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

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24 Summary

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

48 INTRODUCTION

49 Flow regime is the key driver of river and floodplain wetland ecosystems (Bunn and
50 Arthington, 2002; González-Ortegón et al., 2012), and closed systems such as wetlands are the
51 easiest systems in which to determine aquatic community responses to any perturbation
52 (Scheffer and van Nes, 2004). Water regulation modifies hydrological factors and
53 physicochemical conditions, influencing biological production (bottom up control) and the
54 aquatic assemblage structure (Poff and Allan, 1995; González-Ortegón and Drake, 2012). The
55 impacts of flow change have been described across broad taxonomic groups in plants,
56 invertebrates and fish (Fausch and Bramblett, 1991; Poff and Allan, 1995) and in food web
57 structure due to alternative basal resources available for consumers (Wantzen et al., 2002;
58 González-Ortegón et al., 2010; Wang et al., 2011). In addition, the alteration of flow regimes
59 can facilitate the invasion and success of non-native species (Bunn and Arthington, 2002). In
60 this way, after successful establishment of an exotic species in the new habitat, its effects on
61 native species may have diverse intensities, ranging from an apparently non-competitive
62 coexistence with the native counterpart (González-Ortegón et al., 2010) to the extinction of
63 native species (Clavero and Garcia-Berthou, 2005).

64 Food web studies are central in understanding changes in community organisation and
65 ecosystem functioning since they incorporate the ecological interactions of that ecosystem in
66 an integrated way (Sierszen et al., 2006; Pace et al., 2013). The study of food webs requires
67 detailed work of the composition and density of each of the aquatic components and the
68 relationships among each component based on gut contents. However, the diversity in primary
69 producers, the complex mobility of consumers, and the digestion of prey in the stomach can
70 make it difficult to ascertain trophic relations among species in an ecosystem (González-
71 Ortégón et al., 2010; Wang et al., 2011). The use of stable carbon and nitrogen isotope ratios (δ
72 ^{13}C and δ ^{15}N) to identify carbon sources and trophic relationships and the advances in isotopic

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73 mixing models to quantify the contributions of different sources to consumers have greatly
74 facilitated the investigation of aquatic food webs (Parnell et al., 2010). However, there have
75 been relatively few studies estimating the ecological impacts of management practices, such as
76 the effects of the flow regime regulation and the introduction of non-native species in food web
77 dynamics (Kingsford 2000; Coll et al., 2011). The reconstructed wetlands of Veta La Palma (on
78 the west bank of the Guadalquivir estuary, SW Spain), that are used for extensive and semi-
79 extensive aquaculture by regulating water exchange with the Guadalquivir estuary, offer an
80 excellent opportunity for testing how water regulation influences species composition in the
81 aquatic community. Water flow from the estuary allows for recruitment of the non-native
82 species *P. macrodactylus* Rathbun, 1902 (Gonzalez-Ortegón et al., 2010) and this introduced
83 species (Lejeusne et al., 2014) may compete with the native counterpart species *Palaemon*
84 *varians* (Leach, 1814) within the Veta La Palma wetland.

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

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97 MATERIAL AND METHODS

98 In the 3000 ha of reconstructed wetlands at Veta La Palma (VP) two pond management
99 systems are operated (Fig. 1). In mixed ponds, water enters a row of smaller ponds (0.6 ha
100 each) where semi-extensive aquaculture is performed prior to entering the large 70 ha
101 extensive aquaculture ponds; here water flow rates are higher, resulting in a exchange rate in
102 the extensive ponds of 5% day⁻¹. In purely extensive aquaculture ponds, with no prior
103 aquaculture activity, water exchange rates are 0.1% day⁻¹. Water exchange occurs daily during
104 the year, with the exception of the period between November and February. The differences in
105 water exchanges rates between mixed and extensive pond determined the spatial and temporal
106 salinity patterns in these two pond systems (Fig. 2). Three mixed pond systems (A3, B3 and
107 A5) and two purely extensive ponds (A7 and B7) were seasonally sampled 4 times (1-4 May
108 2011, 25-29 July 2011, 1-4 November 2011, and 20-24 February 2012). Daily temperature
109 range and monthly samples of salinity and chlorophyll fluorescence were measured. Three
110 replicate samples were taken for each food web compartment. From the primary producers,
111 three categories were collected: plants, sediment and suspended Particulate Organic Material
112 (POM). The most common plant species at the Veta La Palma wetland, *Spartina densiflora*,
113 *Phragmites australis* and *Ruppia maritime*, were sampled. Benthos was sampled using a
114 cylindrical corer (32cm²) and box corer (240cm²). The top 5 mm of sediment layer was
115 carefully sampled from the benthic corer as a proxy of periphyton. Suspended particulate
116 organic matter (POM) as a proxy of phytoplankton was sampled by taking water samples 5 cm
117 under the pond surface, passing through a 100 µm mesh and then vacuum filtering through pre-
118 combusted GFF filters. Zooplankton tows were performed using mesh sizes of 200 µm and 500
119 µm. 'Nasa' traps (Fyke type, funnel-mouthed bag traps) with 3 mesh sizes: 1 mm, 5 mm and
120 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

144 tissue samples were corrected for lipid content as this was found to influence $\delta^{13}\text{C}$ values (Post
145 et al., 2007). Diet - consumer ^{13}C discrimination ($\Delta^{13}\text{C}$) $\pm$ standard deviation was $1.3 \pm 0.85\text{‰}$
146 for consumers analyzed as muscle tissue. Similarly $\Delta^{15}\text{N}$ was $2.9 \pm 1.24\text{‰}$ for consumers
147 analyzed as muscle tissue (McCutchan et al., 2003)

148 ***Gut contents analysis***

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

157 ***Data analysis***

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

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

196 Overall, the aquatic community composition shows low average dissimilarity in terms of
197 biomass and abundance among ponds (35.6% and 34.3%, respectively), months (37.7% and
198 38.4%, respectively) and water management regime (39.02% and 35.82%, respectively). When
199 differences in aquatic community composition were tested, ANOSIM analyses showed
200 significant differences in terms of abundance among months ($R = 0.52$; $P < 0.05$) and in terms
201 of biomass among water management ($R = 0.55$; $P < 0.01$). There were no spatial differences
202 among ponds ($R = 0.16$ and -0.25 ; $p > 0.05$). The seasonal differences were due to a high
203 abundance of mysids, annelids, nematodes and amphipods in May and to shrimps in
204 November. In the case of water management, high average individual biomass of shrimp
205 species explained the high contribution of this group to the dissimilarity of water management
206 (Fig.4); *P. macrodactylus* was found almost exclusively in mixed ponds only (5.57 g m⁻²) vs.
207 extensive ponds (0.01 g m⁻²). In contrast, the native *P. varians* was found at similar density in
208 both the extensive (5.93 g m⁻²) and mixed (4.18 g m⁻²) ponds. Thus, the comparative analysis
209 between the two shrimp species was focused on the mixed ponds.

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

215 *Gut contents*

216 Gut contents of both species were grouped better by water management ($R=0.47$; $p=0.01$) than
217 by ponds ($R=0.28$; $p>0.05$) or by species ($R = 0.07$; $p>0.05$) (Fig. 5). The low intraspecific
218 variability of gut contents of *P. varians* was explained by differences in water management
219 (21% of dissimilarity; $R = 0.48$; $P=0.2$). These differences were due to a higher presence of
220 ostracods in the gut contents of shrimp from mixed ponds and of isopods and pollen granules
221 in those sampled at extensive ponds (Table 1).

222 *Interspecific Overlap*

223 Similarity of the frequency of occurrence of the different prey in the gut contents was used as a
224 measure of dietary overlap. SIMPER analysis showed a larger trophic similarity in the diet of
225 both species (Mean Bray–Curtis similarity index, $82\% \pm 8.5$). Also inter-specific similarity
226 (84%) was higher than *P. macrodactylus* (81%) and *P. varians* (82%) intra-specific similarities.
227 When differences in diets between both species were tested, ANOSIM analyses did not show
228 significant differences ($R = -0.31$; $P>0.05$). The highest contributions to this trophic overlap
229 were the mysid *Mesopodopsis slabberi* and rest of sediment. On average, the most common
230 prey in *P. varians* (74%) and *P. macrodactylus* (69%) guts was the mysid *M. slabberi* (Table
231 1). Besides that, two other groups of prey were consumed by both species with similar FO:
232 sediment (39% and 44%, respectively) and copepods (28%). The dissimilarity, although low, is
233 explained in the mixed ponds by the higher occurrence of corixids and amphipods found in the
234 gut contents of *P. macrodactylus*, versus a higher occurrence of isopods and the presence of
235 pollen only in *P. varians*.

236 *Isotopic composition: primary producers, potential prey and shrimps*

237 Strong seasonal differences were found in the primary producers from plankton and benthos
238 (Table 2). These differences were explained mainly by an increasing of the ^{15}N values between

239 winter and summer both in POM (from 2.65 to 6.37; $R=0.76$ $p<0.01$) as in sediment (from 8.67
240 to 10.9; $R=0.97$, $p<0.01$). Although less significant, the carbon isotopic signature of POM
241 explained also this seasonal variation.

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

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

254 A comparative analysis of the isotopic signatures between native and exotic shrimps in those
255 ponds where both species were abundant (mixed ponds A3 and B3), showed significant
256 differences ($R=0.39$, $p<0.01$) (Fig. 6b); the more depleted ^{13}C values in *P. macrodactylus* (-
257 19.5 ‰) than in *P. varians* (-18.1 ‰) explained 79% of the interspecific differences in the
258 mixed ponds.

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

263 *Stable Isotope Analysis in R (MixSIAR)*

264 The MixSiar model predicted that both consumers had relatively similar diets in mixed ponds,
265 although spatial (Table 3: low contribution of corixids, polychaetes and spartina plants to *P.*
266 *macrodactylus* diet and of amphipods, copepods and phragmites plants to *P. varians* diet) and
267 seasonal variation were found (Table 4: low contribution of chironomids, ostracods,
268 polychaete, ruppia and spartina plants to *P. macrodactylus* diet). The dietary variation of *P.*
269 *variens* was mostly driven by water exchange with the Guadalquivir estuary (Fig. 7 and Table
270 3): in extensive ponds they consumed more plant material especially phytoplankton (POM:
271 12.3%) and less mysids (5%) while in mixed ponds the diet consisted of less phytoplankton
272 (1.7%) and more mysids (16.4%), despite the presence of the exotic species *P. macrodactylus*
273 (Table 3).

274 Thus, although the credibility intervals of food source contributions increase uncertainty, these
275 models indicated that *P. macrodactylus* was more zooplanktivorous (consumed more copepods
276 and mysids) while *P. varians* tended to be more omnivorous. In addition, the very large range
277 of *P. varians* $\delta^{13}\text{C}$ values showed that this species uses a greater range of food sources (Figure
278 7).

280 DISCUSSION

281 The composition of the aquatic macroinvertebrate community and the trophic niche of
282 *Palaemon varians* in the Veta La Palma wetland were determined by the rates of water
283 exchange with the adjacent Guadalquivir estuary. Flow is a major determinant of
284 physicochemical habitat (e.g. salinity and nutrient composition), which in turn is a major
285 determinant of biotic composition (Bunn and Arthington, 2002). The low flow regime
286 increased the average salinity at extensive ponds due to a higher water residence time than in

287 mixed ponds. In contrast, the high flow of water exchange with the estuary in mixed ponds
288 resulted in similar salinity values between the wetland and the estuarine water at this height of
289 its basin and a higher abundance of estuarine fauna such as mysids and the non-native species
290 *P. macrodactylus* from the estuary (Gonzalez-Ortegón and Drake, 2012; Gonzalez-Ortegón et
291 al., 2010).

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

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

322 The input of estuarine water into the Veta La Palma wetland may explain the seasonal
323 differences in ^{15}N isotopic signals of primary producers in the water column. The Guadalquivir
324 estuary suffers nitrogen hyper-nutrification from intensive agriculture (González-Ortegón and
325 Drake, 2012). Elevated N isotope signatures can act as a ^{15}N -enriched tracer of wastewater
326 inputs to estuaries (McClelland et al., 1997). The seasonal differences (higher ^{15}N values in
327 summer than in winter) and the interaction with the flow regime (higher water exchange with
328 the estuary in mixed ponds) may explain the spatial and water management patterns in the
329 isotopic signature of the consumer *P. varians*. In addition, in the Guadalquivir estuary, *M.*
330 *slabberi* and copepods (main prey of both shrimp species) show a strong link with planktonic
331 primary producers (González-Ortegón and Drake, 2012). The seasonal differences found in the
332 carbon isotopic signature in the phytoplanktonic producers and also in the macroinvertebrates
333 as prey of the both shrimps species indicate that these producers were the main carbon source
334 for the shrimp's prey. However, the fact that seasonal isotopic signature differences were not
335 observed in *P. varians* but were in *P. macrodactylus*, is probably due to probably due to the
336 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.

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

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

374

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385 REFERENCES

- 386 Aguzzi J, Cuesta JA, Librero M, Toja J. Daily and seasonal feeding rhythmicity of
387 *Palaemonetes varians* (Leach 1814) from southwestern Europe. Mar Biol 2005;148:141-147.
- 388 Bunn SE, Arthington AH. Basic Principles and Ecological Consequences of Altered Flow
389 Regimes for Aquatic Biodiversity. Environ Manage 2002;30:492–507.
- 390 Byers JE. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of
391 selection regimes. Oikos 2002;97:449–458.
- 392 Clarke KR, Gorley RN. PRIMER v.6: User Manual/Tutorial. U.K: PRIMER-E Ltd; Plymouth
393 Marine Laboratory; 2006.
- 394 Clarke KR, Warwick RM. Change in marine communities: an approach to statistical analysis
395 and interpretation, 1stedn. Plymouth Marine Laboratory; 1994.
- 396 Clavero M, Garcia-Berthou E. Invasive species are a leading cause of animal extinctions.
397 Trends Ecol Evol 2005;20:110–110.
- 398 Coll M, Schmidt A, Romanuk T, Lotze HK. Food-Web Structure of Seagrass Communities
399 across Different Spatial Scales and Human Impacts (SJ Bograd, Ed.). PLoS ONE 2011;
400 6:e22591.
- 401 Cuesta JA, González-Ortegón E, Rodríguez A, Baldó F, Vilas C, Drake P. The Decapod
402 Crustacean community of the Guadalquivir Estuary (SW Spain): seasonal and inter-year
403 changes in community structure. Hydrobiologia 2006;557:85-95.
- 404 Fausch KD, Bramblett RG. Disturbance and Fish Communities in Intermittent Tributaries of a
405 Western Great Plains River. Copeia 1991:659.
- 406 González-Ortegón E, Pascual E, Cuesta JA, Drake P. Field distribution and osmoregulatory
407 capacity in a temperate European estuary (SW Spain). Estuar Coast Shelf S 2006;67:293–302.

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

411 González-Ortegón E, Drake P. Effects of freshwater inputs on the lower trophic levels of a
 412 temperate estuary: physical, physiological or trophic forcing? Aquat Sci 2012;74:455–469
 413 74:455–469.

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

417 González-Ortegón E, Pascual E, Drake P. Respiratory responses to salinity, temperature and
 418 hypoxia of six caridean shrimps from different aquatic habitats. J Exp Mar Biol Ecol
 419 2013;445:108–115.

420 González-Ortegón E, Giménez L. Environmentally-mediated phenotypic links and
 421 performance in larvae of a marine invertebrate. Mar Ecol Prog Ser 2014;doi:
 422 10.3354/meps10708

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

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

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

431 Leduc D, Probert PK, Duncan A. A multi-method approach for identifying meiofaunal trophic

432 connections. *Mar Ecol Prog Ser* 2009;383:95–111.

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

436 McClelland JW, Valiela I, Michener RH. Nitrogen-stable isotope signatures in estuarine food
437 webs: a record of increasing urbanization in coastal watersheds. *Limnol Oceanogr*
438 1997;42:930-937.

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

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

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

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

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

450 Ramarn T, Chong VC, Hanamura Y. Versatile mysids exploit multiple basal resources:
451 implication of the benthic-pelagic habit in estuarine food webs. *Hydrobiologia* 2014;1-15.

452 Semmens BX, Ward EJ, Moore JW, Darimont CT. Quantifying inter-and intra-population
453 niche variability using hierarchical Bayesian stable isotope mixing models. *PLoS One* 2009;
454 4:e6187.

455 Scheffer M, Nes EH van. Mechanisms for marine regime shifts: Can we use lakes as
 456 microcosms for oceans? *Progr Oceanogr* 2004;60:303–319
 457 Sierszen ME, Peterson GS, Trebitz AS, Brazner JC, West CW. Hydrology and nutrient effects
 458 on food-web structure in ten Lake Superior coastal wetlands. *Wetlands* 2006;26:951–964
 459 Stock BC, Semmens BX. 2013. MixSIAR GUI user manual, version 1.0. Accessible online at:
 460 <http://conserver.iugo-cafe.org/user/brice.semmens/MixSIAR>
 461 Vinson MR, Budy P. Sources of variability and comparability between salmonid stomach
 462 contents and isotopic analyses: study design lessons and recommendations. *Can J Fish Aquat*
 463 *Sci* 2010;68:137-151.
 464 Wantzen KM, Arruda Machado F de, Voss M, Boriss H, Junk WJ. Seasonal isotopic shifts in
 465 fish of the Pantanal wetland, Brazil. *Aquat Sci* 2002;64:239–251.
 466 Wang Y, Yu X, Li W, Xu J, Chen Y, Fan N. Potential influence of water level changes on
 467 energy flows in a lake food web. *Chin Sci Bull* 2011;56:2794–2802.

469 **Figure captions**

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

474 Fig. 2. Daily range of water temperature at the Veta la Palma wetland (continuous line) and the
 475 Guadalquivir estuary (point line) and annual average of salinity and chlorophyll a
 476 concentration ($\mu\text{g L}^{-1}$) in mixed and extensive ponds. Error bars represent standard error of the
 477 mean ($n = 58$ and 24 for mixed and extensive ponds, respectively, per environmental factor).
 478 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 $\pm 1\text{SD}$. Prey species: amphipods, chironomids,

	503	copepods, corixids, mysids, ostracods, annelids, sediment, POM, Ruppia, Spartina and
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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			
	<i>P. varians</i>						<i>P. macrodactylus</i>			<i>P. varians</i>		<i>P. macrodactylus</i>	
	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
<i>P. varians</i>	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
<i>P. macrodactylus</i>	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

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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)	
<i>P. varians</i>															
	<i>Amphipod</i>	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)	
	<i>Chironomid</i>	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)	
	<i>Copepods</i>	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)	
	<i>Corixid</i>	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)	
	<i>M.slabberi</i>	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)	
	<i>Ostracod</i>	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)	
	<i>Phragmites</i>	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)	
	<i>Polychaete</i>	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)	
	<i>POM</i>	^{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)	
	<i>Ruppia</i>	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)	
	<i>Sediment</i>	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)	
	<i>Spartina</i>	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)	
<i>P. macrodactylus</i>															
	<i>Amphipod</i>	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)		-		-		-	
	<i>Chironomid</i>	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)		-		-		-	
	<i>Copepods</i>	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)		-		-		-	
	<i>Corixid</i>	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)		-		-		-	
	<i>M.slabberi</i>	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)		-		-		-	
	<i>Ostracod</i>	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)		-		-		-	
	<i>Phragmites</i>	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)		-		-		-	
	<i>Polychaete</i>	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)		-		-		-	
	<i>POM</i>	1.3 (0-6.6)	18	1.1 (0-6.4)	13	1.1 (0-6.7)	14	1.2 (0-6.5)		-		-		-	
	<i>Ruppia</i>	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)		-		-		-	
	<i>Sediment</i>	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)		-		-		-	
	<i>Spartina</i>	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
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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.

Consumer Source	May		July		November		February	
	N	M (CI)	N	M (CI)	N	M (CI)	N	M (CI)
<i>P. varians</i>								
<i>Amphipod</i>	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)
<i>Chironomid</i>	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)
<i>Copepods</i>	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)
<i>Corixid</i>	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)
<i>M. slabberi</i>	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)
<i>Ostracod</i>	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)
<i>Phragmites</i>	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)
<i>Polychaete</i>	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)
<i>POM</i>	5	0.9 (0.1-4.5)	9	1 (0-6.9)	29	0.9 (0-5.2)	8	0.9 (0-5.6)
<i>Ruppia</i>	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)
<i>Sediment</i>	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)
<i>Spartina</i>	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)
<i>P. macrodactylus</i>								
<i>Amphipod</i>	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)
<i>Chironomid</i>	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)
<i>Copepods</i>	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)
<i>Corixid</i>	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)
<i>M. slabberi</i>	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)
<i>Ostracod</i>	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)
<i>Phragmites</i>	2	1.4 (0-12.6)	2	3.3 (0-31.8)	2	6.2 (0-26.5)	2	2.4 (0-23.4)
<i>Polychaete</i>	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)
<i>POM</i>	3	0.5 (0-3.7)	7	0.7 (0-21.6)	23	0.6 (0-6.6)	6	0.5 (0-6.4)
<i>Ruppia</i>	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)
<i>Sediment</i>	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)
<i>Spartina</i>	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

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