

The effect of water management on extensive aquaculture food webs in the reconstructed wetlands of the Doñana Natural Park, Southern Spain

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Abstract

Extensive aquaculture in coastal and estuarine wetlands can support both increased food production and wider ecosystem services when underpinned by effective management to promote productivity and hence food webs that support both commercial species and biodiversity. Changing hydrology, specifically water movement, within wetlands significantly impacts the physico-chemical properties of the water body and hence can be employed to manipulate productivity and alter patterns of recruitment of commercial species and may also transfer non-native species from the supplying water bodies. The reconstructed wetlands of Veta la Palma in the Doñana Natural Park are subjected to either a 1 % or 5 % d⁻¹ water exchange with water drawn from the adjacent Guadalquivir estuary. This site provides an excellent opportunity for examining the effect of water management on the food webs that support both the birdlife and aquaculture activities for which this habitat is managed. Stable isotopes were used to examine food webs in three replicate lagoons under each water management scheme. In lagoons receiving higher water exchange, phytoplankton productivity appeared to be more important than benthic production in supporting food webs. Increased water exchange also changed the shape of the food webs, facilitated the colonisation of at least one non-native species and increased the importance of non-native species in the diets of large commercially harvested fish (> 60 % of seabass diet). Lagoons with high water flows also had between three and four times greater shrimp biomass than those of low flow lagoons. Non-native fauna were opportunistic omnivores, eating marginally more non-natives in lagoons with greater water exchange. Overall non-native cordgrass *Spartina densiflora* contributed only slightly more to food webs compared with the native reed *Phragmites australis*, despite the lagoon edge occupancy ratio of 9:1, respectively. Non-natives also appear to enhance food provision for large predators and wetland birds, by increasing biomass, without competing for resources with native species, supporting the dual management objectives of aquaculture and waterbird conservation.

Key words: flow regime, nitrogen supply, primary productivity, non-native species, stable isotope, waterbirds.

1.1. Introduction

The strategic guidelines for sustainable development of EU aquaculture from the European Commission (EC 2013) highlight the constraints on growth of the industry and particularly the need for a reduction in administrative barriers. To address these issues, adoption of an ecosystem approach can help illustrate both the possible environmental impacts and the potential ecosystem services supported by aquaculture developments. This can inform spatial planning for future aquaculture development and is particularly important when aquaculture activities are adjacent to or within designated conservation areas, such as Natura 2000 sites, where identification and quantification of likely significant effects on conservation features are a critical step in the approval process. Extensive aquaculture in coastal and estuarine wetlands has a long history in Asia, but is less well-developed in temperate regions, including Europe, where it offers considerable potential for integration of increased aquaculture production with the provision of wider ecosystem services from wetlands. As more than 90% of all European wetlands are estimated to have been lost (Mitsch and Gosselink 2000) with some 60 % being drained and converted to agriculture (Revenga et al. 2000), our study site, Veta la Palma, is an example of how aquaculture can be a driver for the reconstruction of wetlands. Where once extensive cattle ranching occurred on drained wetlands degraded by siltation and the construction of dykes and drainage channels, permanently flooded wetlands have been created. Three thousand hectares of lagoons, each of approximately 70 ha, have been constructed since 1990 for the extensive eco-aquaculture of fish and shrimp. As Veta la Palma is within the Doñana Natural Park boundary, the area is also managed for conservation, with more than a 100 purpose-built islands in the lagoons providing nesting and shelter for the birdlife. The Natural Park is a Ramsar wetland of international importance being a significant transitory area for the six million migratory birds that pass through on the European – West African flyway and a major overwintering site for more than 500,000 waterbirds (UNEP 2011). It is also the most important European wintering site for ducks (Anatidae) (Rendon et al. 2008).

Hydrology is the major factor in determining the structure and function of any wetland with water flow impacting not only the physicochemical conditions but also the biology including species composition and primary productivity (Mitsch and Gosselink 2000). Wetland ecosystems are impacted at all trophic levels by altered flow regimes with changes reported in the relative importance of primary producers (Nilsson and Svedmark 2002; Vis et al. 2007), in invertebrate communities (González-Ortegón and Drake 2012), and fish composition (Poff and Allan 1995; Roy et al. 2005; Xenopoulos and Lodge 2006). In aquaculture increasing water exchange normally improves water quality resulting in better survival and growth of the cultured organism (Pillay 1990). Understanding how environmental factors impact the food web, and in particular primary productivity, is essential in extensive aquaculture as these constrain total harvest rates.

Changes in hydrology can lead to state shifts in ecosystems and may facilitate the invasion success of non-native species (Bunn and Arthington 2002). Non-native species research mostly focuses on their negative environmental impact with media coverage being similarly biased (Chew and Laubichler 2003) and more than 2.9 billion euros are spent annually on the control or eradication of non-native species in the European Union (extracted from Gren et al. 2007; Kettunen et al. 2008). Although it is generally accepted that once a non-native species becomes invasive they can reduce biological diversity, some non-natives are benign and others are economically valuable cash crops. Moreover, recently two reviews have highlighted beneficial interactions between non-native species and some part of the host ecosystem (Rodriguez 2006; Schlaepfer et al. 2011). Therefore careful assessment of both the

positive and negative impacts are needed in order to determine if the cost of control is warranted, taking into account the management objectives of the area.

Stable isotopes have been extensively used in trophic ecology since the early work of DeNiro and Epstein (1978; 1981), who showed that carbon is useful in tracking food sources, and nitrogen in discerning trophic level. Early studies used isotopic similarity to infer consumption of a prey by consumer, more recently isotopic mixing models such as IsoSource (Phillips and Gregg 2003), SIAR (Parnell et al. 2008) and mixSIAR (Stock and Semmens 2013) have enabled the calculation of the most likely proportional contribution of multiple food sources to the tissue of a consumer, and hence, dietary composition. The effect of non-native species on food webs has been studied using stable isotope mixing models to examine both the impact of introducing non-native fish species on other species (Cucherousset et al. 2007) and non-native primary producers on both primary consumers (Levin et al. 2006) and higher trophic species (Currin et al. 2003; Shang et al. 2008). Isotopic analysis has advantages over stomach contents analysis in providing dietary information as it provides a more integrated longer term dietary signal reflecting assimilated not merely ingested material (Al-Maslamani et al. 2009). Although the use of generalist diet-tissue discrimination factors can be problematic in isotopic analysis, uncertainty can be reduced by the use of the mixing model mixSIAR that incorporates this variability in discrimination factors.

The current study examines the effect of increasing water exchange rate on the productivity and composition of food webs in extensive aquaculture lagoons. Stable isotopes are used to illustrate the change in diet of consumers with increased water exchange. The impact of water exchange on recruitment and density of non-native fauna is also studied as is their roles in support of both the extensive aquaculture production and the birds feeding in these lagoons.

2.1. Materials and Methods

The study site at Veta La Palma, in Southern Spain, south of Seville, is located within Doñana Natural Park and sandwiched between the Doñana National Park to the west and the Guadalquivir estuary to the east and south (Fig. 1). In the 1990's, from previous agricultural land, approximately 3000 ha of wetlands were reconstructed in the form of forty large (70 ha) shallow (0.5 m) brackish-water lagoons, complete with bird shelter/nesting islands and a deeper (1 m) peripheral canal. The permanently inundated lagoons at Veta la Palma provide a vital refuge for these ducks and other waterbirds during the dry season and until winter rains re-flood the Doñana marshes bird populations in Veta la Palma can reach 300,000 (Kloskowski et al. 2009). These lagoons are particularly important feeding grounds for great cormorants (*Phalacrocorax carbo*), greater flamingos (*Phoenicopterus roseus*), black winged stilts (*Himantopus himantopus*) and pied avocets (*Recurvirostra avosetta*) (Rendon et al. 2008), and feeding by flamingos, coots and ducks has been shown to have a significant influence on the biomass of both macrophytes and invertebrate populations (Rodriguez-Perez and Green 2006; Rodriguez-Perez and Green 2012). In parallel with the habitat and food support to birds, a total of more than 800 t of semi-extensive and extensively produced fish and shrimp are harvested annually (Walton et al. 2015). Shrimp and some fish bycatch are harvested continuously and fish mostly at the end of each three year cycle when the water levels are lowered, species include seabass *Dicentrarchus labrax* Linnaeus, mullet *Mugil cephalus* Linnaeus, European ditch shrimp *Palaemon varians* Leach, and the oriental shrimp *Palaemon macrodactylus* Rathbun. There are two operational systems for management of the

lagoons for aquaculture; designated high flow and low flow lagoons (Figure 1). In the low flow extensive lagoons aquaculture production is entirely supported by natural productivity. In the high flow extensive lagoons, water comes from a row of small (0.1-0.9 ha) semi-extensive culture ponds where seabass are maintained at 2-4 kg m⁻² and nutrition comes from both inflowing natural production and formulated feeds supplied by demand feeders. The high flow lagoons have enhanced exchange rates of 5 % d⁻¹ whereas the low flow lagoons have lower rates of 1 % d⁻¹. Water exchange rates were provided by Veta La Palma management and estimated by the relationship between the rate of inflowing water and total water volume of the lagoon. Flow rates are recorded using the water height passing across a weir and calibrated by the time taken to fill a known volume. In the winter when increased freshwater flow reduces estuarine salinity, sluice gates are shut and the isolated water recirculated around the farm. Once estuarine salinity is >10 ppt, estuarine water is introduced and a mix of 30:70 recirculated:estuarine water is pumped through the lagoons.

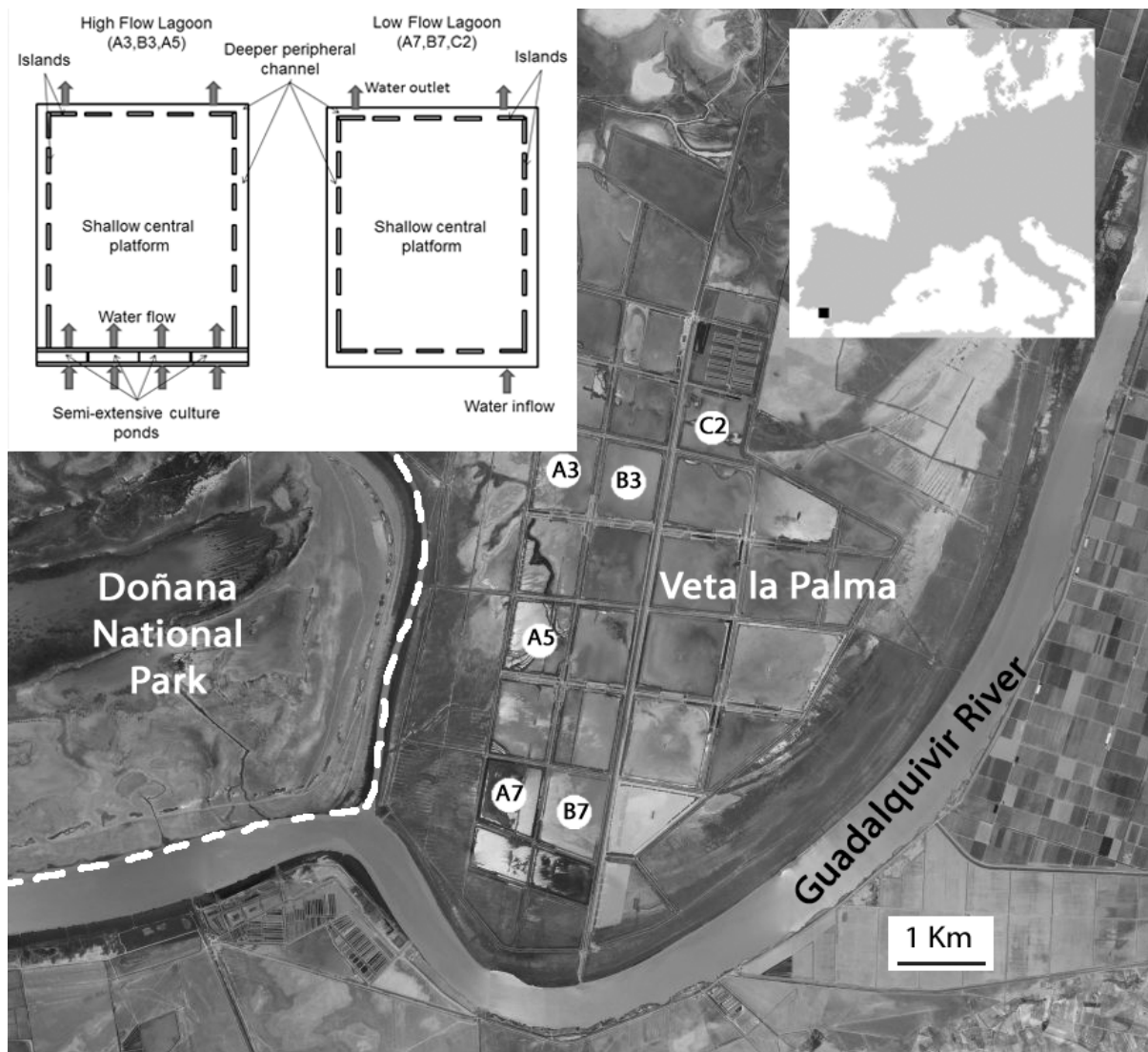


Fig. 1: Satellite image of the sampled lagoons of Veta la Palma, part of the Doñana Natural Park and the boundary (dashed line) that separates it from Doñana National Park. Inserted are the geographic location of Veta La Palma and diagrammatic representation of the high flow and low flow lagoons (not to scale).

Six extensive lagoons (3 high flow and 3 low flow) were sampled 4 times over a year (1-4 May 2011, 25-29 July 2011, 1-4 November 2011, and 20-24 February 2012), with each time period selected to represent the typical conditions of each season. Three replicate samples for isotope analysis were taken with each method, from haphazardly-spaced locations within each lagoon. Benthos was sampled using a cylindrical corer (32 cm²) and box corer (240 cm²). ‘Nasa’ traps (Fyke type, funnel-mouthed bag traps) with 3 mesh sizes: 2 mm, 5 mm and 10 mm, were used to catch nekton, mostly fish and shrimp. Zooplankton tows were performed using mesh sizes of 200 µm and 500 µm. Corixids were collected with a 500 µm D-framed pond net. Biofilm was sampled by scraping the top 1 mm off benthic cores. Submerged parts of plants were brushed and vigorously shaken in distilled water and the resultant suspension vacuum filter through pre-combusted GF/C filters (Whatman) to obtain periphyton samples. Macrophytes were collected by hand from the lagoon verge (*Spartina denisflora* Brognand, *Phragmites australis* (Cav.) Trin. ex Steudel) and in the lagoon (*Ruppia maritima* Linnaeus). Suspended particulate organic matter (SPOM) was sampled by taking water samples 5 cm below the lagoon surface, passed through a 100 µm mesh and then vacuum filtered through pre-combusted GF/F filters (Whatman). Subsurface water was sampled at lagoon inlets and outlets, in supply canals and at the farm/estuary entrance, filtered through GF/F (Whatman) and stored frozen at -20 °C until nutrient analysis using a 5 channel LCHAT Instruments Quick-Chem 8000 autoanalyzer. Salinity, temperature and chlorophyll fluorescence were also measured monthly in each of the six lagoons using a multiparameter sonde (YSI 600 OMS VZ, Ohio, USA).

To examine the impacts of water exchange on the extensive aquaculture production, shrimp biomass was used as a proxy for productivity as it represents the most valuable component of extensive aquaculture harvests. Shrimp biomass was sampled seasonally 4 times during the year (4-8 July 2011, 7-11 November 2011, 20-24 February 2012, 14-18 May) using five deep-sided lift nets (94 cm diameter; 120 cm deep, 1 mm mesh) distributed across the shallow central platform (3 nets) and in the peripheral channel (2 nets).

Flora and fauna samples for stable isotope analysis were rinsed in distilled water before being oven dried at 50 °C for 24 hours. Filter paper with SPOM and periphyton samples were fumigated with concentrated HCl to remove carbonates, and subsequently re-dried. Biofilm/sediment samples were sequentially acidified with 0.1M HCl to remove carbonates and then 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, crab and fish 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:

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

Organic standards, interspersed with samples, had a standard deviation of 0.2 ‰ and 0.4 ‰ for δ¹³C and δ¹⁵N, respectively. The stable isotope data for each species was pooled across sampling events as variance was greater between lagoons than seasons. When C:N ratios were greater than 3.5, the δ¹³C signal of muscle tissue samples were mathematically corrected

for lipid content (Post et al. 2007). Literature values were used for diet - consumer discrimination ($\Delta^{13}\text{C}$ & $\Delta^{15}\text{N}$). For fauna analysed whole, $\Delta^{13}\text{C} \pm$ standard deviation was 0.5 ± 1.32 ‰ and for larger fauna where muscle tissue was analysed a $\Delta^{13}\text{C}$ of 1.3 ± 0.85 ‰ was used (McCutchan et al. 2003). Similarly $\Delta^{15}\text{N}$ was 2.2 ± 1.54 ‰ for fauna analysed whole with mixed diet, 1.4 ± 0.75 ‰ for fauna analysed whole with invertebrate diet, and 2.9 ± 1.24 ‰ for fauna analysed as muscle tissue (McCutchan et al. 2003).

The Bayesian isotope mixing model mixSIAR was used to determine the likely dietary composition of non-native species, the dietary composition of commercial species and the relative importance of primary producers in support of food webs that sustain these consumers. MixSIAR, a recent collaborative venture between the developers of SIAR and mixSIR, was selected as it incorporates both the isotopic variability of both consumers and diet (Parnell et al. 2010), and allows researchers to address hierarchical structure in mixing model analysis (Semmens et al. 2013; Stock and Semmens 2013). Dietary proportions are expressed as the median and 95 % Bayesian credible intervals for each of the two water exchange regimes with lagoons entered as categorical covariates. Selection of possible prey items used in the mixing model, for the non-native species was based on: stomach content analysis performed in a parallel study for the non-native shrimp *P. macrodactylus* and the native shrimp *P. varians* (Moghaddam 2012), the non-native fishes *Fundulus heteroclitus heteroclitus* Linnaeus and *Gambusia affinis* Baird & Girard (Deamer-John 2012), and the literature for the non-native corixid *Trichocorixa verticalis* Fieber and the non-native crab *Rhithropanopeus harrisi* Gould (Kelts 1979; Hegele-Drywa and Normant 2009; Simonis 2012). Important prey items for other fish species were selected using Fishbase (2012). Isotopic values for bass (*Dicentrarchus* spp.) and mullet (Mugilidae) are composed of two species each, *D.labrax* and *Dicentrarchus punctatus* Bloch, and *M. cephalus* and *Liza ramada* Risso, respectively, as isotopic signatures were not significantly different (One way ANOVA, $P < 0.05$).

The indirect contribution of C and N from the non-native cordgrass *Spartina densiflora* and other primary producers to the trophic web supporting both the commercially important predators and the non-native species was also examined. Following the methods of (Shang et al. (2008)) and Al-Maslamani et al. (2012), the trophic position of the consumers in each lagoon was estimated as the difference between the $\delta^{15}\text{N}$ value of the consumer and the mean $\delta^{15}\text{N}$ value of primary producers using the previous discrimination factors of 2.2 ‰ for the initial trophic step and 2.9 ‰ for subsequent steps. The contribution of the primary producers to the food webs supporting the consumers was estimated using these discrimination factors to correct for the diet:tissue discrimination across the difference in trophic level. In order to allow integration of the primary producers signal, the target organism needs to be feeding at least two trophic levels above the primary producers.

3.1 Results

Water exchange appears not to impact water temperature as all lagoons exhibited similar seasonal temperature fluctuations from 10 to 27 °C (Fig. 2). Similarly, fluorescence data indicated no consistent differences in chlorophyll concentration between the high flow and low flow lagoons with algal blooms occurring in spring and again in summer (Fig. 3). However, salinities in the low flow lagoons A7 & B7 differed from the rest being much higher during the summer as a result of reduced water exchange. Water entering the farm from the estuary averaged approximately 200 μM total dissolved inorganic nitrogen (TDIN)

during months when water was exchanged with the estuary and TDIN nutrient levels were significantly reduced (92.5 %) by the time water exited the lagoons (Figure 4). Comparison of water column nutrients prior to, and after exit from, the semi-extensive aquaculture ponds indicated that the addition of feed had only a very minor effect on nutrient supply to the high flow lagoons. In the winter months when water is recirculated and TDIN supply is low (mean 18.6 μM) the fish feed inputs can double the nitrogen supply to the high flow lagoons (mean 29.6 μM) however in terms of annual supply feed inputs remain relatively unimportant. There was a slight but insignificant reduction in nitrate and nitrite in water passing through the semi-extensive ponds, although ammonia levels increase by on average 11.9 μM .

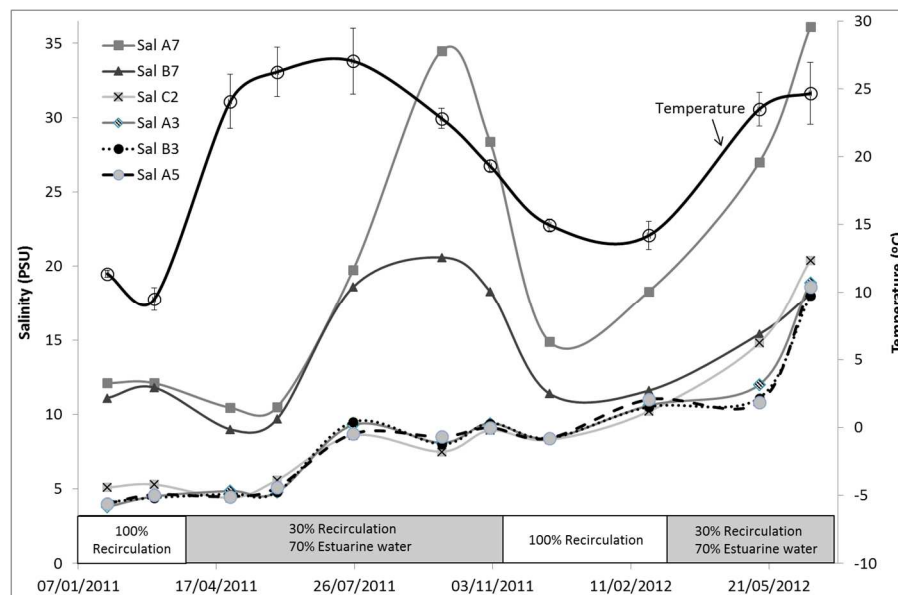


Fig. 2: Average salinity (PSU) in each of the six lagoons sampled and mean water temperature ($^{\circ}\text{C}$) (± 1 S.D.). Bottom indicates the water exchange regime in place throughout the year.

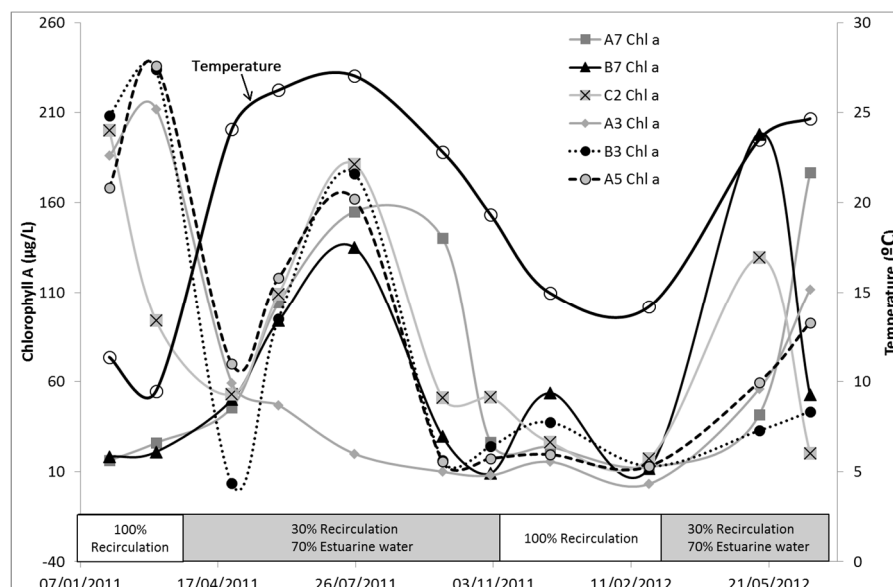


Fig. 3: Chlorophyll A concentration ($\mu\text{g L}^{-1}$) in each of the six lagoons sampled and mean water temperature ($^{\circ}\text{C}$). Bottom panel indicates the water exchange regime in place throughout the year.

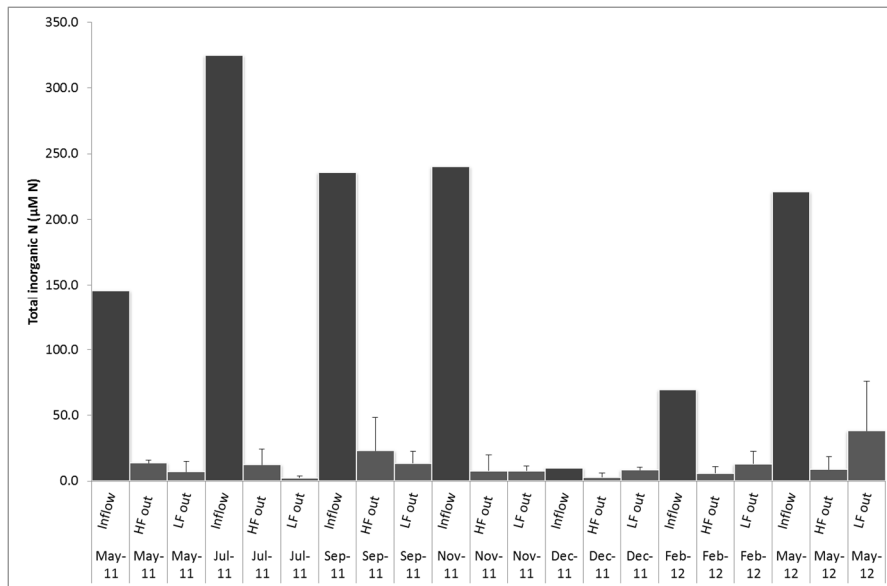


Fig. 4: Total inorganic N concentrations ($\mu\text{M N}$) (mean \pm 1s.d.) in inflowing water in supply canal from estuary and water exiting the high flow (HF) and low flow (LF) lagoons. No water exchange with estuary between November and February.

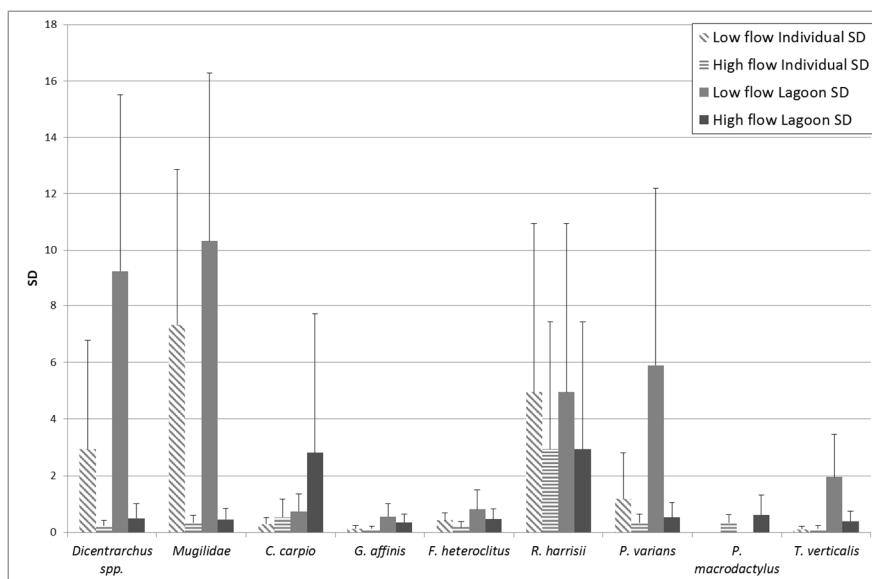


Fig. 5: Estimated mean and standard deviation of dietary variability (SD) apportioned to individuals and lagoons as estimated by mixSIAR.

Shrimp densities were generally higher in high flow lagoons, especially in the summer and autumn when mean densities reached 37.5 and 18.4 g dry wt m^{-2} respectively (Figure 6). Despite biomasses being 3 to 4 fold higher in high flow compared with low flow lagoons, a two way ANOVA with season and lagoon as factors suggested that differences were only just significant ($p = 0.046$) due the high level of variation. *P. macrodactylus* was very rarely found in the low flow systems and biomass never surpassed 0.02 g dry wt m^{-2} . In contrast shrimp biomass in summer in high flow lagoons was predominantly *P. macrodactylus* with a biomass of up to 28 g dry wt m^{-2} .

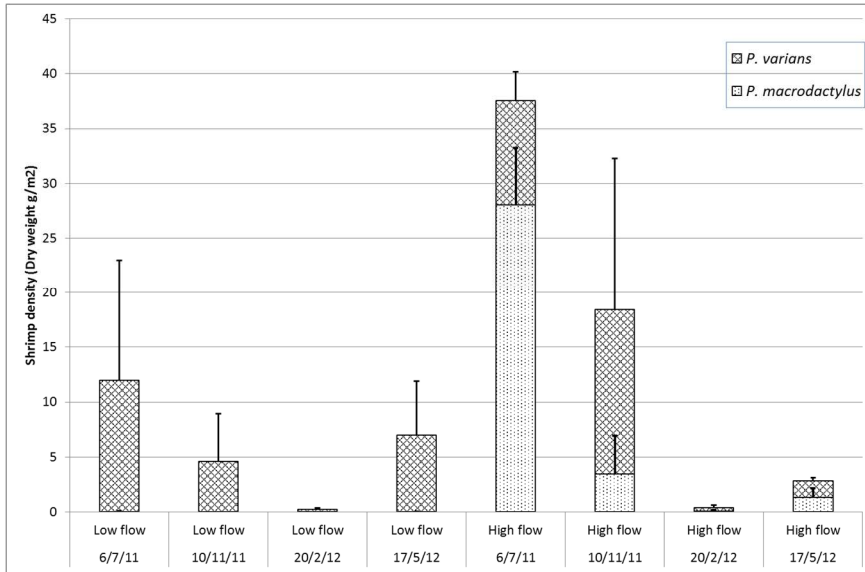


Fig. 6: Seasonal variation in the biomass (dry weight g m^{-2}) of *Palaemon varians* and *Palaemon macrodactylus* in high flow and low flow lagoons (mean \pm 1s.d.)

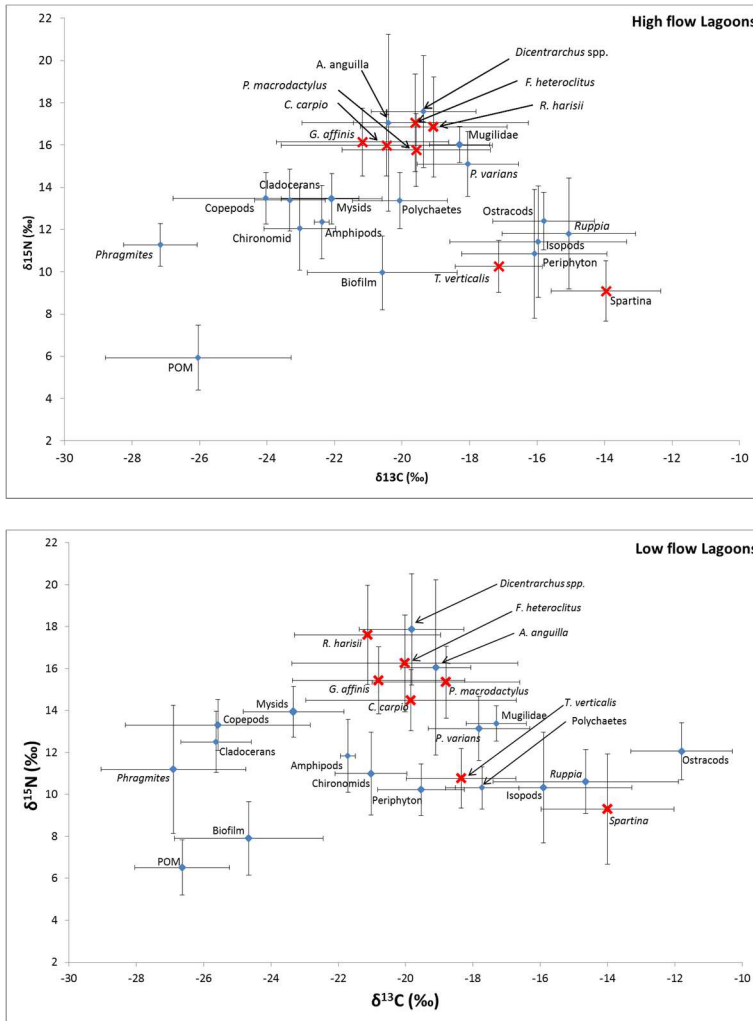


Fig. 7: Mean and standard deviation of the carbon and nitrogen isotopic signature (‰) of the organisms sampled over 4 seasons and 6 lagoons in Veta la Palma ($n = 1234$). Diamonds indicate native species, crosses indicate non-native species.

S. densiflora was the only non-native flora identified during the sampling along with six non-native macrofauna: *T. verticalis*, *R. harrisii*, *P. macrodactylus*, *F. heteroclitus*, *Cyprinio carpio* Linnaeus and *G. affinis*. Although recent publications suggest *G. affinis* is possibly *Gambusia heteroclitus* the Eastern mosquitofish (eg. Diez-del-Molino et al. 2013; Coccia et al. 2014), but genetic tests are needed for certainty. Four faunal species: *T. verticalis*, *F. heteroclitus*, *G. affinis* and *C. carpio* were found in all six lagoons, while *P. macrodactylus* was only occasionally present in the lagoons with the lowest water exchange. Only 10 specimens of *R. harrisii* were caught, restricting analysis to two lagoons. The non-native cordgrass *S. densiflora* was widespread and the dominant lagoon-edge vegetation in all sample sites. The non-native copepod *Acartia tonsa* Dana, and the snail *Potamopyrgus antipodarum* Gray, have also been recorded at this location previously (Frisch et al. 2006; Rodriguez-Perez and Green 2012). Isotope signatures of primary producers ranged from the more depleted -27 ‰ $\delta^{13}\text{C}$ for the C3 reed *P. australis*, to the more enriched value of -14 ‰ $\delta^{13}\text{C}$ for the C4 cordgrass *S. densiflora*, and from +6 ‰ $\delta^{15}\text{N}$ for SPOM to +11 ‰ $\delta^{15}\text{N}$ for the wigeongrass *R. maritima*, with the benthic biofilm values falling between these values (Fig.7). Generally the spread of isotopic signatures was greater in low flow than high flow lagoons (Fig.7). There was no measureable influence of nitrogen from formulated feeds on the isotopic composition of primary producers within the high flow lagoons as would have been expected given that the depleted ^{15}N signatures of the feed were 5.7 ‰ $\delta^{15}\text{N}$. The $\delta^{15}\text{N}$ values of suspended POM in water exiting the semi-extensive ponds (i.e. in the inflow to the high flow lagoons) were slightly depleted but not significantly different compared to that measured in the low flow lagoons over the 4 seasons, (difference in means = -1.11 ‰, $F=4.11$, $p=0.52$). Differences in $\delta^{15}\text{N}$ values were even less marked between POM in the outflows of high flow and low flow lagoons (difference in means = 0.69 ‰ $\delta^{15}\text{N}$, $F=1.24$, $p=0.238$). C:N ratios were also not significantly different between inflow of high flow and low flow lagoons ($F=3.11$, $p=0.085$) and respective outflows ($F=0.42$, $p=0.52$). Likewise no significant differences in $\delta^{15}\text{N}$ signatures could be discerned between biofilm around the inflow of high flow compared with low flow lagoons ($F=0.12$, $p=0.733$) or between biofilm around the outflows of high flow compared with low flow ($F=0.78$, $p=0.387$).

The isotopic composition of the non-native species indicated that they were generalist feeders consuming a wide range of food items, with water exchange regime influencing the relative dietary proportions (Table 1). Non-native species formed significant fractions of the diet of all non-native fish species examined. In both lagoon types periphyton formed 30 % of the diet for the corixid *T. verticalis* with ostracods also important when water exchange was greater and the benthic chironomid larvae important when water exchange was less. The shrimp *P. macrodactylus* was only found predominantly in the high flow lagoons with mysids, and copepods, accounting for approximately 40 % of the diet. Significant dietary items for the non-native crab *R. harrisii* included mysids, chironomids and both shrimp species, with cladocerans also important in the low flow lagoons. The mosquitofish, *G. affinis* was found to eat a wide range of organisms with a quarter of the diet consisting of copepods in both water exchange regimes. Larger prey was predominant in the diet of the killifish, *F. heteroclitus*, with *G. affinis* forming almost 20 % of the diet in low flow lagoons and *P. macrodactylus* and *P. varians* comprising 23 % of the diet in the high flow lagoons. The carp, *C. carpio* had a more omnivorous diet than the other non-native sampled fish species formed mostly of small invertebrates with biofilm and the pond weed *R. maritima* also important in some lagoons.

Table 1: Median and 95% Bayesian credible intervals of the predicted diet of non-native species in low flow and high flow lagoons, as suggested by an analysis of the isotopic signatures of consumers and common prey using the mixSIAR Bayesian mixing model. (L = number of lagoons where consumer was found and n = sample number).

Consumer	Prey	Low flow			High flow		
		Low95%	High95%	Median	Low95%	High95%	Median
<i>T. verticalis</i> (L=6, n=158)	Periphyton	7.5	58.3	31	9.8	50.7	29.9
	Ostracods	0.3	25.7	4.8	6.4	37.8	20.9
	Biofilm	1.4	34.5	11.1	2.9	38.2	16.8
	Amphipods	1.2	34.6	10.9	0.5	24	7.2
	POM	0.1	23	3.8	0.6	17.7	6.5
	Mysis	0.6	28.4	7.6	0.2	17.9	5
	Chironomids	1.6	39.8	13.2	0.2	17.4	4.6
	Copepods	0.1	23.5	3.6	0.1	13.4	2.9
<i>P. macrodactylus</i> (L=3, n=75)	Mysis	-	-	-	4.4	57	27.2
	Copepods	-	-	-	1.2	40.4	15.2
	Amphipods	-	-	-	0.7	39.2	11.9
	Chironomids	-	-	-	0.4	32.9	9.9
	Polychaetes	-	-	-	0.3	26.7	6.3
	<i>T. verticalis</i>	-	-	-	0.3	25.7	6.1
	Ostracods	-	-	-	0.3	21	5.8
	Biofilm	-	-	-	0.2	21.2	4.9
<i>R. harrisi</i> (L=2, n=6)	<i>P. macrodactylus</i>	-	-	-	0.6	40.4	11.1
	<i>P. varians</i>	0.3	33.9	8.4	0.4	35.2	9.7
	Mysis	0.7	40.1	10.9	0.4	36.6	9.1
	Chironomids	0.3	37.7	9.2	0.4	33	8.1
	Copepods	0.4	34.1	8.4	0.3	30.4	8.1
	Cladocerans	0.5	39.2	11.3	0.4	31.8	7.8
	Amphipods	0.3	33.6	7.7	0.3	31	6.9
	<i>T. verticalis</i>	0.3	36.1	8.7	0.3	27.7	5.9
	Isopods	0.3	31.4	6.8	0.2	26.7	5.8
	Ostracods	0.2	30	6.2	0.2	25.8	5.5
<i>F. heteraciltus</i> (L=6, n=141)	<i>P. macrodactylus</i>	-	-	-	1.2	30.6	11.5
	<i>P. varians</i>	0.2	35.4	10.5	1.2	30.2	11.5
	Cladocerans	0.1	21.1	4.2	0.5	39.2	11.3
	Isopods	0.1	24.9	5.6	0.7	40.1	10.9
	Chironomids	0.3	24.8	6.2	0.3	37.7	9.2
	<i>T. verticalis</i>	0.2	25	4.8	0.3	36.1	8.7
	Copepods	0.1	20.7	4.4	0.4	34.1	8.4
	Ostracods	0.3	21	5.3	0.3	33.9	8.4
	Amphipods	0.5	38.2	11.4	0.3	33.6	7.7
	<i>G. affinis</i>	3.4	41	19.3	0.3	31.4	6.8
Mysis	0.6	35.3	11.6	0.2	30	6.2	
<i>G. affinis</i> (L=6, n=67)	Copepods	7.9	41.7	24.4	11.7	43.4	26.4
	Cladocerans	0.5	26.2	8.9	2.5	30.4	15.3
	Mysis	1.4	36.5	14.5	2.3	32.5	14.5
	Chironomids	0.4	22.5	6.8	1.4	25.4	11.1
	<i>P. macrodactylus</i>	-	-	-	0.3	19.9	6.9
	<i>P. varians</i>	0.8	28.9	10.8	0.3	17.5	5.6
	Amphipods	0.4	27.7	8.3	0.2	17.6	4.9
	<i>T. verticalis</i>	0.7	26.2	7.9	0.3	13.8	4.4
	Isopods	0.3	22	5.3	0.2	11.3	2.7
Ostracods	0.2	15.3	3.6	0.1	7	1.7	
<i>C. carpio</i> (L=6, n=33)	Copepods	0.4	26.8	8.5	0.8	39.8	14.1
	Mysis	0.4	28.1	6.8	0.7	40.1	12.3
	Cladocerans	1.2	35.1	12.5	0.4	35.7	11.1
	Chironomids	0.7	33.4	10.6	0.4	28.4	7.1
	<i>P. macrodactylus</i>	-	-	-	0.3	26.4	7
	Amphipods	0.5	35.4	10.3	0.2	26.3	6.3
	<i>P. varians</i>	0.4	26.7	7	0.2	24.9	6.1
	Biofilm	0.8	25.6	8.5	0.3	23	5.4
	<i>T. verticalis</i>	0.4	31.4	8.6	0.3	22.7	4.7
	<i>Ruppia</i>	0.4	22.8	6.3	0.2	19.8	3.6
Ostracods	0.2	19.5	4.6	0.1	19.4	2.9	

For the commercially important native bass species, non-natives formed greater than 60 % of the diet in high flow lagoons and >30 % in low flow systems. The two shrimp species comprised 25 % of the diet in high flow lagoons for the native mullets, whereas in low flow

lagoons median values indicated mullet diet was more evenly balanced with the corixid, *T. verticalis*, being the largest single component (Table 2).

Table 2: Median and 95% Bayesian credible intervals of the predicted diet of commercial species in low flow and high flow lagoons, as suggested by an analysis of the isotopic signatures of consumers and common prey using the mixSIAR Bayesian mixing model. (L = number of lagoons where consumer was found and n = sample number).

	Prey	Low flow			High flow		
		Low95%	High95%	Median	Low95%	High95%	Median
<i>Dicentrarchus</i> spp. (L=5, n=38)	<i>G. affinis</i>	0.8	52.3	14.9	7.7	45.5	30.2
	<i>F. heteroclitus</i>	0.5	44.9	11.2	2.4	38.3	18.5
	<i>P. varians</i>	0.3	43.8	10	0.7	34.3	11.7
	Amphipods	0.4	45.8	9.4	0.6	22.5	7
	<i>C. carpio</i>	0.4	43.9	10.7	0.4	25.4	7
	<i>P. macrodactylus</i>	-	-	-	0.4	25	6.7
	Mugilidae	0.3	44	9.6	0.3	24.3	5.7
	Isopods	0.3	45.5	9.3	0.2	15	3.4
Mugilidae (L=5, n=25)	<i>P. varians</i>	0.3	34.6	6.7	0.9	36.1	14.2
	<i>P. macrodactylus</i>	-	-	1	31.8	11.2	
	Polychaetes	0.4	34.5	8.2	0.4	28.1	8.8
	Amphipods	0.4	34.8	8.1	0.6	29.1	7.9
	<i>T. verticalis</i>	0.2	36.4	8.3	0.4	26.2	7.8
	Ostracods	0.3	31.9	7.1	0.5	21.1	7.2
	Mysis	0.2	32.4	7	0.3	28.3	7
	Biofilm	0.3	32.5	7.1	0.3	22	5.4
	Chironomids	0.2	34.7	7.9	0.1	21.2	5.2
	Copepods	0.3	32.3	6.5	0.2	20.8	4.8
Cladocerans	0.2	32.6	7	0.2	19.4	4.4	
<i>P. varians</i> (L=6, n=160)	Mysis	0.2	33.3	5.8	1	37.1	13.6
	Polychaetes	0.9	48.5	14.4	1.1	38.5	12.8
	Amphipods	0.5	41.3	10.8	0.7	37.8	12.5
	Ostracods	0.5	38.3	11.8	1.2	29.5	12.1
	<i>T. verticalis</i>	0.3	40.9	10.7	0.4	34.3	10.6
	Biofilm	0.4	38.7	10.6	0.4	30.5	9.3
	Copepods	0.2	32.7	5.6	0.7	29.4	8.6
	Chironomids	0.3	35.9	9.3	0.4	27.6	8.2

Variance parameters indicated that dietary variation amongst individuals and lagoons was greatest in low flow lagoons especially with the bass and mullet (Figure 5). For the majority of consumers dietary variability was greater between lagoons than between individual consumers particularly in low flow lagoons.

The indirect contribution through the food web of primary producers' C and N to higher level consumers is shown in Table 3. Averaged contributions to food webs suggested that in high flow lagoons where water exchange was greatest, food webs were supported more by suspended POM (33 %) than in low flow lagoons (20 %). Benthic productivity (biofilm) supported on average ~22 % of the food web regardless of the rate of water exchange. Macrophytes contributed significantly to food webs (on average >40 %) with *P. australis* being more dominant in high flow lagoons and *S. densiflora* playing a greater role in low flow lagoons. However, the model outputs suggest that *R. maritima* and *S. densiflora* are highly correlated in low flow lagoons, implying that mixSIAR was unable to resolve the relative contributions of these two species.

Table3: Median and 95% Bayesian credible intervals of the percentage contribution of each primary producers to the trophic web supporting the consumers in low flow and high flow lagoons, as suggested by an analysis of the isotopic signatures of consumers and primary producers using the mixSIAR Bayesian mixing model. Left hand column contains consumers, and trophic level (TL) in high flow (HF) and low flow (LF) lagoons.

Consumer	Prey	Low flow			High flow		
		Low95%	High95%	Median	Low95%	High95%	Median
<i>P. macrodactylus</i> (TL: HF=2.72, LF=1.66)	POM	-	-	-	11.6	60.2	36.5
	Biofilm	-	-	-	2.1	52.8	21.5
	Phragmites	-	-	-	2.2	40.3	16.9
	Spartina	-	-	-	0.9	29.9	12
	Ruppia	-	-	-	0.4	27.8	7.9
<i>P. varians</i> (TL: HF=2.34, LF=1.66)	POM	1.3	34.1	12.7	8	47	26.6
	Spartina	17.5	64.1	44.7	4.6	46.7	25.2
	Biofilm	1.8	43.1	17.3	1.6	52.4	21.8
	Ruppia	0.6	38.6	11.8	0.8	36.7	12.3
	Phragmites	0.5	28.2	8.6	0.7	29	9.4
<i>F. heteroclitus</i> (TL: HF=2.99, LF=2.83)	POM	9.4	42.8	25	19.4	51	34.6
	Biofilm	4.7	44.5	22.5	10.8	47	28.5
	Phragmites	3	31.7	14.8	6.4	35.2	18.5
	Spartina	11	43.7	26.9	1.4	21.7	9.9
	Ruppia	0.4	24.3	8	0.6	18.4	6.5
<i>G. affinis</i> (TL: HF=2.67, LF=2.52)	POM	7.6	42.5	23.7	18.9	53.1	35.6
	Biofilm	9.2	49.7	28.2	8.5	46.3	26.1
	Phragmites	6.9	38.6	20.8	10.6	42.9	26
	Spartina	3.6	29.4	16	0.2	15.7	5.8
	Ruppia	0.7	24.2	9.2	0.3	15.6	4.6
<i>C. carpio</i> (TL: HF=2.64, LF=1.04)	POM	3.5	43.1	20.1	9.5	58.2	33.1
	Phragmites	2.4	39.7	18.1	4.6	48.1	24.1
	Biofilm	2.8	50.4	22.3	1.8	51.6	20.9
	Spartina	7.7	44.6	25.8	0.7	25.6	9
	Ruppia	0.9	29.9	9.8	0.6	27.8	7.9
Mugilidae (TL: HF=2.70, LF=1.78)	POM	0.6	48.9	12.7	13.5	48.9	30.6
	Biofilm	0.6	52.6	15.6	3.3	48.1	21.7
	Spartina	2.4	65	29.6	3.9	37.1	19.6
	Phragmites	0.6	46.3	11.3	2.1	30.5	13.1
	Ruppia	1	56.8	18.2	1	32.5	11.7
<i>Dicentrarchus</i> spp. (TL: HF=3.55, LF=3.36)	POM	2.1	54.5	23.1	20.3	54.8	37
	Phragmites	2.1	51.2	19.4	9.5	40.7	23.9
	Biofilm	2.8	57.3	24	2.4	40.6	17.8
	Spartina	0.8	39.7	14.5	1.1	23.8	10
	Ruppia	0.5	36.9	11	0.7	22.6	8.7

4.1 Discussion

In common with many estuaries, the Guadalquivir estuary is enriched in nutrients with nitrate levels exceeding 1.5 mg l^{-1} (Lopez-Lopez et al. 2011), but high turbidity restricts light penetration and hence phytoplankton productivity is limited (Ruiz et al. 2013). Once water enters the lagoons the combination of sedimentation and shallow water permits maximum light penetration, stimulating primary production. The resulting reduction in nitrogen concentration as the water passes through the lagoons as a consequence of the primary production suggests that this wetland is absorbing a significant amount of nitrogen. Although variability in chlorophyll concentrations meant that flow rates had no significant impact on chlorophyll a concentration, the primary production must have been greater in high flow lagoons. Both lagoon flow types had equivalent nutrient reduction, but a fivefold difference in exchange rate suggests that nitrogen is absorbed five times more rapidly in high flow lagoons. This is supported by net primary production estimates that suggested summer carbon fixation averaged $50 \mu\text{g l}^{-1} \text{ d}^{-1}$ in high flow lagoons and $25 \mu\text{g l}^{-1} \text{ d}^{-1}$ in low flow lagoons (Walton et al. 2015).

It appears that productivity relies predominantly on the nutrients introduced in the incoming estuarine water, as no increase in nitrate and nitrite was detected in water that passed through the small semi-extensive culture ponds. Ammonia in incoming estuarine water was relatively very low, on average 5.5 μM , and increased by 11.9 μM as it passed through the semi-extensive ponds. In winter when the sluice gates are shut, the ammonia nitrogen from the feed becomes more important, but was only a minor component (9.8 %) of annual TDIN that entered the lagoons which comes mainly from the estuary. The low fish content of the artificial diet resulted in a depleted ^{15}N signal of 5.7 ‰ $\delta^{15}\text{N}$. As a portion of the ingested dietary N will be excreted as ammonia and available to primary producers, this might have been expected to influence the isotopic signatures of those primary producers that absorb it. However no significant depletion was observed in the phytoplankton (POM) or biofilm in area surrounding the semi-extensive culture pond outlets suggesting the supplementary feeding had limited effects in the lagoons and especially by the time the water exited the lagoons.

The aquatic species present in these previously dry wetlands results from recruitment through water exchange with the Guadalquivir estuary. Since the estuary is an international route for shipping, a number of common non-native species have been introduced through ballast water exchange and hull biofouling and now coexist with native species (Cuesta et al. 1996; Gonzalez-Ortegon et al. 2010). All the sampled non-native species have been previously reported in this region and are widely distributed and well established across both Doñana and Western Europe, where they are frequently reported to be in competition with other native species e.g. the corixids, *T. verticalis* with *Sigara lateralis* (Rodriguez-Perez et al. 2009), the fish, *F. heteroclitus* and *G. affinis* with *Aphanius baeticus* (Fernandez-Delgado et al. 1988), the shrimp *P. macrodactylus* with *Palaemon longirostris* (Gonzalez-Ortegon et al. 2010), and the cordgrass, *S. densiflora* with other wetland plants (Castillo and Figueroa 2009). However in these artificial reconstructed wetlands colonisation by native faunal competitors maybe restricted due to their absence in the incoming estuarine water. Previously, the rate of water exchange was shown to influence the invertebrate community in the lagoons of Veta la Palma (González-Ortegón et al. 2015). Lagoons with low flow rates exhibited a more stable wetland community and those high flow rates resulted in a transitory community that was a mixture of the stable wetland and estuarine communities that included estuarine mysids and *P. macrodactylus*. In the current study the results suggest that this change in community brought on by increased water exchange with the estuary, translated into a change in dietary patterns, with different prey being consumed when water exchange increases. This is supported by consistent increases in the trophic level at which consumers feed in high flow compared with low flow lagoons (Table 4). Decreasing trophic niche width as indicated by the variance parameters, increasing trophic level and increasing reliance on suspended POM as a driver of the food web supporting consumers in high flow lagoons, suggest that the input of nutrient rich water is promoting water column production, increasing prey availability permitting consumers to restrict prey composition perhaps following classic A1 optimal foraging theory.

Sampling over a wide range of lagoons demonstrated how trophically integrated non-native species have become, consuming both native and other non-native species, and being consumed by higher predators. To date there is no confirmation of competition for resources between non-natives and related native species found in these wetlands. For example there is no clear evidence from other studies for competition between *T. verticalis* and native corixids (Van de Meutter et al. 2010), and differences in isotopic signatures suggest that there may be some resource partitioning between *T. verticalis* and the co-existing native species *S. lateralis* (Coccia *et al* in prep.). Recently Gonzalez-Ortegon et al (2015) using stomach contents and

stable isotopes showed that *P. macrodactylus* was a pelagic carnivore, while the native *P. varians* had a more benthic diet which changed overlapping with *P. macrodactylus* when the two species co-existed in high flow lagoons where abundance of pelagic prey increased. Densities of *P. varians* were found to be unaffected by co-existence with *P. macrodactylus*. During the winter *P. macrodactylus* is almost entirely absent from all lagoons, but recruitment with influx of estuarine water results in rapid population growth during the summer in high flow lagoons. Peak total shrimp biomass 37.5 g dry weight m⁻² (as mean depth is 0.5m this equates to approximately 70g m⁻²) are achieved in July of which more than 70 % was due to *P. macrodactylus*. Shrimp biomass in the summer was 3-4 fold greater in the high flow lagoons with the higher water flow than in the low flow systems. This increase in total shrimp biomass contributes to increased aquaculture harvest of shrimp and provides an alternative prey for higher consumers, including the large predatory fish and waterbirds. The contribution of non-native species to the diet of large commercially harvested fish species in the lagoons is substantial; the isotopic evidence indicates that more than 60 % of the bass diet in high flow lagoons and 37 % in low flow lagoons are composed of non-native species. Of the non-native species, *P. macrodactylus* is the most widely consumed, playing a significant role in the diets of bass and mullet

An analysis of the literature by Rodriguez (2006) suggested that while the negative impact of species introductions have been widely documented, positive or facultative interactions could be as common, including increased habitat diversity, trophic diversification, pollination, seed dispersal, and competitive or predatory release. Veta la Palma has an important conservation role in providing feeding grounds for the large wetland bird population during the summer months when the main wetlands in the Doñana National Park are dry (Figuerola and Green 2004; Kloskowski et al. 2009), and it is the existence of these reconstructed wetlands that enables a larger and more diverse waterbird community to persist (Kloskowski et al. 2009). In Veta la Palma non-native species are now integral to the ecosystem function, increasing trophic diversity and providing predatory release to native species. The increased stability of the system resulting from the greater species diversity (Ives and Carpenter 2007) could play an important part in maintenance of the very significant ecosystem service in support of waterbird populations

While the other non-native fauna tend to be relatively benign and perhaps even beneficial, the carp, *C. carpio* which feeds at a lower trophic level than the other non-native fish species and in agreement with Blanco et al. (2003) is an opportunistic omnivore that can shift its diet from carnivore, mostly invertebrates, to herbivore or even detritivore (Crivelli 1981). The environmental impact of *C. carpio* was recently reviewed in a meta-analysis which suggested it is an ecosystem engineer increasing water turbidity, nutrients, phytoplankton and zooplankton while decreasing macrophyte and benthic invertebrate density (Matsuzaki et al. 2009) and presumably, also decreasing benthic primary production due to the decrease in light transmission. Thus it may also have consequences for the waterfowl such as the Anatidae that feed on wigeongrass *R. maritima* and other commercially important consumers that target benthic invertebrates.

In the USA there is concern about the ecological impact of the large areas of *Spartina alterniflora* that are being replaced by the invasive non-native *P. australis* particularly with regard to the impact of fisheries supported by these wetlands (Currin et al. 2003). However Weis and Weis (2003), after reviewing the literature, concluded that both species hold equal ecological value, supported similar densities of fauna and were of equal nutritional value. In Veta la Palma the opposite is occurring; large areas of *P. australis* are being replaced by *S. densiflora* and there is evidence that this may have negative consequences (Neira et al. 2007;

Cruz Sueiro et al. 2012). According to aerial surveys, almost 90 % of the lagoon banks at Veta La Palma are now colonised by *S. densiflora* (A.Perez pers comm.), limiting the input of organic material from *P. australis*, although the latter still contributed about the same proportion to the lagoon food webs. Also worth noting is the change in the physical structure of the lagoon verge, from the open *P. australis* beds to the dense stands of *S. densiflora* which could impede the use of the lagoon banks by some waterbird species. The reduction in available space for the saltmarsh bulrush *Scirpus maritimus*, whose seeds are an important food source for many waterfowl (Green et al. 2002), could also have significant impact on the size of the duck population that this wetland can support.

This study is not suggesting that if non-native faunal species could be controlled and similar native species introduced, the resulting ecosystem would not offer similar or even superior ecosystem support to the management objectives as well as the added benefit of preserving indigenous species. However, these non-native faunal species are ubiquitous and eradication would be prohibitively expensive and probably unachievable. Therefore before considering enacting any expensive eradication or control measures, one has to be mindful of the management aims of the area and both the positive and negative ecological impacts of non-native species. In Veta la Palma the management aims are clear and include the provision of livelihoods through low flow production of high quality fish and shrimp, and the provision of habitat for wetland birds that live, feed or shelter here. Generally, the evidence suggests that the novel ecosystem (Hobbs et al. 2006) in Veta la Palma consisting of interacting native and non-native fauna is beneficial to these management aims. However, this does not apply to *S. densiflora* due to its relatively low trophic contribution compared with the space it occupies, for which control measures should be considered. Complete eradication is unlikely to be cost effective (Roberts and Pullin 2008), but maintenance of *P. australis*, at least at present coverage, may be important to aquatic food webs and support to birds. Similarly detrimental are carp although control measures are also probably unfeasible. In all cases monitoring should continue to prevent the future establishment of new non-natives.

In conclusion, increased water exchange in the large low flow lagoons of the Veta La Palma aquaculture wetlands has been shown to increase productivity (g m^{-2}), and the role of planktonic primary production relative to benthic and terrestrial plant sources in support of the food web. The increased productivity related to the greater flow rates is largely down to the increased supply of nutrients present in the estuarine water and not as a result of aquaculture activity that occurs prior to the water entering the lagoons in the high flow system. Increased water exchange not only enhances the dependence of the food web on phytoplankton primary production it also changes the shape of food webs and increases the opportunity for the entrance of estuarine species including non-natives. In lagoons where the flow rate is higher, and resulting extensive aquaculture production is also greater, and shrimp biomass estimates suggest that aquaculture production could be increased by 3 to 4 times if harvest rates were increased. The changing shape of the food web as a result of increased flow rates also leads to an increasing contribution of non-natives to the diets of commercially important species. While non-native fauna are abundant in the wetlands, they appear to be well integrated into the food web and both contribute to supporting the extractive aquaculture activities and provide support for biodiversity by supplying food and habitat for the birds that use these wetlands.

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