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Flow regime in a restored wetland determines trophic links and species composition in the aquatic macroinvertebrate community

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HIGHLIGHTS

- Flow regimen is a major determinant of physicochemical habitat of a wetland.
- Water exchanges wetland-estuary modify its aquatic community and trophic links.
- Omnivory and physiological tolerance key in the resistance of a wetland community.
- Trophic niche of *P.varians* seems not to be shrunk by the presence of *P.macrodactylus*.
- The shrimp *P. varians* has a key role in the stability of the aquatic faunal community.

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ABSTRACT

In a restored wetland (South of Spain), where different flow regimes control water exchange with the adjacent Guadalquivir estuary, the native *Palaemon varians* coexists with an exotic counterpart species *Palaemon macrodactylus*. This controlled m\acrocosm offers an excellent opportunity to investigate how the effects of water management, through different flow regimes, and the presence of a non-native species affect the aquatic community and the trophic niche (by gut contents and C-N isotopic composition) of the native shrimp *Palaemon varians*. We found that increased water exchange rate (5% day^{-1} in mixed ponds *vs.* 0.1% day^{-1} in extensive ponds) modified the aquatic community of this wetland; while extensive ponds are dominated by isopods and amphipods with low presence of *P. macrodactylus*, mixed ponds presented high biomass of mysids, corixids, copepods and both shrimp species. An estuarine origin of nutrients and primary production might explain seasonal and spatial differences found among ponds of this wetland. A combined analysis of gut contents and isotopic composition of the native and the exotic species showed that: (1) native *P. varians* is mainly omnivorous (2) while the non-native *P. macrodactylus* is more zooplanktivorous and (3) a dietary overlap occurred when both species coexist at mixed ponds where a higher water exchange and high abundance of mysids and copepods diversifies the native species' diet. Thus differences in the trophic ecology of both species are clearly explained by water management. This experimental study is a valuable tool for integrated management between river basin and wetlands since it allows quantification of wetland community changes in response to the flow regime.

1. Introduction

Flow regime is the key driver of river and floodplain wetland ecosystems (Bunn and Arthington, 2002; González-Ortegón et al., 2012), and closed systems such as wetlands are the easiest systems in which to determine aquatic community responses to any perturbation (Scheffer and van Nes, 2004). Water regulation modifies hydrological factors and physicochemical conditions, influencing biological production (bottom up control) and the aquatic assemblage structure (Poff and Allan, 1995; González-Ortegón and Drake, 2012). The impacts of flow change have been described across broad taxonomic groups in plants, invertebrates and fish (Fausch and Bramblett, 1991; Poff and Allan, 1995) and in food web structure due to alternative basal resources available for consumers (Wantzen et al., 2002; González-Ortegón et al., 2010; Wang et al., 2011). In addition, the alteration of flow regimes can facilitate the invasion and success of non-native species (Bunn and Arthinghton, 2002). In this way, after successful establishment of an exotic species in the new habitat, its effects on native species may have diverse intensities, ranging from an apparently non-competitive coexistence with the native counterpart (González-

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Ortegón et al., 2010) to the extinction of native species (Clavero and Garcia-Berthou, 2005).

Food web studies are central in understanding changes in community organisation and ecosystem functioning since they incorporate the ecological interactions of that ecosystem in an integrated way (Sierszen et al., 2006; Pace et al., 2013). The study of food webs requires detailed work of the composition and density of each of the aquatic components and the relationships among each component based on gut contents. However, the diversity in primary producers, the complex mobility of consumers, and the digestion of prey in the stomach can make it difficult to ascertain trophic relations among species in an ecosystem (González-Ortegón et al., 2010; Wang et al., 2011). The use of stable carbon and nitrogen isotope ratios ($\delta\ ^{13}C$ and $\delta\ ^{15}N$) to identify carbon sources and trophic relationships and the advances in isotopic mixing models to quantify the contributions of different sources to consumers have greatly facilitated the investigation of aquatic food webs (Parnell et al., 2010). However, there have been relatively few studies estimating the ecological impacts of management practices, such as the effects of the flow regime regulation and the introduction of non-native species in food web dynamics (Kingsford, 2000; Coll et al., 2011).The reconstructed wetlands of Veta La Palma (on the west bank of the Guadalquivir estuary, SW Spain), that are used for extensive and semi-extensive aquaculture by regulating water exchange with the Guadalquivir estuary, offer an excellent opportunity for testing how water regulation influences species composition in the aquatic community. Water flow from the estuary allows for recruitment of the non-native species *P. macrodactylus* Rathbun, 1902 (Gonzalez-Ortegón et al., 2010) and this introduced species (Lejeusne et al., 2014) may compete with the native counterpart species *Palaemon varians* (Leach, 1814) within the Veta La Palma wetland.

This study explores how water flow management in reconstructed wetlands and the introduction of the non-native shrimp *P. macrodactylus* determine aquatic community composition and influence the trophic niche of the native *P. varians*. We estimated density of aquatic fauna, studied gut contents of both shrimps species and analysed food web faunal and source samples seasonally and in individual ponds using isotope mixing models. We hypothesised that different water exchange rates could lead to shifts in the community structure and affect the type of food resources consumed by the two shrimps species in the food webs of the wetland. Secondarily, the density and feeding habits of the native species *Palaemon varians* should be affected mainly by the introduction of the non-native species *Palaemon macrodactylus*.

2. Material and methods

In the 3000 ha of reconstructed wetlands at Veta La Palma (VP) two pond management systems are operated (Fig. 1). In mixed ponds, water enters a row of smaller ponds (0.6 ha each) where semi-extensive aquaculture is performed prior to entering the large 70 ha extensive aquaculture ponds; here water flow rates are higher, resulting in a exchange rate in the extensive ponds of 5% day^{-1}. In purely extensive aquaculture ponds, with no prior aquaculture activity, water exchange rates are 1% day^{-1}. Water exchange occurs daily during the year, with the exception of the period between November and February. The differences in

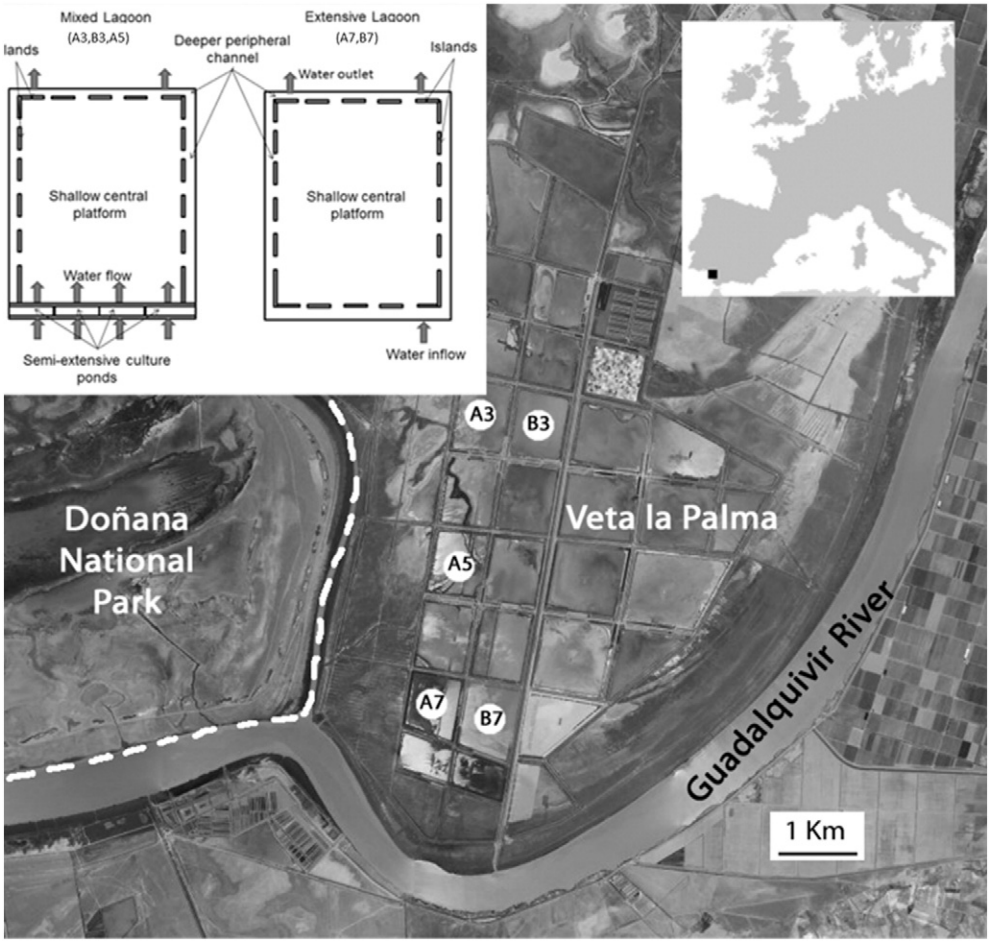

Fig. 1. Satellite image of the sampled ponds of Veta La Palma, part of the Doñana Natural Park and the boundary (dashed line) that separates it from Doñana National Park. Inserted are the geographic location of Veta La Palma and diagrammatic representation of the mixed and extensive ponds.