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Title page

FLOW REGIME IN A RESTORED WETLAND DETERMINES TROPHIC LINKS AND SPECIES COMPOSITION IN THE AQUATIC MACROINVERTEBRATE COMMUNITY

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KEYWORDS

Wetland, water management, flow regime, macroinvertebrates, stable isotope analysis, food webs, invasive species.

Summary

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 macrocosm 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.

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-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*.

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 0.1% day^{-1}. Water exchange occurs daily during the year, with the exception of the period between November and February. The differences in water exchanges rates between mixed and extensive pond determined the spatial and temporal salinity patterns in these two pond systems (Fig. 2). Three mixed pond systems (A3, B3 and A5) and two purely extensive ponds (A7 and B7) were seasonally sampled 4 times (1-4 May 2011, 25-29 July 2011, 1-4 November 2011, and 20-24 February 2012). Daily temperature range and monthly samples of salinity and chlorophyll fluorescence were measured. Three replicate samples were taken for each food web compartment. From the primary producers, three categories were collected: plants, sediment and suspended Particulate Organic Material (POM). The most common plant species at the Veta La Palma wetland, *Spartina densiflora*, *Phragmites australis* and *Ruppia maritime*, were sampled. Benthos was sampled using a cylindrical corer (32cm^2) and box corer (240cm^2). The top 5 mm of sediment layer was carefully sampled from the benthic corer as a proxy of periphyton. Suspended particulate organic matter (POM) as a proxy of phytoplankton was sampled by taking water samples 5 cm under the pond surface, passing through a 100 µm mesh and then vacuum filtering through pre-combusted GFF filters. Zooplankton tows were performed using mesh sizes of 200 µm and 500 µm. ‘Nasa’ traps (Fyke type, funnel-mouthed bag traps) with 3 mesh sizes: 1 mm, 5 mm and 10 mm, were used to catch fish and macroinvertebrates, mostly shrimps.

Shrimp biomass was sampled seasonally 4 times during the year (4-8 July 2011, 7-11 November 2011, 20-24 February 2012, and 14-18 May 2012). Five deep-sided lift nets (94cm diameter; 120cm deep) with a 1mm mesh were placed in each of the five sampled ponds, two in the peripheral canal and three on the main platform. Net catches were placed in plastic bags on ice until arriving at the VP laboratory where counts and wet weight were recorded for each shrimp species.

Stable isotope analysis

Flora and fauna samples were rinsed in distilled water before being oven dried at 50°C for 24 hours. POM samples on the GFF filters were treated with concentrated HCl to remove carbonates, and subsequently re-dried. Sediment samples were sequentially acidified with 0.1M HCl to remove carbonates the oven dried. The dried sediment was rinsed with distilled water and the supernatant carefully pipetted off once the sediment had settled, before final oven drying. Muscle tissue was separated from other tissue in shrimp samples. All samples were homogenised, weighed into tin cups (D1008, Elemental Microanalysis Ltd, UK) and analysed for carbon and nitrogen content and stable isotope ratios using a PDZ Europa Scientific Roboprep elemental analyser coupled to a PDZ Europa Hydra 20/20 stable isotope ratio mass spectrometer (Crewe, UK) at the Stable Isotope Facility, University of California, Davis. Stable isotope ratios in the samples are expressed as delta notation (δ, ‰), deviations from the isotopic ratios found in Pee Dee belemnite and atmospheric nitrogen so that

$$\delta_{sample} = 1000\left(\frac{R_{sample}}{R_{std}} - 1\right)$$

For prey items where C or N content was so low that it decreased the precision of the isotopic analysis, mean values pooled across samples from the same pond or from the same pond system and its standard deviation were instead. When C:N ratios were greater than 3.5, muscle tissue samples were corrected for lipid content as this was found to influence $\delta^{13}C$ values (Post et al., 2007). Diet - consumer ^{13}C discrimination ($\Delta^{13}C$) ± standard deviation was 1.3 ± 0.85‰ for consumers analyzed as muscle tissue. Similarly $\Delta^{15}N$ was 2.9 ± 1.24‰ for consumers analyzed as muscle tissue (McCutchan et al., 2003)

Gut contents analysis

The feeding habits of *P. varians* and *P. macrodactylus* were assessed by analysing gut contents under a binocular microscope. Spatial differences in their diet of both species were studied by selecting individuals at each pond where both species inhabit. Gut contents were studied in individuals collected during April and July 2011. Length frequency distribution for the analysed individuals of *P. varians* and *P. macrodactylus* and percent of gut fullness are given in Supplementary Information (Fig. A.1 and Fig. A.2). Prey were identified to lowest taxon possible and assigned to the following categories: copepods, mysids, amphipods, isopods, ostracods, nematods, cladocerans, corixidae and sediment.

Data analysis

The MixSiar Bayesian stable isotope mixing model (Semmens et al., 2009; Stock and Semmens, 2013) was used to determine probability distributions for the proportional contribution of the food sources to the diet of each shrimp species. Pond, water management (mixed and extensive) and month were used as main effects; when water management was tested, the design had “pond” as a factor nested in “type of flow regimes”. Individual effects (as a random effect) were included in all analyses. However, the variation in diet for individuals was quite low indicating that the majority of the total variation in shrimps' diets was driven by water management or month. Trace plots and the diagnostic tests Gelman-Rubin, Heidelberger-Welch, and Geweke were used to determine if the model had converged (Stock and Semmens, 2013).

For each species of shrimp in each pond and month, the estimated median contribution (the median source contribution value for each source) and 95% Bayesian credible intervals of the likely contribution of each prey item to the tissue composition of the consumer were calculated. A multivariate approach to the analysis of seasonal, spatial (ponds) and water management differences in the community structure, diet composition and isotopic composition of macroinvertebrates was followed using the PRIMER 6.1 (Plymouth Routines in Multivariate Ecological Research) computer software pack. Multivariate data analysis was carried out by non-metric multidimensional scaling (MDS) ordination with the Bray-Curtis similarity measurement for density and diet composition, and Euclidian distance similarity for isotopic data calculated on fourth root transformed data (Clarke and Gorley, 2006). Pairwise Bray–Curtis similarity coefficients were calculated to provide a rough measure of dietary breadth of each species and of inter-specific differences (see González-Ortegón et al., 2010). Main prey categories responsible for similarity and dissimilarity in each considered group were identified using SIMPER (Clarke and Warwick 1994). Relative importance of temporal, spatial and water management changes in the community structure and isotopic composition of the community were estimated by calculating the average similarity of samples: (a) monthly samples, for seasonal changes; (b) among ponds, for spatial variation; and (c) among mixed and extensive ponds (average samples), for water management variations. ANOSIM tests were carried out to determine significant differences among month, ponds and water management changes in the aquatic community, isotopic signature in primary producers, prey and shrimps and in the diet composition.

RESULTS

Fauna composition and densities

The aquatic macroinvertebrates community of reconstructed wetlands of Veta La Palma during the study was strongly dominated by crustaceans; copepods (6440 ind m^{-2}) and mysids (635 ind m^{-2}) were the most abundant groups (Fig.3) while, in terms of biomass, shrimps (5.05 gm^{-2} of *P. varians* and 2.79gm^{-2}of *P. macrodactylus*), isopods (0.37 gm^{-2}, especially *Lekanesphaera* sp.) and mysids (0.18 gm^{-2}) dominated the community (Fig.3).

Overall, the aquatic community composition shows low average dissimilarity in terms of biomass and abundance among ponds (35.6% and 34.3%, respectively), months (37.7% and 38.4%, respectively) and water management regime (39.02% and 35.82%, respectively).When differences in aquatic community composition were tested, ANOSIM analyses showed significant differences in terms of abundance among months ($R = 0.52$; $P<0.05$) and in terms of biomass among water management ($R = 0.55$; $P<0.01$). There were no spatial differences among ponds ($R=0.16$ and -0.25; $p>0.05$). The seasonal differences were due to a high abundance of mysids, annelids, nematodes and amphipods in May and to shrimps in November. In the case of water management, high average individual biomass of shrimp species explained the high contribution of this group to the dissimilarity of water management (Fig.4); *P. macrodactylus* was found almost exclusively in mixed ponds only (5.57 g m^{-2}) *vs.* extensive ponds (0.01 g m^{-2}). In contrast, the native *P. varians* was found at similar density in both the extensive (5.93 g m^{-2}) and mixed (4.18 g m^{-2}) ponds. Thus, the comparative analysis between the two shrimp species was focused on the mixed ponds.

When we tested the differences in the aquatic community using the fauna collected by lift nets, spatial differences between ponds were detected, in addition to seasonal and water management differences. Most of the differences were found between the mixed pond B3 and the extensive ponds A7 and B7 (both of them $R=0.5$, $p<0.01$), and the mixed pond A3 and the extensive ponds A7 and B7 (both of them $R=0.2$, $p<0.01$).

Gut contents

Gut contents of both species were grouped better by water management (R=0.47; p=0.01) than by ponds (R=0.28; p>0.05) or by species (R = 0.07; p>0.05) (Fig. 5). The low intraspecific variability of gut contents of *P. varians* was explained by differences in water management (21% of dissimilarity; R = 0.48; P=0.2). These differences were due to a higher presence of ostracods in the gut contents of shrimp from mixed ponds and of isopods and pollen granules in those sampled at extensive ponds (Table 1).

Interspecific Overlap

Similarity of the frequency of occurrence of the different prey in the gut contents was used as a measure of dietary overlap. SIMPER analysis showed a larger trophic similarity in the diet of both species (Mean Bray–Curtis similarity index, 82% ± 8.5). Also inter-specific similarity (84%) was higher than *P. macrodactylus*(81%) and *P.varians* (82%) intra-specific similarities. When differences in diets between both species were tested, ANOSIM analyses did not show significant differences (R = -0.31; P>0.05). The highest contributions to this trophic overlap were the mysid *Mesopodopsis slabberi* and rest of sediment. On average, the most common prey in *P. varians* (74%) and *P. macrodactylus* (69%) guts was the mysid *M. slabberi* (Table 1). Besides that, two other groups of prey were consumed by both species with similar FO: sediment (39% and 44%, respectively) and copepods (28%). The dissimilarity, although low, is explained in the mixed ponds by the higher occurrence of corixids and amphipods found in the gut contents of *P. macrodactylus*, versus a higher occurrence of isopods and the presence of pollen only in *P. varians*.

Isotopic composition: primary producers, potential prey and shrimps

Strong seasonal differences were found in the primary producers from plankton and benthos (Table 2). These differences were explained mainly by an increasing of the ^{15}N values between winter and summer both in POM (from 2.65 to 6.37; R=0.76 $p<0.01$) as in sediment (from 8.67 to 10.9; R=0.97, $p<0.01$). Although less significant, the carbon isotopic signature of POM explained also this seasonal variation.

In the same way than POM, seasonal differences of carbon isotopic signature of potential prey of *P. varians* and *P. macrodactylus* were higher than spatial ones. These differences were more significant between winter and summer (R=0.42, p=0.02).

Isotopic signatures of the consumer *P. varians* showed significant differences with water management (R=0.59, $p<0.01$) and among ponds (R=0.32, p=0.01) (Fig. 6 and Table 2). Among ponds, the differences were found exclusively between extensive and mixed ponds: mainly between the extensive pond B7 with all the mixed ponds (R=0.7-0.9, $p<0.05$) and between the extensive pond A7 and the mixed pond B3 (R=0.5, $p<0.05$). In both cases, 70% of this spatial difference was explained by higher ^{15}N values for *P. varians* in mixed (15.3 ‰) versus extensive (12.8 ‰) ponds. In the case of the exotic species *P. macrodactylus*, a significance variance occurred among months (R=0.37, p=0.01). This seasonal difference was explained by lower ^{15}N values in winter (15‰) than in the rest of months (16.2‰).

A comparative analysis of the isotopic signatures between native and exotic shrimps in those ponds where both species were abundant (mixed ponds A3 and B3), showed significant differences (R=0.39, $p<0.01$) (Fig. 6b); the more depleted ^{13}C values in *P. macrodactylus* (-19.5 ‰) than in *P. varians* (-18.1 ‰) explained 79% of the interspecific differences in the mixed ponds.

In summary, seasonal differences were explained by a higher ^{15}N values found in the primary producers from water column and in *P. macrodactylus* in summerversus winter, while spatial differences were due to higher ^{15}N values found in *P. varians* in mixed ponds versus extensive ponds.

Stable Isotope Analysis in R (MixSIAR)

The MixSiar model predicted that both consumers had relatively similar diets in mixed ponds, although spatial (Table 3: low contribution of corixids, polychaetes and spartina plants to *P. macrodactylus* diet and of amphipods, copepods and phragmites plants to *P. varians* diet) and seasonal variation were found (Table 4: low contribution of chironomids, ostracods, polychaete, ruppia and spartina plants to *P. macrodactylus* diet). The dietary variation of *P. varians* was mostly driven by water exchange with the Guadalquivir estuary (Fig. 7 and Table 3): in extensive ponds they consumed more plant material especially phytoplankton (POM: 12.3%) and less mysids (5%) while in mixed ponds the diet consisted of less phytoplankton (1.7%) and more mysids (16.4%), despite the presence of the exotic species *P. macrodactylus* (Table 3).

Thus, although the credibility intervals of food source contributions increase uncertainty, these models indicated that *P. macrodactylus* was more zooplanktivorous (consumed more copepods and mysids) while *P. varians* tended to be more omnivorous. In addition, the very large range of *P. varians*δ^{13}C values showed that this species uses a greater range of food sources (Figure 7).

DISCUSSION

The composition of the aquatic macroinvertebrate community and the trophic niche of *Palaemon varians* in the Veta La Palma wetland were determined by the rates of water exchange with the adjacent Guadalquivir estuary. Flow is a major determinant of physicochemical habitat (e.g. salinity and nutrient composition), which in turn is a major determinant of biotic composition (Bunn and Arthington, 2002). The low flow regime increased the average salinity at extensive ponds due to a higher water residence time than in mixed ponds. In contrast, the high flow of water exchange with the estuary in mixed ponds resulted in similar salinity values between the wetland and the estuarine water at this height of its basin and a higher abundance of estuarine fauna such as mysids and the non-native species *P. macrodactylus* from the estuary (Gonzalez-Ortegón and Drake, 2012; Gonzalez-Ortegón et al., 2010).

Anthropogenic alteration of this reconstructed wetland allowed the invasion of non-native species from a well-established population in the adjacent estuary (Cuesta et al., 2006; González-Ortegón et al., 2010). This alteration may put even previously well-adapted native species at a competitive disadvantage with non-native species (Byers, 2002) and affect the resistance of this wetland community. This resistance is clearly observed in the native community in this wetland, especially in the native European shrimp *P. varians*. In spite of different regimes of water exchange, *P. varians* was found at similar average density both in the extensive and mixed ponds in contrast to *P. macrodactylus* which was found almost exclusively in the mixed ponds. The physiological tolerance of salt-marshes species is a determinant factor of the resistance of a wetland community under the input of estuarine water. Although the oxygen concentration is unlikely to be a limiting factor in shallow water ecosystems with water exchange, salinity and temperature among other physical factors may abruptly change (Bunn and Arthington, 2002). The shrimp species *P. varians* and *P. macrodactylus*, like many estuarine species which are more tolerant to large fluctuations of these environmental factors, should be well adapted to inhabit areas under physiological stress (González-Ortegón et al., 2006). Lejeusne et al., (2014) reported that *P. macrodactylus* was more tolerant to rapid increase in temperature, and consistently consumed less oxygen over a broad range of temperatures and salinities than *P. varians*. However, a comparative physiological study under multiple factors showed an oxygen independence in *P. varians* irrespective of the water temperature and the higher oxygen regulation in warmer waters than

P. macrodactylus (González-Ortegón et al., 2013). In this way, the higher temperature variability over short periods in closed wetland systems compared with estuaries may explain the absence of estuarine shrimp species *P. macrodactylus* and *P. longirostris* in the extensive ponds with limited water exchange (Gonzalez-Ortegón et al., 2006; 2010). Also, the broader physiological tolerance and more efficient metabolism of *P. macrodactylus* compared to the estuarine species *P. longirostris* (González-Ortegón et al., 2010; 2013; Lejeusne et al., 2014) and the continuous supply of *P. macrodactylus* recruits pumped directly into the mixed ponds from the Guadalquivir source population, accompanied with the availability of estuarine prey such mysids would explain the successful colonisation (high abundance) of this largely carnivorous non-native species (González-Ortegón et al., 2010) in the mixed ponds.

The input of estuarine water into the Veta La Palma wetland may explain the seasonal differences in ^{15}N isotopic signals of primary producers in the water column. The Guadalquivir estuary suffers nitrogen hyper-nutrification from intensive agriculture (González-Ortegón and Drake, 2012). Elevated N isotope signatures can act as a ^{15}N-enriched tracer of wastewater inputs to estuaries (McClelland et al., 1997). The seasonal differences (higher^{15}N values in summer than in winter) and the interaction with the flow regime (higher water exchange with the estuary in mixed ponds) may explain the spatial and water management patterns in the isotopic signature of the consumer *P. varians*. In addition, in the Guadalquivir estuary, *M. slabberi* and copepods (main prey of both shrimp species) show a strong link with planktonic primary producers (González-Ortegón and Drake, 2012). The seasonal differences found in the carbon isotopic signature in the phytoplanktonic producers and also in the macroinvertebrates as prey of the both shrimps species indicate that these producers were the main carbon source for the shrimp´s prey. However, the fact that seasonal isotopic signature differences were not observed in *P. varians* but were in *P. macrodactylus*, is probably due to probably due to the influence of recruitment of *P. macrodactylus* from the estuary in the summer-autumn months, in contrast to the resident population of *P. varians*. While the spatial difference in *P. varians* may be attributed to a higher influx of enriched nitrogen sources in mixed ponds than in extensive ponds.

Intraspecific variability may have important implications for how populations respond to different environmental contexts (González-Ortegón and Giménez, 2014). The trophic shift noted in the native *P. varians*, revealed by its isotopic composition, appears to be the result of a change of feeding strategy. The large range of food source intakes predicted by the MixSiar models correspond with an opportunistic trophic behaviour, where the main variability in the dietary contribution of *P. varians* was driven by water management. This native species is mainly benthonic in the extensive ponds, but was able to diversify to feed on pelagic prey (mysids and copepods) in the mixed ponds, where the densities of these prey are higher, despite competition from the more carnivorous *P. macrodactylus* which is also feeding mainly on mysids.

Although the analysis of gut contents did not provide clear differences in the diet of both species, it did confirm the range of ingested species. Gut contents can be highly variable due to the difficulty in identifying partially digested prey, the variation in assimilation rates, feeding habits, seasonal or diel collection times, body size, individual dietary (Vinson and Budy, 2010). In addition, these authors highlighted that occurrence of empty guts can increase variation in diet measurements. In agreement with our study, Aguzzi et al (2005) observed that the most *P. varians* in the Veta La Palma wetland showed a low level of gut fullness. Although the variability of prey isotopic signature values, probably due to the wide utilization of basal food resources by their prey (Lebreton et al. 2012; Ramarn et al. 2014), increased the uncertainty of dietary composition, the use of stable isotopes provided a better integrated analysis of the diet of both shrimps species than the complementary gut content analysis.

However, to further reduce uncertainty, future studies could be combined with other trophic markers such as fatty acids (Leduc et al. 2009).

In conclusion, the rate of introduction of the estuarine water determined the physicochemical conditions and the aquatic community composition within the Veta La Palma wetland. Seasonal variation in the primary producers and the spatial differences in the consumer *P. varians* make the estuarine waters as a significant source of nutrient and primary producers in this wetland. The resistance of the aquatic community of this wetland was strongly determined by the omnivorous feeding habits and extreme physiological tolerance of its species to shallow and lentic habitats. In this way, the native European species *P. varians* plays an important role in the stability of the aquatic faunal community. The trophic niche of *Palaemon varians* appears not to be shrunk by the presence of the potential competitor *P. macrodactylus*, in fact diversifying and spreading to more pelagic prey when these prey densities increase, resulting in some dietary overlap with *P. macrodactylus*.

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REFERENCES

Aguzzi J, Cuesta JA, Librero M, Toja J. Daily and seasonal feeding rhythmicity of *Palaemonetes varians* (Leach 1814) from southwestern Europe. Mar Biol 2005;148:141-147.

Bunn SE, Arthington AH. Basic Principles and Ecological Consequences of Altered Flow Regimes for Aquatic Biodiversity. Environ Manage 2002;30:492–507.

Byers JE.Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. Oikos 2002;97:449–458.

Clarke KR, Gorley RN. PRIMER v.6: User Manual/Tutorial. U.K: PRIMER-E Ltd; Plymouth Marine Laboratory; 2006.

Clarke KR, Warwick RM. Change in marine communities: an approach to statistical analysis and interpretation, 1stedn. Plymouth Marine Laboratory;1994.

Clavero M, Garcia-Berthou E. Invasive species are a leading cause of animal extinctions. Trends Ecol Evol 2005;20:110–110.

Coll M, Schmidt A, Romanuk T, Lotze HK. Food-Web Structure of Seagrass Communities across Different Spatial Scales and Human Impacts (SJ Bograd, Ed.). PLoS ONE 2011; 6:e22591.

Cuesta JA, González-Ortegón E, Rodríguez A, Baldó F, Vilas C, Drake P. The Decapod Crustacean community of the Guadalquivir Estuary (SW Spain): seasonal and inter-year changes in community structure. Hydrobiologia 2006;557:85-95.

Fausch KD, Bramblett RG. Disturbance and Fish Communities in Intermittent Tributaries of a Western Great Plains River. Copeia 1991:659.

González-Ortegón E, Pascual E, Cuesta JA, Drake P. Field distribution and osmoregulatory capacity in a temperate European estuary (SW Spain). Estuar Coast Shelf S 2006;67:293–302.

González-Ortegón E, Cuesta JA, Pascual E, Drake P. Assessment of the interaction between the white shrimp, *Palaemon longirostris*, and the exotic oriental shrimp, *Palaemon macrodactylus*, in a European estuary (SW Spain). Biol Invasions 2010;12:1731–1745.

González-Ortegón E, Drake P. Effects of freshwater inputs on the lower trophic levels of a temperate estuary: physical, physiological or trophic forcing? Aquat Sci 2012;74:455–469 74:455–469.

González-Ortegón E, Subida MD, Arias AM, Baldó F, Cuesta JA, Fernández-Delgado C, Vilas C, Drake P. Nekton response to freshwater inputs in a temperate European Estuary with regulated riverine inflow. Sci Total Environ 2012;440:261–271.

González-Ortegón E, Pascual E, Drake P. Respiratory responses to salinity, temperature and hypoxia of six caridean shrimps from different aquatic habitats. J Exp Mar Biol Ecol 2013;445:108–115.

González-Ortegón E, Giménez L. Environmentally-mediated phenotypic links and performance in larvae of a marine invertebrate. Mar Ecol Prog Ser 2014;doi: 10.3354/meps10708

González-Ortegón E, Baldó F, Arias A, Cuesta JA, Fernández-Delgado C, Vilas C, Drake P. Freshwater scarcity effects on the aquatic macrofauna of a European Mediterranean-climate estuary. Sci Total Environ 2014;in press.

Kingsford RT. Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia. Austral Ecol 2000;25:109–127.

Lebreton B, Richard P, Galois R, Radenac G, Brahmia A, Colli G, Grouazel M, André C, Guillou G, Blanchard GF. Food sources used by sediment meiofauna in an intertidal *Zostera noltii* seagrass bed: a seasonal stable isotope study. Mar Biol 2012;159:1537-1550.

Leduc D, Probert PK, Duncan A. A multi-method approach for identifying meiofaunal trophic connections.Mar Ecol Prog Ser 2009;383:95–111.

Lejeusne C, Latchere O, Petit N, Rico C, Green AJ. Do invaders always perform better? Comparing the response of native and invasive shrimps to temperature and salinity gradients in south-west Spain. Estuar Coast Shelf Sci 2014;136:102–111.

McClelland JW, Valiela I, Michener RH. Nitrogen-stable isotope signatures in estuarine food webs: a record of increasing urbanization in coastal watersheds. Limnol Oceanogr 1997;42:930-937.

McCutchan JH, Lewis WM, Kendall C, McGrath CC. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 2003;102: 378-390.

Pace ML, Carpenter SR, Johnson RA, Kurtzweil JT. Zooplankton provide early warnings of a regime shift in a whole lake manipulation. Limnol Oceanogr 2013;58:525–532

Parnell AC, Inger R, Bearhop S, Jackson AL. Source Partitioning Using Stable Isotopes: Coping with Too Much Variation (S Rands, Ed.). PLoS ONE 2010;5:e9672

Poff NL, Allan JD. Functional Organization of Stream Fish Assemblages in Relation to Hydrological Variability. Ecology 1995;76:606

Post D, Layman C, Arrington D, Takimoto G, Quattrochi J, Montaña C. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 2007;152:179-189.

Ramarn T, Chong VC, Hanamura Y. Versatile mysids exploit multiple basal resources: implication of the bentho-pelagic habit in estuarine food webs. Hydrobiologia2014;1-15.

Semmens BX, Ward EJ, Moore JW, Darimont CT. Quantifying inter-and intra-population niche variability using hierarchical Bayesian stable isotope mixing models. PLoS One 2009; 4:e6187.

Scheffer M, Nes EH van. Mechanisms for marine regime shifts: Can we use lakes as microcosms for oceans? Progr Oceanogr 2004;60:303–319

Sierszen ME, Peterson GS, Trebitz AS, Brazner JC, West CW. Hydrology and nutrient effects on food-web structure in ten Lake Superior coastal wetlands. Wetlands 2006;26:951–964

Stock BC, Semmens BX. 2013. MixSIAR GUI user manual, version 1.0. Accessible online at: http://conserver.iugo-cafe.org/user/brice.semmens/MixSIAR

Vinson MR, Budy P. Sources of variability and comparability between salmonidstomach contents and isotopic analyses: study design lessons and recommendations. Can J Fish Aquat Sci 2010;68:137-151.

Wantzen KM, Arruda Machado F de, Voss M, Boriss H, Junk WJ.Seasonal isotopic shifts in fish of the Pantanal wetland, Brazil. Aquat Sci 2002;64:239–251.

Wang Y, Yu X, Li W, Xu J, Chen Y, Fan N. Potential influence of water level changes on energy flows in a lake food web. Chin Sci Bull 2011;56:2794–2802.

Figure captions

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.

Fig. 2. Daily range of water temperature at the Veta la Palma wetland (continuous line) and the Guadalquivir estuary (point line) and annual average of salinity and chlorophyll a concentration (µg L^{-1}) in mixed and extensive ponds. Error bars represent standard error of the mean (n = 58 and 24 for mixed and extensive ponds, respectively, per environmental factor). Data of the Guadalquivir estuary from González-Ortegón et al., in press.

Fig. 3.Spatial differences between mixed and extensive ponds in numerical abundance (individuals per 1 m^{-2}) and biomass (g. m^{-2}) of ostracods, annelids, copepods, mysids, amphipods, corixids, isopods and chironomids in the Veta La Palma wetlands. Grey and Black colour Mixed and Extensive ponds, respectively.

Fig. 4.nMDS ordination of all biomass samples based on Bray–Curtis similarity matrix of ponds and months in the Veta La Palma wetland considered in the study and the correlation circle (r=1) and vectors of two shrimps species *Palaemon varians* and *P.macrodactylus* included in the analysis. Triangle up = mixed ponds; Triangle down= extensive ponds.

Fig. 5. nMDS ordination of samples based on Bray–Curtis similarity matrix of prey frequency of occurrence (FO %) data (square root transformed) for *Palaemon varians* (Pv) and *Palaemon macrodactylus* (Pm) in the Veta La Palma wetland. Triangle up = mixed ponds; Triangle down= extensive ponds.

Fig. 6. MDS plots based on the Euclidean distance of monthly individual variation of δ13C and δ15N isotopic signatures of *Palaemon varians* tissue from mixed and extensive ponds (A) and of *Palaemon varians* and *Palaemon macrodactylus* tissue from the three mixed ponds (A3, B3 and A5) at Veta La Palma wetland. Triangle up = mixed ponds; Triangle down= extensive ponds. Feb February, May May, Jul July, Nov November.

Fig. 7. Stable isotope input for Veta La Palma wetland. Consumer data (the shrimps*P. varians* and *P. macrodactylus*) are smaller dots and source data are labelled. Upper plot: isotope signatures of individual variation of *P.varians* and *P.macrodactylus* in relation to mixed and extensive ponds; Middle plot: isotope signatures of individual variation of *P. varians* and *P. macrodactylus* in relation to each pond separately; Lower plot: isotope signatures of individual variation of *P.varians* and *P.macrodactylus*in relation to the months. Error bars indicate combined source and discrimination uncertainty ±1SD.Prey species: amphipods, chironomids,

copepods, corixids, mysids, ostracods, annelids, sediment, POM, Ruppia, Spartina and Phragmites.

Table 1. Frequency of occurrence (%) of main items found in *Palaemon varians* and *Palaemon macrodactylus* guts contents at each pond of Veta La Palma wetland and month.

Month	July								April			
	P. varians					*P. macrodactylus*			*P. varians*		*P. macrodactylus*	
	Mixed			Extensive		Mixed			Mixed		Mixed	
Pond	A3	A5	B3	A7	B7	A3	A5	B3	A3	B3	A3	B3
N° guts	24	23	31	36	36	30	35	36	9	5	8	5
Items												
Copepods	50	34.8	13.3	25	16.7	46.7	16.7	19.4	0	11.1	20	0
Mysids	66.7	100	63.3	72.2	72.2	73.3	75	58.3	80	88.9	80	100
Amphipods	0	0	0	0	2.8	0	4.2	0	0	0	0	0
Isopods	0	0	3.3	2.8	13.9	0	0	2.8	0	22.2	0	0
Ostracods	25	26.1	40	5.6	5.6	23.3	16.7	33.3	0	22.2	20	0
Nematods	12.5	17.4	10	8.3	19.4	20	4.2	11.1	0	11.1	20	0
Cladocerans	0	0	0	0	2.8	0	0	0	0	0	0	0
Corixidae	0	0	3.3	0	8.3	6.7	0	5.6	0	0	0	0
Pollen	0	4.3	0	0	5.6	0	0	0	7.1	0	0	0
Sediment	40	17.4	43.3	47.2	47.2	38.9	50	44.4	0	77.8	0	0

Table 2. ANOSIM comparison to analyse seasonal, spatial and flow regime isotopic variations based on the Euclidean distance of the d13C and d15N isotopic signatures for primary producers, macroinvertebrates prey, and the consumers *P. varians* and *P. macrodactylus*. Values obtained by the ANOSIM are Global R statistic. The values highlighted in bold are statistically significant ($P < 0.05$).* = $R \geq 0.5$ = overlapping but different.

	Month		Pond		Water management	
	R	P	R	P	R	P
Primary producers	**0.31**	0.005	0.01	0.400	0.09	0.120
POM	**0.62***	0.001	-0.15	0.964	0.02	0.311
d13C	**0.22**	0.009	-0.03	0.590	0.17	0.040
d15N	**0.71***	0.001	-0.15	0.930	-0.06	0.750
Sediment	**0.27**	0.006	0.07	0.222	**0.19**	0.036
d13C	-0.05	0.680	0.03	0.320	-0.03	0.560
d15N	**0.45**	0.003	-0.03	0.540	0.10	0.110
Plants	0.16	0.047	0.01	0.442	0.06	0.184
d13C	-0.08	0.840	**0.44**	0.003	**0.33**	0.005
d15N	0.18	0.049	-0.11	0.850	-0.01	0.440
Macroinvertebrates	**0.33**	0.002	**0.15**	0.039	**0.17**	0.021
d13C	**0.31**	0.002	0.15	0.054	**0.15**	0.044
d15N	**0.18**	0.025	0.14	0.051	0.09	0.110
P. varians	0.04	0.331	**0.32**	0.011	**0.59***	0.001
d13C	0.11	0.130	-0.01	0.510	-0.06	0.760
d15N	0.01	0.400	**0.35**	0.009	**0.78***	0.001
P. macrodactylus	**0.37**	0.017	0.01	0.400	-	-
d13C	0.24	0.130	0.08	0.250	-	-
d15N	**0.31**	0.020	-0.07	0.710	-	-

Table 3. Predicted diet proportions of *P. varians* and *P. macrodactylus* in mixed (A3, A5 and B3) and extensive (A7 and B7) ponds derived from an analysis of the isotopic signatures of consumers and common prey at Veta La Palma wetland using the mixSIAR Bayesian mixing model. Values are in units of percent contribution to total diet. The median diet proportion (M) are given along with 95% posterior intervals (CI); N = sample number; Proportions higher than 10% are shown in bold. Differences in the dietary proportions of a food sources between the two shrimp species are represented by (a) and (aa), which indicates that the median value of a food resource is not found at 90 and 95% CI, respectively, in *P. varians* between Mixed and Extensive ponds. (b) the median value of a food resource of a shrimp species in mixed ponds is not found within the 90% CI respectively, of that same food resource of the other shrimp species.

		Mixed Ponds		A3		A5		B3	Extensive ponds		A7		B7
Consumer	Source	M (CI)	N	M (CI)	N	M (CI)	N	M (CI)	M (CI)	N	M (CI)	N	M (CI)
P. varians													
	Amphipod	5.2 (0.1-22.6)	2	[b]5 (0.1-22.3)	2	5.4 (0.1-28.1)	2	[b]4.6 (0.1-20.1)	4.5 (0.1-19.8)	4	4 (0.1-24.5)	2	3.5 (0.1-18.9)
	Chironomid	5.2 (0.3-17.7)	5	4.8 (0.3-18.5)	6	4.8 (0.3-17.7)	6	4.8 (0.3-18.9)	5.5 (0.3-22.7)	3	4.9 (0.2-26.8)	9	4.4 (0.1-25.7)
	Copepods	9 (1.6-22.6)	8	[b]9.3 (1.6-24.6)	2	[b]9 (1.5-23.5)	3	[b]8.2 (1.4-21.3)	5.3 (0.3-19.6)	4	5.7 (0.2-27.4)	4	3.5 (0.1-16.8)
	Corixid	5.5 (0.5-19)	44	5.2 (0.5-19)	46	5.1 (0.4-18.8)	39	5.3 (0.5-22.1)	5.8 (0.5-24.3)	44	5.1 (0.2-27.3)	46	5.1 (0.2-26.5)
	M.slabberi	**16.4** (4.3-35.8)	8	**16.5** (3.9-36.9)	4	**17.6** (4.2-39.9)	3	**16.2** (3.7-37.4)	[a]5.5 (0.2-20.9)	3	5.3 (0.1-25.8)	5	4 (0.1-18.9)
	Ostracod	**10.7** (1-27.5)	4	**10.7** (0.9-29.3)	4	9.4 (0.9-24.9)	4	**11.4** (1-30.8)	5.6 (0.5-25)	4	5.1 (0.2-25.3)	4	4.7 (0.1-24.6)
	Phragmites	2.5 (0.1-11.7)	4	[b]2.3 (0.1-11.6)	4	[b]2.5 (0.1-12.8)	4	[b]2.2 (0.1-11)	2.8 (0.1-14.5)	4	2.1 (0-12.4)	4	2.1 (0-12.4)
	Polychaete	9.7 (1-29.8)	11	9.7 (0.9-31.5)	11	9.4 (0.9-30)	11	9.7 (0.9-31.3)	6.8 (0.7-27)	11	6.2 (0.3-37)	11	5.7 (0.3-31.8)
	POM	[aa]1.7 (0.1-8.3)	18	1.6 (0.1-8.5)	13	1.6 (0.1-8.7)	14	1.5 (0.1-8.1)	[aa]**12.3** (2.9-27.5)	7	9.9 (1-24.5)	7	**16** (4.5-36.2)
	Ruppia	**11.5** (1.1-27.9)	2	**11.1** (0.9-28.1)	2	**11** (0.9-28.4)	2	**12.5** (1-31.9)	10.4 (0.4-30.8)	2	9.4 (0.2-33.9)	2	**11.5** (0.2-40.9)
	Sediment	5.5 (0.5-18.4)	6	5.4 (0.5-19.7)	8	5.5 (0.5-20.9)	6	5.1 (0.5-19.1)	6.7 (0.5-25.7)	5	6 (0.2-31.4)	5	5.8 (0.3-30.3)
	Spartina	4.9 (0.2-17.8)	4	4.8 (0.2-18.5)	4	4.6 (0.2-17.7)	4	4.7 (0.2-18.9)	**11.3** (1.1-31)	4	**11.7** (0.5-37.8)	4	**10.8** (0.4-38.3)
P. macrodactylus													
	Amphipod	9.6 (0.8-27.9)	2	**10.1** (0.8-30.1)	2	9.3 (0.7-31.1)	2	9 (0.8-27)	-		-		-
	Chironomid	4.5 (0.2-19.9)	5	4.1 (0.2-20.8)	6	4 (0.2-23.2)	6	4.2 (0.2-19.1)	-		-		-
	Copepods	**15.6** (3.6-32.9)	8	**16.7** (3.5-36.4)	2	**18.2** (3-43.6)	3	**12.7** (2.8-28.4)	-		-		-
	Corixid	2.6 (0.2-14.1)	44	[b]2.4 (0.1-13.6)	46	[b]2.2 (0.1-13.5)	39	[b]2.5 (0.1-14.6)	-		-		-
	M.slabberi	**16.2** (3.8-36.5)	8	**16.9** (3.4-41.1)	4	**15.6** (2.8-43.5)	3	17 (3.6-40.1)	-		-		-
	Ostracod	7.5 (0.5-22.1)	4	6.9 (0.4-21.9)	4	5.8 (0.4-19.8)	4	8.6 (0.4-25.9)	-		-		-
	Phragmites	9.7 (0.5-25.6)	4	9.6 (0.4-24.8)	4	**10.8** (0.4-32.3)	4	8.3 (0.4-21.9)	-		-		-
	Polychaete	5.2 (0.3-20.8)	11	[b]4.8 (0.2-21.3)	11	[b]4.4 (0.2-19.9)	11	5.7 (0.3-24.1)	-		-		-
	POM	1.3 (0-6.6)	18	1.1 (0-6.4)	13	1.1 (0-6.7)	14	1.2 (0-6.5)	-		-		-
	Ruppia	**10.1** (0.5-24.6)	2	9.4 (0.4-23.8)	2	8.1 (0.4-21.8)	2	**12.1** (0.4-28.8)	-		-		-
	Sediment	3 (0.2-16.8)	6	2.7 (0.1-16)	8	[b]2.6 (0.1-17.5)	6	2.9 (0.1-17)	-		-		-
	Spartina	2.2 (0.1-14.4)	4	[b]1.9 (0.1-13.3)	4	[b]1.8 (0.1-12.9)	4	2.2 (0.1-15.7)	-		-		-

Table 4

Table 4 Predicted diet proportions of *P. varians* and *P. macrodactylus* in the studied months derived from an analysis of the isotopic signatures of consumers and common prey at mixed ponds of Veta La Palma wetland using the MixSIAR Bayesian mixing model. The median diet proportion (M) are given along with 95% posterior intervals (CI); N = sample number; Proportions higher than 10% are shown in bold. Differences in the dietary proportions of a food sources between the two shrimp species are represented by (^{b}) and (^{bb}), which indicate that the median value of a food resource is not found within the 90% or 95% CI, respectively, of that same food resource of the other shrimp.

	May		July		November		February	
Consumer Source	N	M (CI)	N	M (CI)	N	M (CI)	N	M (CI)
P. varians								
Amphipod	5	7.5 (0.4-21.9)	16	7.8 (0.4-32.8)	16	6.6 (0.3-22.8)	5	7.5 (0.3-34.6)
Chironomid	12	**13.3** (0.6-28.5)	4	**12.8** (0.5-43.5)	7	**11.3** (0.5-31.7)	6	**10.7** (0.4-27.4)
Copepods	4	^{b}**12.8** (1.3-29.5)	4	**10.0** (0.8-29.0)	4	9.1 (0.9-24.5)	9	**10.4** (0.9-32.6)
Corixid	9	5.6 (0.5-16.6)	141	6.4 (0.5-27.4)	5	7.7 (0.5-53.4)	64	6.7 (0.5-30.6)
M. slabberi	6	**12.0** (0.5-30.3)	5	**10.5** (0.4-40.1)	7	9 (0.4-28.0)	5	**10.9** (0.4-37.3)
Ostracod	4	**11.6** (2.1-21.0)	4	9.8 (0.9-22.5)	4	**14.1** (1.2-31.2)	4	**11.3** (1-26.6)
Phragmites	2	1.1 (0-5.8)	2	1.2 (0-13.9)	2	^{b}1.2 (0-9.0)	2	1.2 (0-10.7)
Polychaete	11	9.1 (0.6-23.6)	11	8.1 (0.5-30.5)	11	8.3 (0.5-30.3)	11	8.6 (0.5-35)
POM	5	0.9 (0.1-4.5)	9	1 (0-6.9)	29	0.9 (0-5.2)	8	0.9 (0-5.6)
Ruppia	5	**10.1** (0.6-22.8)	2	7.7 (0.5-21.5)	9	8.8 (0.4-26.2)	9	8.6 (0.5-26.7)
Sediment	8	3.3 (0.2-16.0)	8	3.2 (0.2-20.1)	8	2.7 (0.2-12.1)	6	2.9 (0.2-13.8)
Spartina	2	5.1 (0.3-16.7)	2	4.1 (0.3-16.9)	2	4.3 (0.3-21.9)	2	4 (0.3-16.2)
P.macrodactylus								
Amphipod	3	5.6 (0.1-23.5)	3	7.6 (0.1-52.9)	3	6.8 (0.1-47.6)	2	5.7 (0-48.9)
Chironomid	7	^{b}6.2 (0.1-25.1)	3	^{b}4.0 (0.1-44.1)	4	^{b}4.4 (0.1-32.0)	3	^{b}2.7 (0-19.6)
Copepods	4	^{bb}**31.3** (7.4-54.1)	3	9.6 (0.2-47.0)	3	**12.3** (0.4-45.9)	3	**10.4** (0.1-44.3)
Corixid	4	4.1 (0.1-20.4)	100	5.8 (0.1-41.2)	3	7.9 (0.2-45.7)	22	4.9 (0.1-39.0)
M. slabberi	4	**17.5** (1.9-41.6)	4	**11.4** (0.3-64.1)	4	**12.1** (0.3-54.7)	3	**17.2** (0.4-77.8)
Ostracod	4	^{b}6.3 (0.2-16.5)	4	^{b}4.6 (0.1-20.5)	4	^{b}9.2 (0.2-30.9)	4	**10.0** (0.1-38.1)
Phragmites	2	1.4 (0-12.6)	2	3.3 (0-31.8)	2	6.2 (0-26.5)	2	2.4 (0-23.4)
Polychaete	11	^{b}3.9 (0.1-16.9)	11	^{b}3.6 (0.1-39.2)	11	^{b}3.6 (0.1-30.4)	11	^{b}3.5 (0-47.3)
POM	3	0.5 (0-3.7)	7	0.7 (0-21.6)	23	0.6 (0-6.6)	6	0.5 (0-6.4)
Ruppia	3	^{b}5.3 (0.1-19.2)	2	^{b}2.8 (0-17.5)	2	^{b}3.2 (0-21.1)	2	^{b}3.2 (0-25.5)
Sediment	6	2.7 (0.1-17.8)	6	2.8 (0-54.0)	6	1.8 (0-14.6)	2	1.7 (0-16.1)
Spartina	2	^{b}1.9 (0-13.6)	2	^{b}1.6 (0-14.7)	2	^{b}1.6 (0-17.1)	2	1.4 (0-19.6)

Figure 1

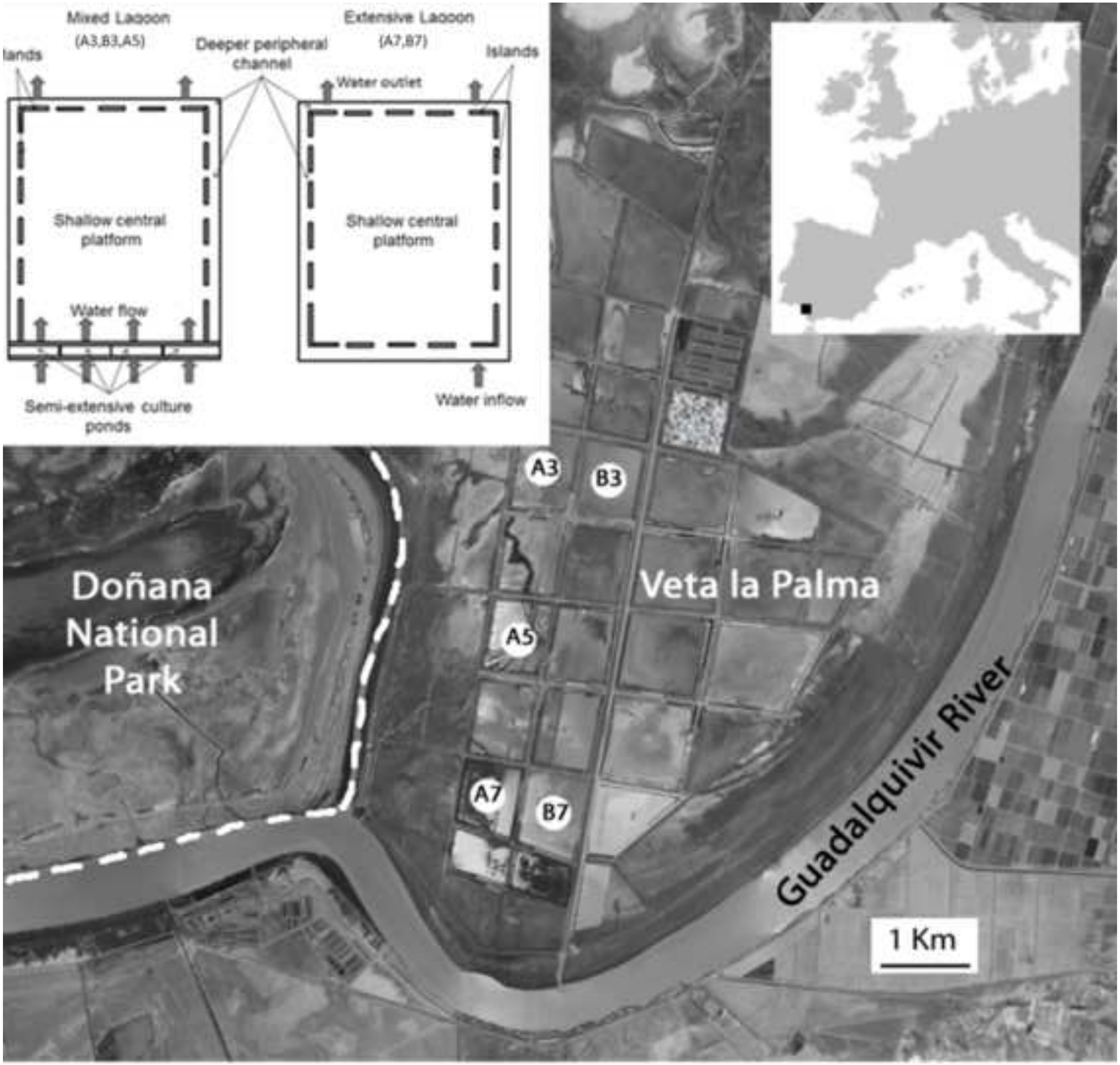

Mixed Lagoon
(A3,B3,A5)
lands
Deeper peripheral channel
Extensive Lagoon
(A7,B7)
Islands
Water outlet
Shallow central platform
Water flow
Shallow central platform
Semi-extensive culture ponds
Water inflow
A3
B3
A5
A7
B7
Doñana National Park
Veta la Palma
Guadalquivir River
1 Km

Figure 2

Click here to download high resolution image

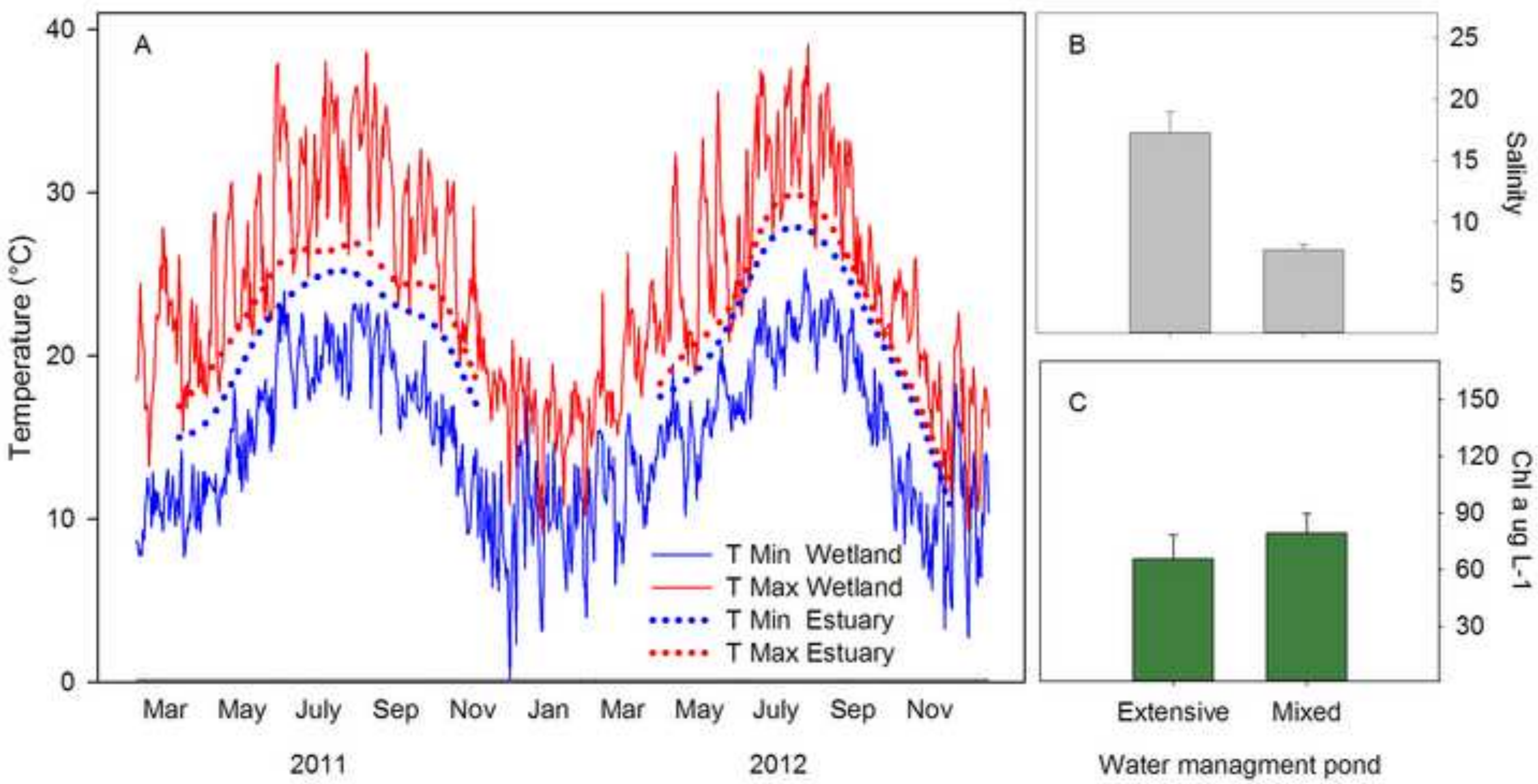


Figure 3

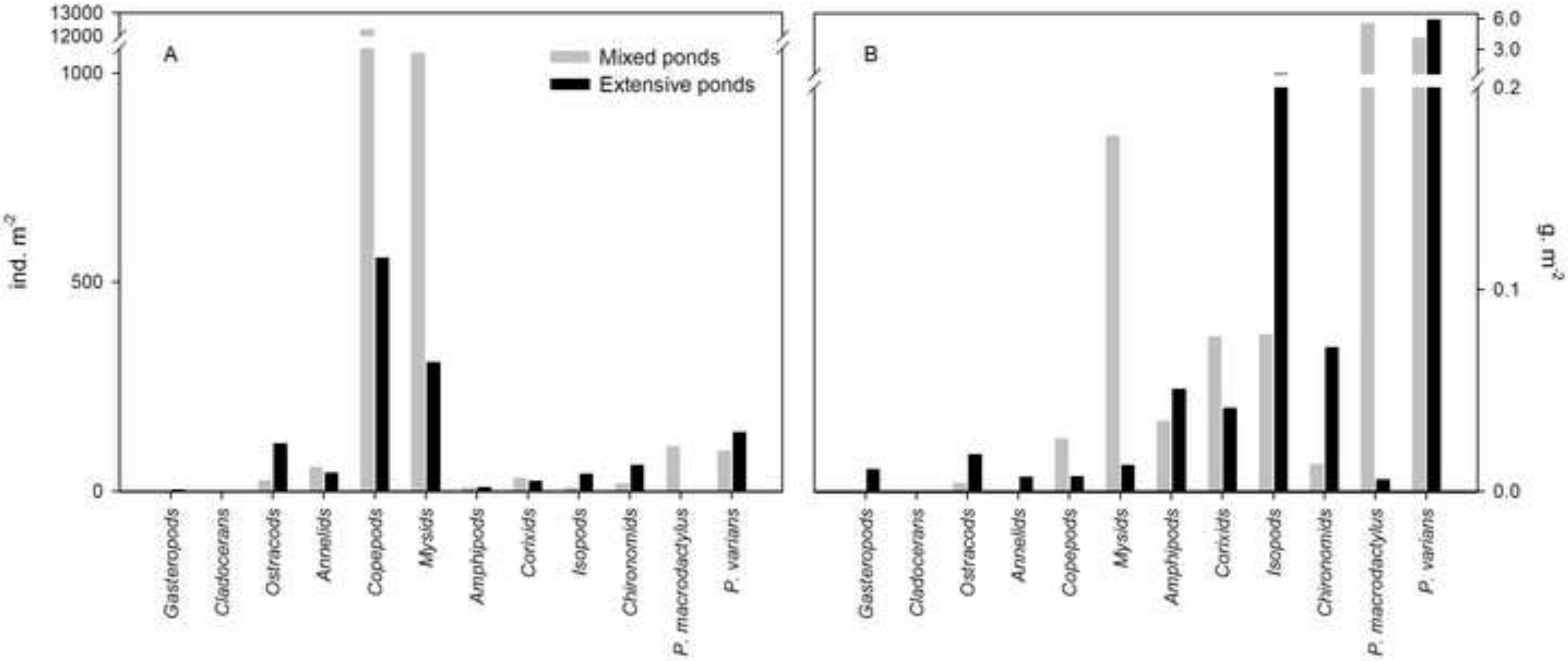

A
B
Mixed ponds
Extensive ponds
ind. m-2
g. m-2
13000
12000
1000
500
0
6.0
3.0
0.2
0.1
0.0
Gasteropods
Cladocerans
Ostracods
Annelids
Copepods
Mysids
Amphipods
Corixids
Isopods
Chironomids
P. macrodactylus
P. varians

Figure 4

Click here to download Figure: Fig 4.docx

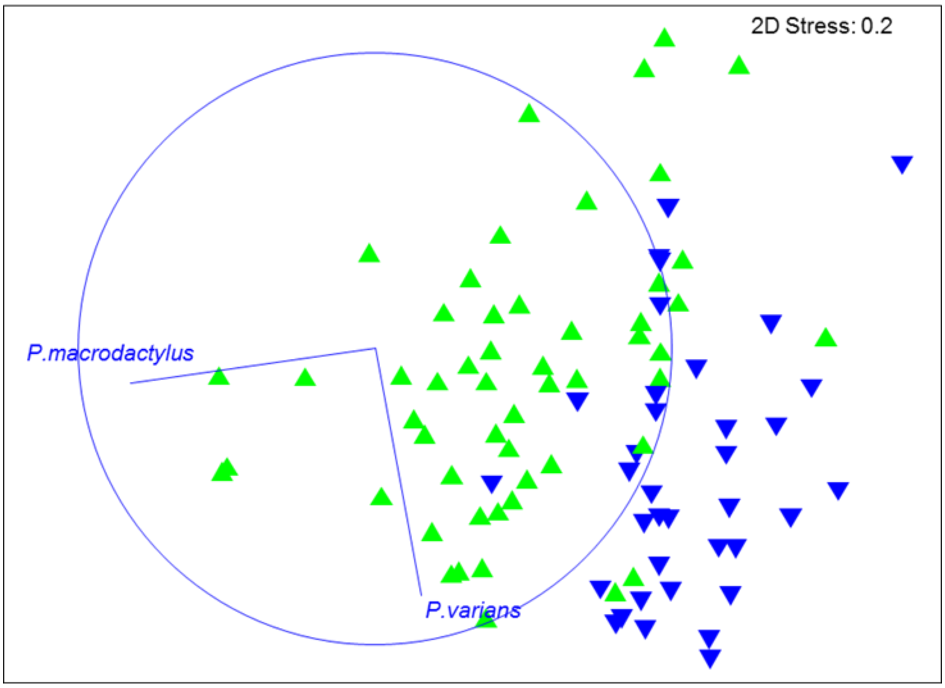


Figure 5

Click here to download high resolution image

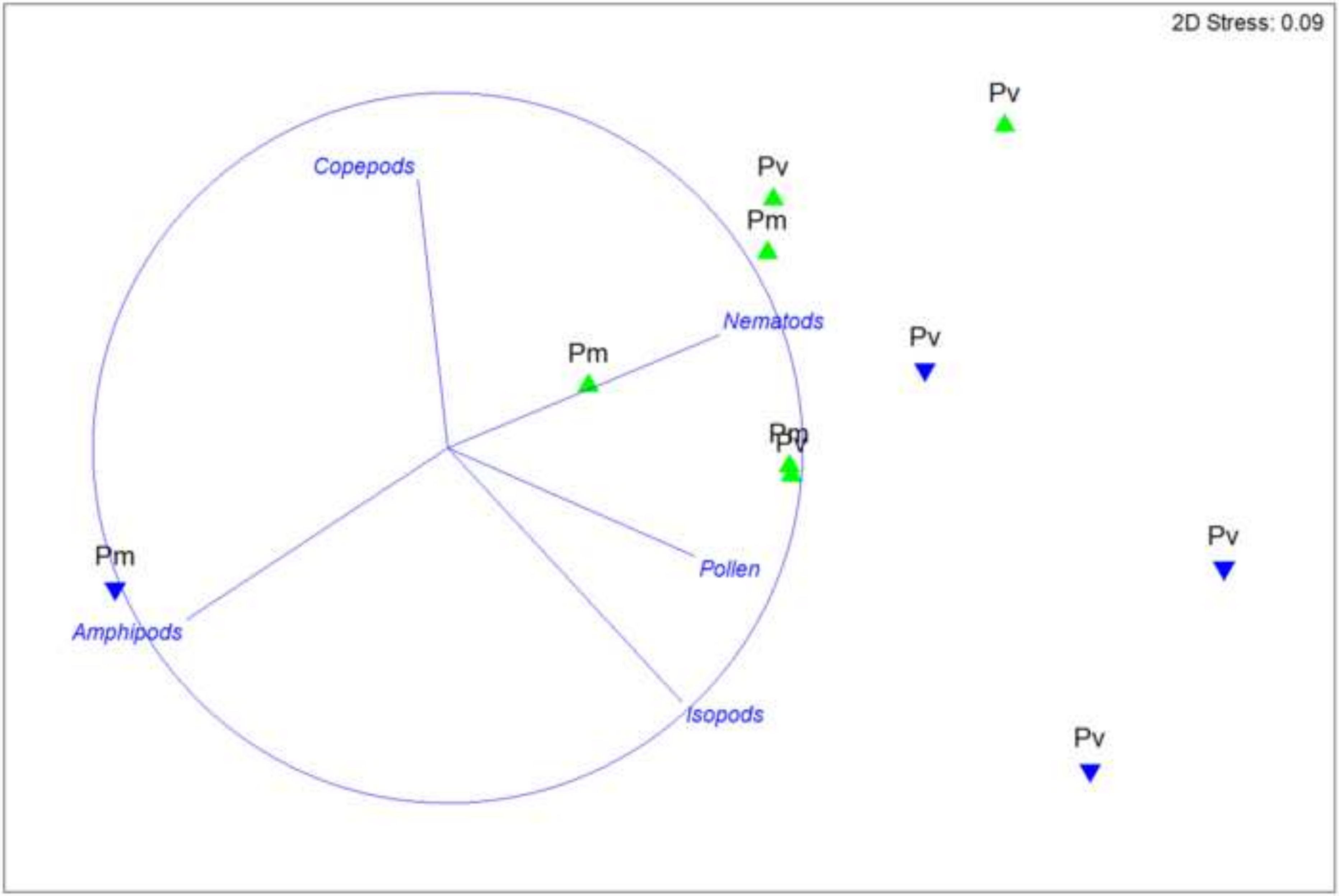


Figure 6

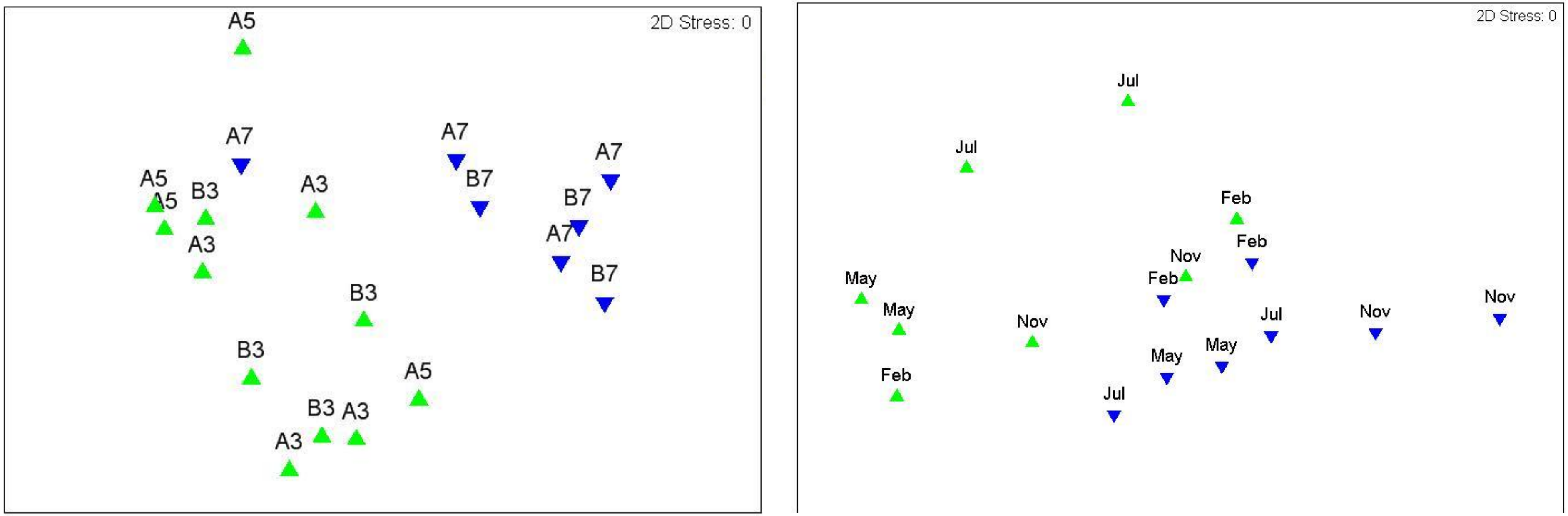
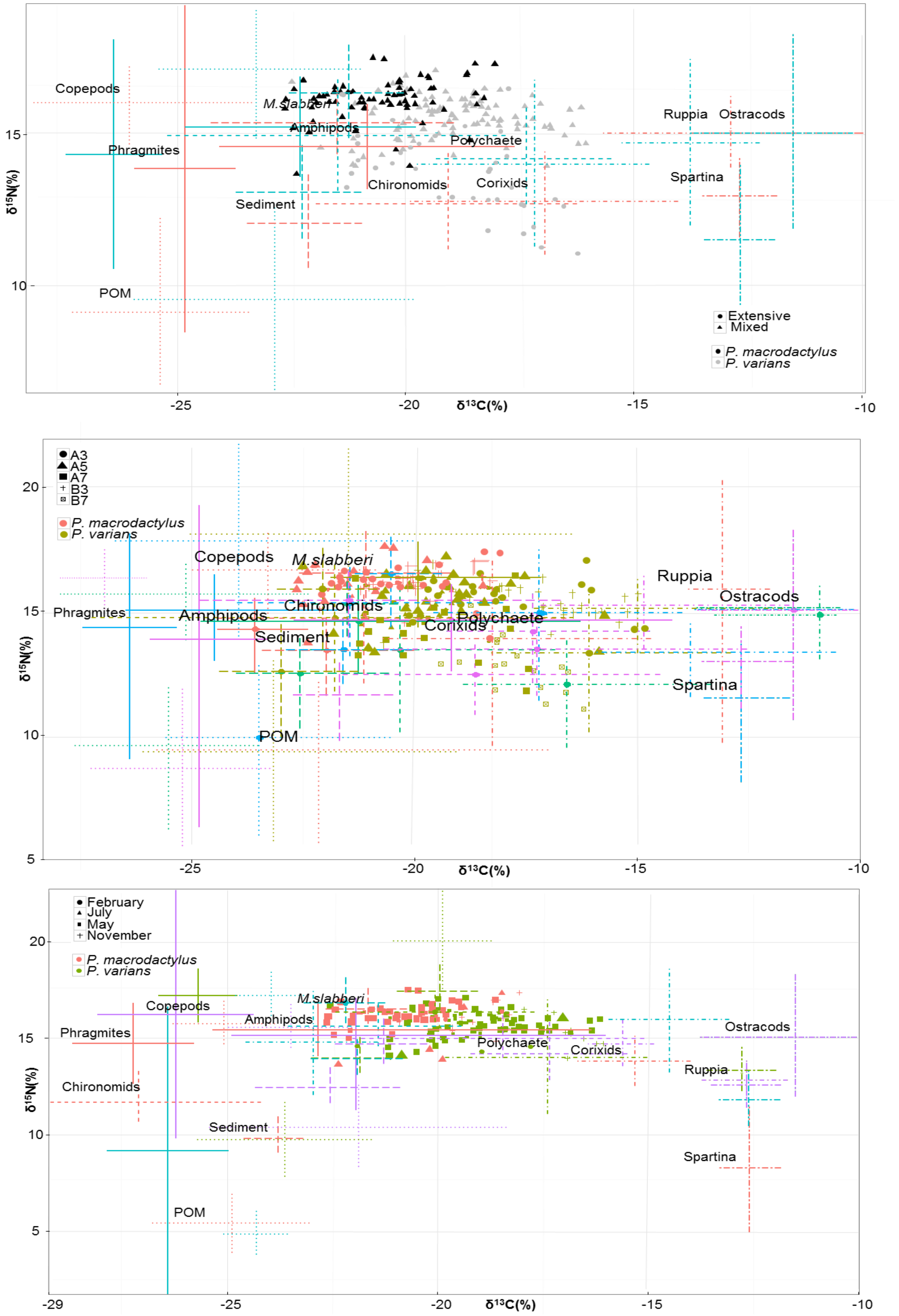

2D Stress: 0
A5
A7
A7
A7
A5
A5
B3
A3
B7
B7
A7
A3
B7
B3
B3
A5
B3
A3
A3
2D Stress: 0
Jul
Jul
Feb
Feb
Nov
Feb
May
May
Nov
Jul
Nov
Nov
May
May
Feb
Jul

Figure 7


Copepods
M.slabberi
Amphipods
Phragmites
Polychaete
Chironomids
Corixids
Sediment
Ruppia
Ostracods
Spartina
POM
15
10
δ¹⁵N(%)
-25
-20
δ¹³C(%)
-15
-10
Extensive
Mixed
P. macrodactylus
P. varians
A3
A5
A7
B3
B7
P. macrodactylus
P. varians
Copepods
M.slabberi
Ruppia
Ostracods
Phragmites
Amphipods
Chironomids
Polychaete
Corixids
Sediment
Spartina
POM
20
15
10
5
δ¹⁵N(%)
-25
-20
δ¹³C(%)
-15
-10
February
July
May
November
P. macrodactylus
P. varians
M.slabberi
Copepods
Amphipods
Phragmites
Ostracods
Polychaete
Corixids
Ruppia
Chironomids
Sediment
Spartina
POM
20
15
10
5
δ¹⁵N(%)
-29
-25
-20
δ¹³C(%)
-15
-10