



# Evaluation of seasonal variability in the food-web properties of coastal lagoons subjected to contrasting salinity gradients using network analyses



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## ABSTRACT

Salinity is a major factor influencing the abundance and composition of species and the overall organization of natural communities but its relevance in the maintenance of important functional processes such as energy flows, trophic structure, resilience and stability is lesser known. Estuarine communities from coastal lagoons in the Ebro Delta (Tancada, Encanyissada and Clot; Catalonia, NW Mediterranean) are subjected to anthropic variability in their salinity regime and offer a suitable setting for investigating differences in ecosystem functioning. To this aim, we conducted seasonal sampling of estuarine communities (from phytoplankton to birds) and we describe the structural and functional changes in carbon flows and trophic relationships using ecological network analysis (ENA). Results showed that summer biomass of *Ruppia cirrhosa* (annual species) in the two higher salinity lagoons is sufficient to sustain fish and invertebrate communities, whereas in winter they become plant-limited and enhanced detrital consumption is necessary for balancing the trophic models. In contrast, consumers in the low salinity lagoon dominated by *Potamogeton pectinatus* (pseudo-annual species) were not limited by plant abundance and seasonal differences in NPP:biomass ratios, total system throughput (TST), and ascendancy were the lowest, suggesting more stable functioning. The biomass of phytoplankton was low compared to that of benthic macrophytes, but accounted for similar rates of primary production (from 0.21 to 0.54 g C m<sup>-2</sup> d<sup>-1</sup> and from 0.01 to 1.96 g C m<sup>-2</sup> d<sup>-1</sup>, respectively) and contributions to the TST (from 7.2 to 33.9% and from 0.6 to 39.3%, respectively). Therefore, seasonal variability in ecosystem fluxes was both controlled by the influence of salinity on plant species and by fluctuations in the abundance of phytoplankton. The combined effect of nutrients and salinity was found to have a strong influence on the ratio between pathways originated from phytoplankton and from benthic producers ( $R = 0.99$ ,  $p < 0.05$ ). Overall, our results suggest that plant persistence could help to stabilize ecosystem functioning by providing a permanent source of food and habitat to consumers, and by removing some nutrients from the water column.

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## 1. Introduction

Species in an ecosystem are connected through trophic relationships that form highly complex networks varying in structure and strength. The resilience of these networks depends on the interaction between the physicochemical environment and inherent variables of the system such as seasonal habitat productivity, resource abundance, and consumer behavior and demography (Briand and Cohen, 1984). Recent increases in the availability of computational tools have facilitated the development of multispecies trophic modeling approaches able to characterize the

structure and function of ecosystems and estimate higher-level properties (Straile, 2002) and help implementing efficient management policies (Clark et al., 2001). Among multi-species techniques, ecological network analysis (ENA) provides a descriptive evaluation of all the possible linkages between the different components of the system and gives information on ecological conditions for a snapshot in time (Dame and Christian, 2006). In aquatic systems, ENA exploration has been typically approached with the ECOPATH software (Polovina, 1984) which uses biomass estimates and food-consumption relationships to analyze energy flow between species (or groups of species) that represent the trophic network of a particular ecosystem. It assumes mass balance for the trophic network so that the production of any given prey is equal to the biomass consumed by predators plus the biomass caught (if any) minus any exports from the system. Mass balance modeling has

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been successfully used to identify trophic impacts (Baird et al., 2004) and offer reliable information about how the nature of the ecosystem itself may have changed through time (Baird et al., 1998).

Transitional waters such as coastal lagoons with narrow connections with the sea are typically characterized by strong seasonal cycles resulting from periodical rainfall and wind-forcing events that affect the circulation and the residence time of water (Kjerfve, 1994). In addition, these environments are often severely influenced by human activities such runoff from agricultural and industrial sources, urban development, species exploitation (fisheries and hunting), and climate change induced sea level rise (Gedan et al., 2009). Typically, nutrient additions associated with freshwater discharge stimulate the development of fast-growing macroalgal mats and/or epiphytes that shade submersed macrophytes (Dalla Via et al., 1998). In latter stages of eutrophication, restricted environments often develop high phytoplankton crops due to low hydraulic flushing and turnover rates (Monbet, 1992). Because aquatic macrophyte flora develops in relation to salinity (Adams et al., 1992), variations in freshwater supply will also affect the plant species composition, diversity and primary production of the system and cascade up to associate animal communities (Montague and Ley, 1993). Therefore, such changes on community organization may compromise the overall stability of ecosystems, depending on both the intensity and variability ranges of stressor conditions through the natural cycle of organisms.

Coastal lagoons in the Ebro Delta (Southern Catalonia, NW Mediterranean, see Fig. 1) were declared Natural Park in 1983 but are mostly surrounded by rice fields (ca. 70% of the total Delta surface) and in practice, they are still subjected to persistent human influence. From the 1960s to late 1980s, wastewater rich in nutrients and agricultural chemicals (e.g., PCBs, DDTs and HCB) was disposed into the lagoons during May–November (Comín et al., 1991), enhancing phytoplankton production and decimating submersed macrophytes by 80% of the original area, with the consequent decline of fish and waterfowl populations (Comín et al., 1990, 1991). Since 1990, the regional water and Natural Park authorities implemented a new water management strategy consisting in bringing freshwater from the Ebro River (without completely eradicating wastewater inputs from rice fields) to decrease nutrients and organic matter loading and provide habitat for sporting waterfowl. These recurrent inflows of freshwater from late spring to fall reversed the natural hydrological dynamics of the lagoons, resulting on lower salinities during the summer period, and higher during the winter, but each with distinctive seasonal mean values and annual ranges of variability (Tancada: from ca. 17‰ in summer to 33‰ in winter; Encanyissada: from ca. 11‰ in summer to 30‰ in winter; and Clot: 6‰ in summer to 14‰ in winter) that diverge from otherwise more natural marine conditions (see Prado et al., 2013). Increased inputs of freshwater also favor the successful establishment of non-native fish (Caiola and Sostoa, 2002; Rodríguez-Climent et al., 2013) and invertebrates that threaten the persistence of local species and may have important economic consequences (Oscoz et al., 2010).

Network flow models were constructed and ENA used to examine changes in trophic structure and ecosystem-level properties in summer (period with lowest salinities) and winter (period with highest salinities) resulting from the overall effect of anthropic salinity regimes (i.e., mean seasonal salinities and annual variability ranges). The main goal was to utilize predictable ranges of variability in seasonal salinities to evaluate possible differences in trophic transfers and ecosystem metrics using ECOPATH as a modeling tool, and then provide management recommendations that integrate the functional properties of whole food-web. Specifically, six networks were developed, one for summer and one for winter for each of the three lagoons and examined for differences in their food-web structure, trophic fluxes and critical ecosystem

properties that describe the ecological status and the stability of these ecosystems. All the lagoon models had a similar number of compartments (from 12 to 16) but were very variable in terms of biomass estimates. A correlative approach was also used to investigate the importance of physicochemical factors on the functional ecosystem descriptors obtained from the different models.

## 2. Materials and methods

### 2.1. Study sites

The study was conducted in three coastal lagoons of the Ebro Delta receiving freshwater inflows from irrigation channels from May to December as well as marine water through connecting channels. The Encanyissada lagoon (418 ha;  $3.3 \times 10^6 \text{ m}^3$ ) is connected to Alfacs Bay through a natural outlet and to the Clot lagoon (56 ha;  $4.5 \times 10^5 \text{ m}^3$ ) through an artificial channel and the Tancada lagoon (185 ha;  $1.5 \times 10^6 \text{ m}^3$ ) is connected to the bay through three narrow channels (Fig. 1), resulting on an average tidal range of about 20 cm (Ibáñez et al., 1997). Salinity monitoring since 2007 shows polyhaline winter waters in the Encanyissada and Tancada lagoons and mesohaline in the Clot lagoon whereas in summer, ranges are lower but still polyhaline in the Tancada, mesohaline in the Encanyissada and oligohaline in the Clot lagoon (for more details see Prado et al., 2013). The annual macrophyte, *Ruppia cirrhosa* is the only submersed vegetation in the Tancada and is also the main plant species in the Encanyissada lagoon with some mixed areas with *Potamogeton pectinatus* (pseudo-annual species; i.e., persist all year but experiences certain decline in winter). In contrast, the oligo-mesohaline regime of the Clot lagoon allows well-developed populations of *P. pectinatus* interspersed with *R. cirrhosa* and mixed stands of *P. pectinatus* and *Najas Marina* in some small areas (Prado et al., 2013). Water nutrients are similar among the lagoons (annual averages of  $35.6\text{--}57.6 \mu\text{g L}^{-1} \text{ NO}_2 + \text{NO}_3$ ;  $16.8\text{--}22.4 \mu\text{g L}^{-1} \text{ PO}_4$ ) except for higher levels of ammonia in the Tancada lagoon ( $285 \mu\text{g L}^{-1} \text{ NH}_4$  vs.  $34\text{--}35 \mu\text{g L}^{-1} \text{ NH}_4$  in the Clot and Encanyissada; see Prado et al., 2013). The three lagoons are similar in depth (80 to 90 cm) in all monitoring sites, with water temperature ranging from  $25\text{--}28^\circ\text{C}$  in summer to  $9\text{--}12^\circ\text{C}$  in winter.

### 2.2. Collection of samples

Plants species (*N. marina* in the Clot lagoon, *P. pectinatus* in the Clot and the Encanyissada lagoons and *R. cirrhosa* in the three lagoons) were collected from five sites at each lagoon ( $n = 15$  per site and season) using a 16 cm diameter PVC core and then kept within labeled plastic bags and transported to the laboratory. Removal of epiphytes was done with a razor blade. At each site, sampling of free floating macroalgae not attached to the plant canopy (always *Chaetomorpha linum*) was conducted by randomly throwing a  $50 \times 50$  plastic box opened at the top and bottom, five times, and collecting all the floating biomass within the box ( $n = 15$ ). Plants, epiphytes and macroalgae were dried at  $60^\circ\text{C}$  until constant weight, weighted to the nearest 0.01 g and expressed in  $\text{g DW m}^{-2}$ . Dry weight biomasses per unit area were then transformed to  $\text{g C m}^{-2}$  using a carbon equivalency factor of 0.38 for *R. cirrhosa* and 0.40 for *P. pectinatus* (Prado et al., unpublished data), 0.32 for *N. marina* (Baldantoni et al., 2004), 0.20 for *C. linum* (Menéndez et al., 2002) and 0.16 for epiphytes (Prado et al., unpublished data).

The top 5 cm of sediments ( $n = 5$  per lagoon) were collected using a 4.2 cm diameter plastic containers and transported to the lab. Samples were homogenized and then dried and incinerated for determination of the organic matter (OM) content. A carbon equivalency factor of 0.17 (Prado et al., unpublished data) was

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