other areas they consider of interest. The distribution of the fishing effort was estimated as daily average density of anchored fishing gear in the lagoon (according to data from Barcala et al., 2005; ANSE, 2013, Marcos et al., 2015). We compiled the data from 74 localities and grouped in 20 zones for average calculations to relate with averaged Kinetic energy in the same zones (Fig. 4d). The grid used for currents and kinetic energy calculation in the Mar Menor is shown in Fig. 4b. Monthly averaged kinetic energy was calculated for the entire water column in each of the 8865 elements of the grid. For the statistical analyses, a matrix was constructed from the monthly mean kinetic energies by extracting the monthly values from the node whose coordinates were closest to those of the fishing effort stations. Spatial-temporal variability in kinetic energy was analysed using PERMANOVA in the Primer 7 package (Anderson, 2005), considering the factors zone (with 20 levels), month (with 12 levels) and season (with four levels). All the analyses were performed on the Euclidean distance matrices after square root transformation of the data. To analyse the relationship between fishing effort and kinetic energy the averaged values of the fishing effort for the locations in each zone were plotted against the average kinetic energy in the same zones and the best-fit regression was estimated using Excel.

4. Results

Kinetic energy density distribution showed a stronger small-scale spatial variability than a temporal one (Table 3, Fig. 5). Differences between zones are highly significant ($p = 0.001$), but they depend on the season ($p = 0.006$). However, the analyses do not detect differences between months nested in seasons, neither between seasons ($p = 0.77$ and $p = 0.56$, respectively). That is to say that, throughout the year, although the general spatial patterns are maintained, and the average kinetic energy of the systems is maintained, there exist only slight seasonal changes in kinetic energy in some localities with respect to others (Fig. 5).

By relating the distribution of mean kinetic energy in the lagoon to the distribution of fishing effort (Fig. 6), the results of the regression analyses showed that fishing effort distribution maintains a positive and highly significant relationship with kinetic energy in the area (Fig. 7). This relationship is linear for kinetic energies lower than 1 J/m^3 (Fig. 7b) and turns logarithmic at higher energies (Fig. 7a). Two outliers, locations 1 and 33 in zone 1 (northern end of the lagoon), were excluded from the regression due to their anomalous behaviour, potentially attributed to the substantial spatial variability in kinetic energy and fishing effort within that specific area. This variability, occurring at a spatial scale below 500 m in diameter, aligns with grid cell dimensions and gear length, emphasizing the sensitivity of results to slight coordinate deviations.

5. Discussion and conclusions

Here we show the existence of statistic correlation between kinetic energy and fishing effort distribution in a coastal lagoon. It could suggest that thermodynamic principles could be at the basis of the biological production of coastal marine ecosystems and coastal lagoons. Hence, for the Mar Menor coastal lagoon as the example, we thus showed that biological production (using fishing effort concentration as a proxy) at the local scale is closely related to the energy flow generated by the environmental gradients whose intensity in coastal lagoons is determined by their geomorphological characteristics. The kinetic energy and its spatial distribution in the coastal lagoon should thus be considered for explaining biological productivity in addition to the physic-chemical variables such as nutrient loads and chlorophyll concentration in the water column. Therefore, changes in hydrological (like fresh water

inputs through sewage stations, rainfall, or runoff) or geomorphological characteristics (like depth, coastal works, modifications in the inlets, etc.), induced both by human activities or climate change, will lead to changes in such gradients and the productivity of the lagoons. However, the mechanisms explaining why biological productivity is higher in areas with high kinetic energy are still unknown and further studies are needed.

The role of thermodynamic gradients in biological production and the mechanisms that intervene in their maintenance and in the transformation of the energy involved are beginning to be known at lower levels of biological organisation (Gust et al., 2001; Demirel, 2014; McKinlay et al., 2020). An example can be taken from cellular level, where proton motive force (pmf) is created over membranes by photosynthetic and catabolic processes, and where pmf can be used to synthesize ATP (Munekage et al., 2004; Simon et al., 2008; Wilson et al., 2021). In this case there is a clear mechanism on how the gradient, that is, the pmf, can be used for the production of biomass, and therefore productivity. In the case of cells, said gradient is maintained in a steady state (i.e., internal entropy remains constant) by biological activity itself, consuming energy, by different mechanisms like proton pumping, quinone/quinol cycling or by a redox loop (Simon et al., 2008). In the case of ecosystem-scale physicochemical gradients, particularly those that give rise to hydrodynamic kinetic energies, the maintenance of gradients depends on hydrological, climatic and geomorphological conditions, but there is no known mechanism on how kinetic energy in the water mass can be directly exploited for biomass production. Therefore, the high productivity along hydrodynamic gradients in the water mass needs to be explained in another way, until now unknown, perhaps through indirect mechanisms that relate the fronts and hydrodynamic with processes that concentrate the biomass or facilitate the availability of nutrients. The field of possibilities is wide and is open to further investigation.

The relationship between energy flow generated by gradients and estimators of the biological productivity would allow a purely thermodynamic approach to the study of the organisation of coastal lagoon ecosystems. These environmental gradients will be determined by the hydrological and geomorphological characteristics of each lagoon, which establishes a direct relationship between human actions (for example in the communication channels between the lagoons and the adjacent sea, or those that modify the geomorphology of the coastline or introduce changes in the depth and size of the lagoons) and the consequences on biological production and fishing yields. With this approach, it could be possible to assess which actions can increase the intensity of the gradients and associated energy fluxes or, on the contrary, reduce them homogenising the system. There are actions that can increase temporally energy flow, for example, by favouring the exchange of water in the channels of communication with the sea through dredging operations, but which in the medium or long term can lead to the homogenisation of the system and the loss of such gradients and, therefore, fishing yields. Indeed, operations in the inlets to regulate the interchanges of water with the sea are considered essential for maintaining the lagoon biota (Quignard, 1984), as seen to prevent dystrophic summer crises affecting the Scardovary lagoon fisheries in the Po River Delta (Rossi, 1984), or to avoid sea level rise as in the case of Aqua Alta in a climate change scenario in the lagoon of Venice (Umgiesser, 2020). Furthermore, the opening or closing of channels of communication between lagoons and the open sea is common practice in the management of coastal lagoon fisheries, for example in Eraitino in Greece (Pérez-Ruzafa and Marcos, 2012), Foz de Almarem and dos Salgados in the Portuguese Algarve (Coelho et al., 2007) or in the eighteenth century in the Mar Menor in the Mediterranean coast of Spain (Jimenez de Gregorio, 1984). These actions are often associated with contradictory effects on fishing yields (Pérez-Ruzafa and Marcos, 2012). In the same way, dredging the existing inlets is also a common practice to improve coastal lagoon fisheries in the Gulf of Mexico (Castro, 1984). Furthermore, clogging of the inlets and lack of maintenance of the channels

leading to a rise in salinity, poor seawater circulation or limited water renewal have been related to the drastic change in species composition and drop in the catch of some lagoons (Ben-Tuvia, 1984; Katselis et al., 2003; Mehanna, 2007; Tsihrintzis et al., 2007). By the contrary, in Albanian lagoons in the Adriatic Sea (Peja et al., 1996), or in the Mar Menor in the western Mediterranean (Marcos et al., 2015), the dredging of inlets produced a drop in fishing yields.

These contradictory and complexity of effects can be explained by the subtle balance that must be maintained between increasing flows and preserving gradients if these flows are to be sustainable over time.

We believe that the approach we present could be applicable not only to coastal lagoons, but also to other environments, such as ocean fronts and upwelling areas, where energy fluxes are closely related to physicochemical gradients that increase total ecosystem biomass, affecting fishery abundance and yield and explaining the distribution of fishing effort, marine birds and mammals (Podestá et al., 1993; Acha et al., 2004; Bost et al., 2009; Alemany et al., 2014; Tijani et al., 2015; Woodson and Litvin, 2015; Nieto et al., 2017; Oh et al., 2019).

Considering the great importance of coastal lagoons for the goods and services they produce worldwide, while being among the ecosystems most threatened by human pressures and climate change, an approach based on thermodynamic principles may be essential to anticipate expected changes resulting from such pressures, many of them related to the homogenisation of thermal and/or saline gradients. Using a precautionary principle, it is important to preserve the spatial pattern of the kinetic energy in the water body, bearing in mind that interventions that simplify the fine-scale spatial structure of kinetic energy (thus increasing internal entropy) may have serious negative impacts that have not been foreseen so far. In this context, further research and comparison of different lagoons, or of the same lagoon under different conditions, or in other marine areas such as estuaries, ocean fronts and upwellings, will be necessary to better understand these relationships in order to design management tools to improve fisheries and regulate or prevent ecosystem responses to human impacts or climate change.

CRediT authorship contribution statement

Angel Pérez-Ruzafa: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Gregorio José Molina-Cuberos:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Formal analysis. **Miriam García-Oliva:** Software, Methodology, Investigation, Formal analysis. **Georg Umgiesser:** Writing – review & editing, Writing – original draft, Validation, Supervision, Software, Methodology. **Concepción Marcos:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Funding acquisition, Formal analysis.

Declaration of competing interest

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

Data availability

The full data that we extracted from the reviewed studies in Fig. 1 are available in Supplementary file Table 1). Modelling data generated in this work are available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.171264>.

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