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Artificial coastal lagoons at solar salt-working sites: a network of habitats for specialised, protected and alien biodiversity.

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Abstract

There are concerns that novel structures might displace protected species, facilitate the spread of non-indigenous species, or modify native habitats. It is also predicted that ocean warming and the associated effects of climate change will significantly increase biodiversity loss within coastal regions. Resilience is to a large extent influenced by the magnitude of dispersal and level of connectivity within and between populations. Therefore it is important to investigate the distribution and ecological significance of novel and artificial habitats, the presence of protected and alien species and potential vectors of propagule dispersal. The legacy of solar salt-making in tropical and warm temperate regions is regionally extensive areas of artificial hypersaline ponds, canals and ditches. Yet the broad-scale contribution of salt-working to a network of benthic biodiversity has not been fully established. Artisanal, abandoned and historic salt-working sites were investigated along the Atlantic coast of Europe between southern England (50^{o}N) and Andalucía, Spain (36^{o}N). Natural lagoons are scarce along this macrotidal coast and are vulnerable to environmental change; however it is suspected that avian propagule dispersal is important in maintaining population connectivity. During bird migration periods, benthic cores were collected for infauna from 70 waterbodies across 21 salt-working sites in 5 coastal regions. Bird ringing data were used to investigate potential avian connectivity between locations. Lagoonal specialist species, some of international conservation importance, were recorded across all regions in the storage reservoirs and evaporation ponds of continental salinas, yet few non-indigenous species were observed. Potential avian propagule transport and connectivity within and between extant salt-working sites is high and these artificial habitats are likely to contribute significantly to a network of coastal lagoon biodiversity in Europe.

KEY WORDS

Climate change, Transitional waters, Coastal lagoons, Artificial habitats, Avian connectivity, Brackish lagoons, Structures, Environmental change, Non-indigenous species, Salinas. Ocean Sprawl

1.0 Introduction

It is predicted that ocean warming and the associated effects of climate change will significantly increase biodiversity loss within coastal regions (Hawkins *et al.* 2012; 2016). Transitional waters, which include estuaries, rias and lagoons, are highly productive and extremely important ecosystems that support a wide range of vital services (Munari & Mistri, 2008; Basset *et al.* 2013). Resilience to biodiversity loss is, to a large extent, influenced by the magnitude of dispersal and level of connectivity within and between populations. Yet transitional waters are relatively closed environments and therefore particularly vulnerable and exposed to environmental change. Associated with the development of coastal regions is the creation of novel structures and artificial habitats that become colonised by species assemblages that can differ with native populations. Interactions between native and artificial habitats in coastal regions and their potential contribution to species population resilience are poorly understood and mostly consider hard structures communities (Airoldi & Beck, 2007; Buleri & Airoldi, 2008; Airoldi *et al.* 2009; Mineur *et al.* 2012; Herbert *et al.* 2017). Here we consider the importance of soft-sediment benthic communities within artificial lagoons at salt-working sites along the Atlantic European seaboard and whether they contain species of biodiversity importance and contribute to a network of Coastal lagoon habitat.

1.1.Coastal lagoons

Coastal lagoons are important features and habitats within transitional water ecosystems where connectivity is particularly constrained. They have been defined as 'shallow bodies of enclosed, brackish or salt water separated from an adjacent coastal sea by a barrier of sedimentary material' (Barnes, 1980, 1989a), and artificial coastal lagoons also occur (Bamber *et al*. 1992). Globally, lagoons comprise 13% of the coastline, yet only 5% of the European coast is lagoonal, the smallest proportion of any continent (Cromwell, 1971: Barnes, 2000). In the Mediterranean region lagoons are relatively numerous and of significant area (Chauvet, 1988; Tagliapietra & Volpi Ghirardini, 2006; Zaldivar *et al*. 2006). However, in macrotidal regions, such as the North-east Atlantic, natural lagoons are unusual and particularly restricted in distribution (Barnes, 1980, 1989a, 1995). In a changing climate, coastal lagoons may experience significant variation in rainfall, temperature and fluctuations in sea level that could change the salinity and thermal regime of the habitat. The rate of colonisation and establishment of populations at new and potentially distant habitat will be very low as water exchange between lagoons and with the open sea can be infrequent (Ghezzo *et al*. 2015) and propagule dispersal distance in the water column is small. Establishing mechanisms of connectivity between lagoonal habitats is a conservation priority (Barnes, 1988) and for isolated habitat generally has been an enduring problem in biogeography (MacArthur & Wilson, 1967; Lomolino, 2000; Nolby *et al*. 2015).

There is variation in the degree of specialisation to transitional waters, with euryhaline and eurythermal species being adapted to cope with a wide range of salinity and temperature, respectively. Yet with increasing specialisation and adaptation to a narrower range of abiotic conditions, such as those that can be experienced within lagoonal habitats, there is an increasing risk of population decline and extinction. There has been much debate about the existence of specialisation and diversity within transitional and brackish waters (Remane, 1934, 1940; Barnes, 1989ab, Bamber *et al.* 1992, Barnes, 1994; Cognetti & Maltagliati, 2000; Telesh *et al.* 2011); however for coastal lagoons of the British Isles, Barnes (1989b) recognised the presence of 38 specialist lagoonal species i.e. species more characteristic of lagoon-like habitats than of freshwater, estuarine brackish waters or the sea. These comprise a wide range of invertebrate groups, including insects, algae and plants belonging to the charophyceae. In a survey of 166 British coastal lagoons, Bamber *et al*. (1992) found that lagoons showed greater environmental variability than estuarine waters and the open sea and identified six suites of species that included euryhaline lagoonal specialists, and stenohaline marine lagoonal specialists common in southern Britain. Invertebrate and plant lagoonal specialists differ from estuarine species in their adaptation to the stresses associated with reduced tidal exchange, including hypoxia, thermal and pH stratification, and more extreme temporal variation in temperature and salinity. Tolerance to these conditions ensures their survival in these habitats where competition and predation from marine and estuarine species is reduced (Bamber *et al*. 1992).

In the United Kingdom and Ireland, sites containing stenohaline marine lagoonal specialist species are particularly scarce and given high conservation status (Barnes, 1989a; Bamber et al. 1992 Gilliland & Sanderson, 2000; Joyce *et al.* 2005; Beer & Joyce, 2013; JNCC, 2015). As these sites are vulnerable to being lost as a result of coastal development and climatic changes there is an imperative to establish mechanisms of dispersal of lagoonal specialists and the distribution of potential habitat to ensure adequate population connectivity. Many of these lagoonal species may have found refugia in southern Europe and the Mediterranean basin during the last glacial period (Barnes, 1994). Literature searches of the distribution of six ‘specialised’ lagoonal invertebrate species of conservation importance in the UK (Table 1) indicated that they also primarily occupy lagoonal habitat and brackish waters throughout their range, which extends from the Mediterranean and Baltic Sea north and west to the British Isles. If larger source populations of these species are present on European coasts then it is important to identify habitats and evidence of potential dispersal vectors that could facilitate species colonisation, establishment and range expansion in a changing climate.

1.2. Potential avian mediated dispersal

It has been proposed that successful medium and long-distance dispersal of lagoonal specialists must rely on avian and anthropogenic transport (Barnes, 1988). Several species e.g. *Gammarus insensibilis*, juvenile *Cerastoderma glaucum, Nematostella vectensis* and *Idotea chelipes* are found within floating masses of the filamentous algae *Cladophora* sp. and *Chaetomorpha linum*, and dispersal could be enabled by its attachment to bird feet (Barnes, 1988; Sheader *et al*. 1997). The presence of internal and external invertebrate propagules and their potential for long-distance dispersal has been demonstrated for several species of migratory birds (Green & Figuerola 2005; Sánchez *et al*. 2007; Brochet *et al.* 2010; Casper *et al*. 2012). Geographical discontinuities in the genetic structure of the lagoon cockle (*Cerastoderma glaucum*) and experiments associated with its potential avian transportation support long-distance dispersal by birds (Tarnowska *et al*. 2010; 2012ab; Sromek *et al*. 2016). Furthermore, there have been observations of migratory shorebirds flying with the cockle *C. edule* clamped to their toes (Green & Figuerola, 2005). Indirect genetic evidence supports avian long-distance dispersal of the lagoon mud snail *Ecrobia ventrosa* in Lake Sawa, an inland brackish lake in Iraq (Haase *et al*. 2009). Viable eggs of both native parthenogenetic brine shrimp (*Artemia*) and invasive North American *Artemia. franciscana* were found within faeces of migratory wading birds feeding on salinas (salt-working ponds) in the Algarve (Portugal) and Cadiz (Spain) (Green *et al*. 2005).

If waterfowl are a likely vector for the dispersal of these species, then along the Atlantic coast of Europe, the spring and autumn migration of an estimated 15.5 million wading birds along the East Atlantic flyway (Stroud *et al*. 2004) may provide opportunity for local, regional and long-distance dispersal of specialist and non-specialist lagoonal species. There are few natural lagoons along the macrotidal Atlantic coast of Europe and distances between potentially suitable sites are large (Figure 1). However there remain extensive clusters of active salt-working sites (salinas) around estuaries and bays that have saline ponds of varied sizes and which are frequented by large numbers of water fowl. Smaller, artisanal salinas occur in France, Portugal and Spain and more intensive industrial-scale salinas occur in southern Iberia. Relatively little is known about the broad-scale patterns of benthic invertebrate assemblages of continental Atlantic salinas and whether they harbour significant populations of specialised lagoonal fauna and plants. With the demise of artisanal salt-working, increasing abandonment and economic diversification, large areas of potential habitat are threatened (Rodrigues *et al*. 2011). On the south coast of England, a few salt-working ponds known as ‘salterns’ that fell in to disuse in the 19th Century, have been modified by the creation of higher embankments where exchanges of sea water are managed via sluices. These sites are now classified as coastal lagoons and harbour protected lagoonal specialist species.

1.3.Hypothesis and Objectives

Our main research question is, given the paucity of natural lagoons along the European Atlantic seaboard, is there a network of artificial lagoon habitat that could facilitate both within and cross-regional colonisation of specialist lagoonal species? We hypothesise that salt-working sites could provide this habitat as they are currently prevalent along this coastline which is frequented by migratory wading birds that may act as dispersal vectors.

We have three main objectives:

(i) Characterise and compare habitats and benthic species assemblages at salt-working sites in different locations and regions of the north-east Atlantic coast. It is important to compare habitats to establish suitability of establishment of lagoonal specialist species.

(ii) Compare the abundance of specialist lagoonal species between habitat types, locations and regions. This is important as some habitats in salinas are in decline and gaps in any regional network will impact on connectivity. Some of these species are of international conservation importance, while the spread of non-native species is also of concern and interest.

(iii) Evaluate evidence for potential avian long distance dispersal of lagoonal species that could maintain connectivity, colonisation and persistence of populations within and at the species range periphery.

2.0 Materials and Methods

2.1 Study area and the salt-making process

The study extended along the Atlantic coast of Europe (Figure 1) between southern England (50^{o} N) and Andalucía, Spain (36^{o} N). This is a warm-temperate region, although the central southern part of England is at a boundary with cooler Arctic-Boreal conditions that extend from the North Sea (Forbes, 1858; Southward *et al*.1995). Along this coast, there are historical salt-working sites in southern England, clusters of smaller, artisanal salinas in France, Portugal and Spain and more intensive industrial-scale salinas occur in southern Iberia. Coastal sites can consist of local yet sometimes large-scale interventions of intertidal and maritime habitats that have created extensive areas of mud embankment, channels, canals and saline ponds of various sizes. Although salt-making processes vary, in southern Europe it typically involves three types of pond that are constructed in the ground at different levels to enable the flow of water between them. The ponds and reservoirs of artisanal salinas are lined with clay and separated by mud embankments. In the springtime, sea water either flows through a sluice opened at high tide or is pumped into a large storage reservoir. During the main salt making-season (April-September) water is channelled via sluices in to evaporation pans and then finally into the crystallisation ponds, where the salt concentration increases to near saturation point (Masero, 2003; Rodrigues *et al*. 2011). The brine is eventually discharged or is pumped in to smaller crystallisation ponds where further evaporation occurs and the salt is harvested. In the Bay of Cadiz, water from the main storage reservoir circulates around narrow convoluted channels where it evaporates and is finally diverted in to the crystallisation pans. Salinity in the storage reservoirs is typically between 30-60 ‰ and >200 ‰ in the crystallisation ponds (Amiral & Costa 1999; Masero, 2003). Diagrams of two selected sites that illustrate the types and proximity of the different water bodies are shown in Supplementary Information (S1). At active salinas, winter maintenance may involve drainage, cleaning and repairs to the ponds, pans and reservoirs. In the British Isles, there is no extant solar salt-making and the only legacy of a ‘partial-solar’ process is the remains of a few ‘salterns’ on the south coast of England. At these sites, solar evaporation was attempted in favourable summers prior to boiling the remainder of the brine to produce salt (Lloyd, 1967; Tubbs, 1999). This process was discontinued in the late 19th Century and many of the remaining structures and embankments are modified or incorporated within coastal protection schemes.

Samples were obtained from active and abandoned continental sites that were private artisanal salinas or open salt-working museums (Table 2). One salina at Figueira da Foz (Portugal) had diversified to grow *Salicornia*. Large industrial-scale salt-working sites in Andalucía were excluded from the study due to access difficulties. On the south coast of England, two artificial lagoons (Brownsea Island lagoon and Bembridge lagoon) are in very close proximity to known historical salterns were included, but where salt-working has not been confirmed. These sites are of comparable size and known to have similar physical characteristics to the modified and enlarged historical salterns (Bamber et al. 1992; Herbert et al. 2010). Photographs of selected sites illustrating types of water body are presented as Supplementary Information (S2)

2.2 Field sampling

The survey period coincided with shorebird migration to ensure that sampled species or smaller propagules could potentially be attached to or ingested by birds and potentially be dispersed to other areas. Sites in southern England, France and northern Portugal were sampled in March and April 2011 whereas southern Portugal and Andalucía (Spain) was sampled in April 2012. For seasonal comparison, samples from the English and French sites were also sampled in September 2011.

To characterise species assemblages, seven water bodies (ponds) were sampled in each of two locations within five regions along the European coast (Table 2). At each location, the seven accessible water bodies were sampled across two salinas; however in location 'Solent South' a third site was sampled to ensure an equivalent number of ponds from the location. Ponds sampled were storage reservoirs, abandoned reservoirs, the 1st evaporation pans at salinas and the modified salterns and artificial lagoons on the south coast of England. At active salinas, sampling of storage reservoirs was prioritised as they are the largest water bodies with a salinity range most likely to be similar to natural lagoons. However, at any active salina, storage reservoirs are the least numerous type of water body, so 1st evaporation pans and abandoned reservoirs were also sampled to ensure adequate replication of potentially suitable habitat. Crystallisation ponds at active salinas were not sampled as these were too small and hypersaline in summer for a meaningful comparison with other larger lagoonal habitats and had often been drained over the winter.

At each pond, three benthic core samples were obtained for invertebrates using a 10cm diameter hand-held suction-corer to a sediment depth of 15 cm; (a total of 210 cores were taken across the 70 ponds). The number of cores was limited to 21 per location as there were restrictions on the number of cores permitted at protected and privately owned sites. All core samples were processed using a 0.5mm sieve and retained material was immediately preserved in labelled pots containing buffered 4% formalin in seawater. At each pond, a hand-sample of macrophtye vegetation was washed through the sieve and invertebrates retained and preserved. A qualitative survey for swimming macrofauna was also carried out in each pond using a 1 mm mesh hand net. A sediment core sample from each pond was taken for analysis of total organic content and particle size distribution. Field measurements of salinity and water temperature were measured using a YSI portable hand-held meter. When possible, maximum salinity values from each water-body were obtained from site records. Water depth was measured with a metre rule and the macrophyte cover in each pond was estimated by eye. Macroalgae of genera *Ulva* and *Cladophora* were not were identified to species level.

2.3 Laboratory analysis

Preserved samples were washed in clean seawater and all invertebrates were picked out of the material under a dissecting stereo microscope and placed within a separate labelled tube containing 70% industrial methylated spirit (IMS). All fauna within each sample was identified to species level and the total number of individuals of each taxon was counted. Nomenclature is according to the World Register of Marine Species (WORMS, 2017).

2.4 Sediment analysis

Sediment samples were placed in a muffle furnace at 550^{o}C for 48 hours for the determination of sediment organic content by loss on ignition. Particle size distribution of all sediment samples was determined by measuring the proportion of each fraction retained on a stack of standard sieves after shaking.

2.5 Invertebrate data analysis

The total number of invertebrates of each species recorded within the three benthic cores from each pond was combined. The main focus of analysis was the presence of specialist species in the different types of pond sampled and the characterisation of assemblages at scales of ‘Location’ and Region’.

Differences in numbers of seven specialist lagoonal species (Table 1), representing three phyla, were measured using ANOVA. Variation in assemblages at location and regional scales, were analysed using one-way ANOSIM performed separately using the ‘adonis’ function in R-package ‘vegan’ (Oksanen *et al*. 2007). To partition the variation in community at each of the location and regional scales to environmental covariates, a permutational analysis of variance (PERMANOVA) was performed on a Bray-Curtis dissimilarity index using sqrt transformed data. Significantly correlated variables ($p < 0.05$) were removed from the analysis. A discriminant Canonical Analysis of Principal Coordinates (CAP) was also carried out in PRIMER-e on the Bray-Curtis similarity matrix (Anderson *et al*., 2008). The CAP process was run separately to characterise those differences between locations and regions.

2.6 Potential avian connectivity

To establish the likelihood of connectivity between coastal salt-working locations, bird ring recovery data was obtained through the European Union for Bird Ringing (EURING) Data Bank (du Feu et al. 2009; EURING, 2016). Recovery data was obtained from the area within the EURING Place Code closest to the survey salinas and lagoons as possible. Not all of these records will have been from salt-working sites, although ringing of migratory coastal birds in these areas is often carried out in salinas. Data from the entire EURING data base was obtained for migratory water bird species known to frequent the salinas and lagoons: Eurasian spoonbill (*Platalea leucorodia*), Greater flamingo (*Phoenicopterus roseus),* Black-winged stilt (*Himantopus himantopus*), Black-tailed godwit (*Limosa limosa*), Pied avocet (*Recurvirostra avosetta*) and Common redshank (*Persicaria maculosa*). From the data base, the number of sightings or captures of ringed birds of each species in a salt-working area and later recovered or re-sighted, either in the same or a different area was recorded.

3.0 Results

3.1 Environmental data

At active continental sites, salt production had yet to commence when surveys were conducted in March and April. However temperatures within some Iberian reservoirs had already reached 31^{o}C and salinities were in excess of 50 ‰. Water depth in the different ponds varied from 5-50cm. The reservoirs at salinas surveyed on Île de Ré and Île d'Oléron (France South) were significantly smaller than in other regions. The sediment was >90% clay at half of the sites surveyed and remaining sites contained ≥10% sand, with an exceptionally high sand content in the UK sites at Brownsea and Lymington (53.8%). Mean organic content was <10% for all sites with the exception of 29% at Figueira da Foz (Portugal). Macrophyte cover was very variable within locations and regions and mostly consisted of green algae *Ulva* spp. *Cladophora* or *Cheatomorpha linum.* The highest mean macrophyte cover occurred at Figueira da Foz (mean 77%) and Île de Ré (mean 50%) (France-South), and the lowest macrophyte cover occurred at the Algarve where most sites had ≤1% cover. Abiotic data from the sites is presented as Supplementary Information (S3).

3.2 Benthic assemblages – general description

Overall species richness was relatively low, with a total of 53 invertebrate species identified in spring samples across all study sites, including 24 arthropods, 14 annelids, 6 molluscs, 2 cnidarians and one nemertean (Table 3). Additionally, the amphipod *Gammarus locusta* and Hemipteran *Sigara selecta* were recorded in samples obtained from French sites in September 2011. Two plant lagoonal specialists (*Ruppia* sp. and *Lamprothamnium papulosu*m) and the anemone *Nematostella vectensis* were recorded, which are included in the IUCN Red List of threatened species (IUCN, 2015). The polychaete *Desdemona ornata,* anostracan *A. franciscana* and manila clam *Ruditapes philippinarum* were the only known non-native species recorded within soft sediments. Benthic invertebrates on hard structures were not included in the main analysis; however the non-native barnacles *Austrominius modestus* and *Amphibalanus amphitrite* and polychaete *Ficopomatus enigmaticus* were recorded on sluice gates and pilings at Iberian salinas.

Species richness was significantly greater in samples from UK sites (H= 21.9,df 4, $p<0.001$) yet pairwise tests between other regions were not significant. Benthic core samples at the UK sites were generally dominated by polychaetes *Hediste diversicolor* and *Capitella capitata,* oligochaetes (*Tubificoides* spp.), amphipod *Monocorophium insidiosum* and bivalve *Abra tenuis.* Overall species richness of insect taxa was greater at continental sites but not significantly so. Pairwise tests following Two-way ANOVA indicated that autumn abundance across both French regions was significantly greater than in spring samples ($P<0.05$), however seasonal differences in abundance at UK sites were not significant. Macrophyte washings, mainly from *Cladophora* sp., revealed lagoonal specialist species *G.*

insensibilis, I.chelipes, M. insidiosum, L. hookeri, C. glaucum and *E. ventrosia*. Juveniles fish of species *Syngnathas rostellatus* and. *Liza* sp. were recorded in macrophyte washings from Île d'Oleron and Figuirera da Foz respectively (Table 3).

3.3 Presence of lagoonal specialists in water body types

Specialist lagoonal species were found within cores in all types of pond sampled (Figure 2), although only *E.ventrosa* was recorded in abandoned reservoirs. There were significant differences in the abundance of *N.vectensis* ((H = 24.5, df 3, p<0.001), *M.insidiosum* (H = 10.494,df 3, p=0.015) and *I.chelipes* (H = 10.41, df 3, p=0.015) although pairwise comparisons were inconclusive. The lagoonal specialist amphipod *Gammarus insensibilis* was also recorded from macrophyte washings in reservoirs at Île de Ré and Aveiro. The non-native anostracan *A. franciscana* was found in cores from evaporation pans in Cadiz and in macrophyte washings from a reservoir at Batz. The lagoonal charophyte *L.papulosum* was recorded in a reservoir in Aveiro and *Ruppia* was found within reservoirs in all regions except Iberia South. Shorebird predation on invertebrate fauna was observed in all pond types in each region.

3.4 Regional analysis of specialist species

Specialist lagoonal species were recorded within all five regions (Table 3; Figure 3). The lagoon cockle *C.glaucum* was ubiquitous throughout whereas the anemone *N.vectensis* was only recorded in the UK. Significant differences between regions were found for *N.vectensis* (H = 25.808, df 4, p<0.001); *I.chelipes* (H = 11.328, df 4, p=0.023) and *M.insidiosum* (H =

23.762, df 4, p = <0.001), for which there were significant pairwise differences (p<0.05) between the UK and France North and UK and France South.

3.5 Analysis of community structure

ANOSIM analysis comparing community structure between locations indicated significant differences between assemblages in 33 out of 45 locations compared pairwise (p>0.05). A one-way ANOSIM test across Regions indicated that there were significant differences in community structure (global R = 0.275, p=0.001). Pairwise tests showed difference in community structure were largest between sites in the UK and all other regions. Differences were also evident between north Iberia and both French regions (north and south). PERMANOVA (Table 4) indicates that most variation in assemblages can be explained by region and water body type.

Figure 4 presents the CAP output to discriminate samples between regions. Clear grouping is evident in samples from the different locations, although to a lesser extent between continental sites. Overlaid Pearson rank correlated species vectors (correlation > 0.5) indicate that sites from the UK are characterised by higher abundances of annelid worms, notably *Hediste diversicolor*, *Streblospio shrubsolii* and *Tubificoides benedii*, and the anemone *Nematostella vestensis*. Higher abundances of chironomid larvae were found in Iberian sites. CAP results indicate that the optimal number of PCO axes required to explain the highest proportion of variance in the data is 11 (m = 11). This explains approximately 88.3% of variation within the data, with 54.3% of samples correctly classified (i.e. classified into the correct group based on the data).

3.6 Analysis of bird ring recoveries

Of a total of 56,358 recovery records of the selected species across Europe (EURING Data Bank, 18.03.2016), 972 (1.7%) were from Atlantic salt working regions and 80% of these were for Eurasian spoonbill. There is evidence of intra-regional movement of all species (Table 5) except for Greater flamingo which was restricted to within southern Iberian areas. Eurasian spoonbills move between all the continental salt-working areas and there is a single recovery of a bird that had moved within lagoonal areas in the UK. Evidence of movements of Black-winged stilt and Pied avocet were similar and mostly within and between northern and southern France and within areas in southern Iberia. Black-tailed godwit and Common redshank initially sighted in lagoonal areas in southern England were subsequently recorded in salt-working areas in northern and southern France; however no initial sightings of birds of any of the selected species from southern continental regions were later observed in Britain. Most recorded bird movements were between southern Spain and the French coast (Figure 5), although precise migratory pathways are not shown.

4.0 Discussion

Artificial structures, currently and historically associated with solar salt-working were found to contain coastal lagoonal biodiversity of international conservation importance. These include specialised and protected lagoonal invertebrates and macrophytes and non-native species. Lagoonal specialists and internationally protected species were found in historic salterns and also in larger storage reservoirs and evaporation pans in all continental regions. Differences in macrobenthic assemblages, and the prevalence of lagoonal specialist species were identified between different types of waterbody within each location. Although detailed comparison between natural and artificial sites is beyond the scope of this work, the presence of coastal lagoonal invertebrate indicator species at continental salt working sites demonstrates that these habitats should be classified as coastal lagoons. Evidence of bird movements between locations could theoretically explain the dispersal of lagoonal invertebrate propagules within and between regions and potential connectivity between isolated lagoonal habitats. These habitats could therefore contribute to a network of coastal lagoon habitat along the Atlantic coast of Europe that confers a measure of ecological resilience in response to environmental change.

At active salinas, storage reservoirs, which were the largest and least hypersaline water-bodies, contained highest invertebrate species richness, supporting previous observations (Vieira & Amat 1997; Amiral & Costa 1999). The physiological stress incurred at higher salinities must limit species richness of assemblages and differences between larger and smaller ponds. Moreover, heavy mortality amongst invertebrates, including *H. diversicolor* and *C.volutator,* occurs at salinities above 40‰ (Mason, 1986). Yet across Atlantic Europe, greatest dissimilarity in macrobenthic assemblages was between the salterns and the active salinas.

The number of active salinas is declining rapidly in parts of coastal Europe and diversification of use is increasing (Amat *et al.* 2007; Rodrigues *et al*. 2011). Industrial salinas and some former artisanal saltworking sites that have now been developed for aquaculture were not sampled, so study sites may not have been regionally representative of artificial habitat, especially in southern Spain. However, inspection of lists of species from salinas converted to aquaculture (Arias & Drake, 1994, 2004; Drake & Arias, 1997) reveal that they do contain lagoonal specialists (e.g. *G.insensibilis; M.insidiosum, I.chelipes*) so site diversification may not contribute to population decline for some taxa.

At active salinas, maintenance and repairs to reservoirs and evaporation pans, including drainage, are carried out between the autumn and early spring, so recent disturbance may have limited species presence. Data was obtained in the spring and autumn bird migration period when biological production in the ponds is not at its peak (Arias & Drake, 1994) therefore maximum site abundances and richness may have been underestimated in this study. At English and French sites sampled in 2012, abundances in September, at the end of the production period, were greater than in the spring and this pattern is likely to occur across Iberia also. When sampled in spring, macrophyte cover, which has been shown to influence invertebrate assemblages and is important in determining abundances of Hydrobiidae, *Chironomous salinus* and *Microdeutopus gryllotalpa* (Drake & Arias, 1997), was more prevalent at salinas in the south of France. However latitudinal sampling bias may have been incurred as spring production in the south of the region is more advanced than in the north. Predation by large numbers of migratory shorebirds that visit Atlantic salinas during the winter months (Rufino *et al.* 1984; Batty 1992; Pérez-Hurtado & Hortas 1992; Masero, 2003; Pedro & Ramos, 2009) could also account for lower invertebrate abundances during the spring sampling period.

Comparative analyses of lagoonal macroinvertebrates reveal very high levels of population variability at all spatial and temporal scales (Mason, 1986; Bamber et al.1992; Carvalho *et al.* 2005; Joyce *et al.* 2005; Sanchez *et al.* 2006), so abundance is likely to vary considerably between sites and years. For example some lagoonal species recorded in salinas of Andalucía (Arias & Drake, 2004) were not found. Due to isolation and chance dispersal, recruitment in lagoonal assemblages can be insufficiently high to offset local extinctions (Barnes, 1988), which may account for this variability. Species reproductive performance and size of lagoonal populations may also have been determined by levels of parasitic trematode infection and interactions with abiotic condition (Gates, 2006; Kube *et al*. 2006). Spatio-temporal variation in abundance could affect the frequency and probability of avian transportation of propagules. This might be particularly important for species that are frequently associated with algae, as this was less prominent in the spring compared to the late summer and early autumn. This would favour a southward dispersal of weed-associated fauna, as birds return from their summer breeding grounds and head for wintering in lower latitudes.

Estuarine areas provide opportunistic habitats for non-indigenous species (NIS) due to their low species richness and proximity to human activities such as aquaculture and global trade (Paavola *et al*. 2005; Airoldi & Beck, 2007; Zaiko *et al*. 2007). With the exception of *A.franciscana*, the few NIS species recorded within evaporation pans at continental salinas is likely due to an intolerance of very high salinities. Significantly, NIS recorded in this study were from salterns on the south coast of England where salinities are similar to full sea water. These observations are consistent with the *'Biodiversity increasing invasibility hypothesis'* (see discussion in Zaiko *et al*. 2007), that predicts more invasive species in species-rich communities; brackish lagoons and hypersaline ponds are relatively species-poor, yet the larger salterns would be the least stressed of the range of habitats sampled. Apart from *A. franciscana*, avian or anthropogenic long-distance dispersal may also explain the distribution of the non-native polychaete *Desdemona ornata* found in salterns on the south coast of England and from the Santo André lagoon on the Portuguese coast (Felix et al. 2015). The absence of European native *Artemia salina* from the UK is unsurprising since salt production has ceased and salinities within the salterns seldom reach >35 ‰. However, the species type-locality is salterns from the south coast of England where it was first identified in 1775

(Kuenen & Baas-Becking (1938) (in Sorgeloos, 1980; Tubbs, 1999). Its origins are unknown, however although avian long-distance-dispersal is a possibility, trade in ‘Bay-Salt’, a dirty salt imported for refining from the Bay of Bourgneuf (France) is also a possibility. The internationally vulnerable and protected anemone *N. vectensis* was found only in the English salterns, yet genetic evidence increasingly suggests anthropogenic introduction from North America, possibly via ship fouling (Pearson *et al*. 2002; Rietzel *et al.* 2008; Darling *et al*. 2009) or from imported Pacific oysters. This species has not yet been recorded from lagoons in continental Europe, although some habitats would appear suitable.

4.1 Regional variation

Although the sample size was small, the significant differences in assemblages between locations are consistent with other studies that have observed considerable habitat and taxonomic heterogeneity in lagoon ecosystems owing to large spatial variability and patchiness (Bamber *et al*. 1992; Basset *et al*.2006). Apart from latitudinal differences in temperature and consequential effects on salinity within reservoirs, the reduction in species richness and abundance of macroinvertebrates from the south coast of England to the continental regions is likely to be due to high levels of disturbance from active solar salt-making processes and maintenance interventions that affect the quality of habitat. The salterns are generally larger than the reservoirs of active salinas and are therefore mostly likely to have greater richness, and strong species: area relationships have been found in other lagoons (Bamber *et al*. 1992; Basset *et al*. 2006). However, abandonment of salinas can result in further loss in species diversity (Arias & Drake, 2004) and since 1987, Portugal and Spain have incurred a 55% and 74% loss of active salinas respectively; coastal Andalucía has incurred losses of 82% (Amat *et al*. 2007). The main difference between active and abandoned sites is not the structure *per se* but change in the hydrological regime. Abandoned sluices and channels quickly silt up due to lack of maintenance and flows reduce. Rainfall and evaporation then becomes more important than inflow of sea water. On the south coast of England, some saltern reservoirs abandoned in the 19th Century have been enlarged and their historic embankments incorporated within larger flood prevention schemes (Bamber *et al*. 2001). Management interventions at these sites are relatively infrequent and usually confined to sluices that maintain inflow of water and the quality of the lagoonal habitat. Yet at operating salinas, water levels within the reservoirs and ponds are varying continuously during the salt-making season.

4.2 Connectivity

How isolated lagoonal populations are sustained and potential barriers to dispersal and recruitment are overcome is uncertain. Potentially, ecological connectivity between different types of water body within salinas and between water storage reservoirs of different salinas could be locally high as the structures can be in very close proximity (<100m) and flooding during heavy rain and high tides is probable. It is possible that propagules (eggs, larvae, seeds and adults) might be transported between salinas through sluices and adjacent channels. Insects that complete their life cycles in the water may fly short distances between sites to lay eggs. Pelagic larval stages vary between days and several weeks (Shanks *et al*. 2003), so propagules could enter storage reservoirs when filled from the adjacent sea. Transport from reservoirs in to adjacent channels and the wider estuary may be possible as leakages and seepages are not inconceivable. Natural lagoons along this coast are scarce, and where these habitats are separated by tens or hundreds of km, successful transportation of propagules within the water column is likely to be highly infrequent. Although, primarily lagoonal, some species e.g. *C glaucum*, are found in other brackish habitats and sheltered bays and estuaries, including the Baltic Sea (Table 1) so other potential habitat along this coast for these species may occur. This is of particular importance for successful avian transportation of propagules between the Iberian coast and southern France, and northern France and the UK, where there are the largest gaps between salinas and other lagoons.

Other work has shown that the presence of lagoonal specialist species can be surprisingly localised and restricted, despite apparently suitable habitat in close proximity (Barnes, 1988; Gilliland & Sanderson, 2000). High levels of genetic differentiation have been found between lagoonal populations of *I. chelipes* (Jolly *et al*. 2003) and *N.vectensis* (Pearson *et al*. 2002) on the south coast of England, suggesting significant barriers to gene flow. The stochastic nature of dispersal and successful recruitment can result in large variation between assemblages, as was observed in this study.

Several lagoonal specialist invertebrate species were recorded amongst filamentous green algae which could become attached to bird feet. Notwithstanding bird movements from brackish seas and lagoons to the east of the study area, migrations within and between extant and historical saltworking sites may contribute significantly to the network of coastal lagoon biodiversity in Europe. However it is not possible to confirm actual connectivity between sites without more detailed observations of attached propagules and genetic studies. These salinas maintain a continuity of habitat for lagoonal specialists and provide important habitats for prey species for migratory shorebirds along the East Atlantic flyway, as has been demonstrated for Greater flamingos (Amat *et al*. 2005).

5.0 Conclusions

The environmental legacy of solar-salt making on the Atlantic coast of Europe, and possibly elsewhere, is a potential network of coastal lagoon habitat. Salinas are likely to provide important ‘stepping stones’ for propagule transport and benthic species dispersal as natural lagoon habitat is infrequent. The use of these ponds, abandonment and level of intervention of the hydrological regime are important in influencing the type of benthic assemblages and the number of specialist and scarce species present. The future management of these sites will affect the size, quality and connectivity of the network, including suitability for water birds, which will have implications for invertebrate species population resilience and adaptation to environmental change.

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Table 1. Results of literature search for habitat preferences and European distribution of selected ‘specialist’ lagoonal invertebrates of conservation importance in the UK, plus the non-native *A.franciscana.* Searches conducted in Web of Science (Web of Science, 2017) using terms: ‘Lagoon’ ‘Estuary’, ‘Brackish’, ‘Seas’, ‘Intertidal’ and ‘Habitat’.

Table 2. Sampling Regions, Locations and Sites. A total of seven water bodies (ponds) were sampled at each of two locations. The seven pond samples at each location were obtained from two sites, except for location ‘Solent South’ where an additional third site was sampled. Water Body types: Sal/L~salterns and lagoons; R ~storage Reservoirs; E1 ~ 1st Evaporation pan; AB ~ Abandoned reservoir.

		No. of Sites (Studies)					
Group	**Species**	**Lagoons (a)**	**Salt pans (exc. Salterns) (b)**	**Brackish bays and fjords (c)**	**Estuary (d)**	**Intertidal (e)**	**Region (No. different sites of each habitat type)**
Cnidaria	*Nematostella vectensis*	20 (4)	0	0	0	0	England (20^{a})
Crustacea: Anostraca	*Artemia franciscana*	0	4 (3)	0	0	0	Atlantic Spain (3^{b}), Portugal (1^{b})
Crustacea:Amphipoda	*Gammmarus insensibilis*	27 (16)	0	2 (2)	1 (1)	1 (1)	England (19^{a}), Portugal (2^{a},1^{e}) Mediterranean Sea (5^{a},1^{b}, 1^{e}), Black Sea (1^{a},2^{c})
Crustacea:Amphipoda	*Monocorophium insidiosum*	7 (10)	0	1(6)	0	1 (1)	Mediterranean Sea (7^{a},1^{c},1^{e})
Crustacea:Isopoda	*Idotea chelipes*	5 (4)	0	1 (6)	1 (1)	0	England (3^{a}), Mediterranean Sea (2^{a}) Baltic Sea (6^{c}) , Wadden Sea (1^{d})
Crustacea: Isopoda	*Lekanespaheara hookeri*	35 (10)	0	0	1 (1)	1 (1)	England (28^{a}), Mediterranean Sea (5^{a}), Atlantic Spain (1^{d,e}), Portugal (2^{a})
Mollusca:Gastropoda	*Ecrobia ventrosa*	32 (17)	1 (1)	5 (5)	0	0	England (20^{a}), Atlantic Spain (1^{b}), Mediterranean Sea (6^{a}), Portugal (2^{a}), Denmark (1^{a},1^{c}) Baltic Sea (3^{a},3^{c}), Skagerrak (1^{c})
Mollusca:Bivalvia	*Cerastoderma glaucum*	81 (40)	1 (1)	11 (12)	6 (4)	13 (2)	England (39^{a},10^{e,f}), Scotland (2^{a}), Wales (2^{a}), Ireland (13^{a}, 2^{e,f}), Portugal (4^{a},3^{d}), Mediterranean (21^{a},1^{b}, 1^{c}, 1^{d},1^{e}), Baltic (10^{c}), Wadden Sea (2^{d}),
	Total	**207 (101)**	**6 (5)**	**20 (31)**	**9 (7)**	**16 (5)**	

				No. Water Body sampled			
Region	**Location**	**Sites**	**Position**	**Sal/L**	**R**	**E1**	**AB**
UK	Solent North	Lymington, former salterns	50 ^{o} 44 21.06N; 01 ^{o} 32 15.36W	4	0	0	0
		Brownsea Island lagoon	50 ^{o} 41 30.15N; 01 ^{o} 57 34.99W	3	0	0	0
	Solent South (Isle of Wight)	Bembridge lagoon	50 ^{o} 41 22.37N; 01 ^{o} 05 52.63W	2	0	0	0
		Newtown lagoon, former saltern	50 ^{o} 41 22.37N; 01 ^{o} 05 52.63W	2	0	0	0
		Yarmouth lagoon, former saltern	50 ^{o} 42 11.98N; 01 ^{o}30 23.58W	3	0	0	0
			Region Total	**14**	**0**	**0**	**0**
France (N)	Batz-sur-Mer	Private artisanal salinas	47 ^{o} 17 40.10N; 02 ^{o}28 19.50W	0	0	2	0
		Private artisanal salinas	47 ^{o} 17 26.30N; 02 ^{o} 28 12.50W	0	3	2	0
	Nantes	Ile de Noirmoutier, private artisanal salina	46 ^{o} 59 53.50N; 02 ^{o}17 30.90W	0	3	0	1
		Barre-de-Monts, Écomusée Davioud, artisanal salina	46 ^{o} 52 26.30N; 02 ^{o} 06 10.08W	0	1	0	2
			Region Total	**0**	**7**	**4**	**3**
France (S)	Île de Ré	Écomusée, artisanal salina & museum	46 ^{o} 13 14.70N; 01^{o} 27 28.80W	0	1	2	0
		Private artisanal salina	46 ^{o} 13 13.80N; 01 ^{o} 31 09.10W	0	0	4	0
	Île d’Oléron	Écomusée Port des Salines, artisanal salina & museum	45 ^{o} 51 45.10N; 01^{o} 13 45.00W	0	0	3	0
		Private artisanal salina	45 ^{o} 57 28.20N; 01^{o} 14 58.80W	0	1	3	0
			Region Total	**0**	**4**	**10**	**0**
Iberia (N)	Aveiro	Muncipal artisanal salina	40 ^{o} 38.39.00 N; 08^{o} 39.50.00W	0	2	1	0
		Aveiro University, artisanal salina	40 ^{o} 37.58.00 N; 08^{o} 39.46.00W	0	1	3	0
	Figueira da Foz	Corredor da Cobra museum	40 ^{o} 06.43.00 N; 08^{o} 49.57.00W	0	4	0	0
		Private artisanal salina	40 ^{o} 07.56.00 N; 08^{o} 50.26.00 W	0	3	0	0
			Region Total	**0**	**10**	**4**	**0**
Iberia (S)	Algarve	Odiaxere, abandoned artisanal salina	37 ^{o} 08.01.00N; 08^{o} 38.50.00W	0	0	0	4
		Castro Marim, artisanal salina	37 ^{o} 13.94.00N; 07^{o} 26.07.00W	0	2	0	1
	Cadiz	Salinas San Vicente, artisanal salina	36 ^{o} 28.68.00N; 06^{o} 10.28.00W	0	3	0	0
		Salinas de Chiclana, artisanal salina	36 ^{o} 26.24.00N; 06^{o} 09.98.00W	0	2	2	
			Region Total	**0**	**7**	**2**	**5**

Table 3. Mean faunal species density (ind.m^2) and percentage cover of macrophytes at each location within the five regions in spring 2011 (UK, France North, France South) and 2012 (Iberia South). At each location, seven ponds were sampled, with three cores (10 cm diameter) obtained from each. Species additionally or exclusively present within macrophyte samples are shown as ‘W’; other qualitative observations of species are indicated as ‘P’; Standard Error shown in () ; additional taxa recorded in September 2011 as ‘S’.

Region	**UK**		**(France North)**		**France (South)**		**Iberia N (North)**		**Iberia (South)**	
Location Name	**Solent South**	**Solent North**	**Batz**	**Nantes**	**Île de Ré**	**Île d’Oléron**	**Aveiro**	**Figueira da Foz**	**Algarve**	**Cadiz**
Taxa										
TRACHEOPHYTA										
Ruppia spp.	<5%			<5%	<10%	<5%	<5%	10%	<1%	
CHAROPHYTA										
Lamprothamnium papulosum							<5%			
CHLOROPHYTA										
Chaetomorpha linum	<5%	<5%			<10%					
Cladophora sp		<5%	20%	10%	20%	20%	<5%	65%	<1%	30%
Ulva sp.	5%	<5%	20%	<5%	20%	10%	<5%			5%
CNIDARIA										

Nematostella vectensis	273 (147.6)	279 (238.4)								
Sagartia troglodtytes	61 (53.9)	6 (6.1)								
NEMERTEA										
Ramphogordius sanguineus		6 (6.1)								12 (12.1)
ANNELIDA										
Polychaeta										
Capitella capitata	3646 (2351)	1056 (1041.4)	S				340 (208.2)	18 (18.2)		679 (398)
Cauleriella zetlandica	42 (30.7)									
Desdemona ornata	18 (18.2)	6 (6.1)								
Hediste diversicolor	867 (521.9)	2147 (1517.7)	152 (144.7)	12 (12.1)			61 (60.7)	W	P	340 (167.6)
Malacoceros fuliginosus	18 (18.2)					6 (6.1)				6 (6.1)

Paradoneis lyra										12 (12.1)
Polydora cornuta	67 (66.7)		S				18 (18.2)			
Pygospio elegans		6 (6.1)								
Spio filicicornis	0	6 (6.1)								
Streblospio shrubsolii	127 (51.6)	61 (60.7)	S							12 (7.8)
Oligochaeta										
Enchytraeidae indet.	0	6 (6.1)								
Tubificoides benedii	3537 (1100.8)	849 (828.1)								6 (6.1)
Tubificoides pseudogaster	279 (177.5)	2584 (1951.3)	49 (48.5)				12 (12.1)	73 (72.8)		127 (87.9)
CRUSTACEA										
Anostraca										

Artemia franciscana				W						18 (18.2)
Amphipoda										
Monocorophium insidiosum	382 (157.8)	461 (334.5)				S	261 (260.8) W			1589 (754.7)
Corophium volutator	613 (339.8)	146 (124.6)								
Gammarus insensibilis		24 (24.3)			W	30 (17.9) W	6 (6.1) W			
Gammarus locusta			W							
Melita palmata										133 (72)
Microdeutopus gryllotalpa	55 (27.4)	30 (30.3)	6 (6.1)		W	W	85 (78.1) W			922 (547.5)
Isopoda										
Cyathura carinata										36

										(23.5)
Idotea chelipes	6 (6.1)	24 (12.6)	42 (35.9) W		W		W			
Lekanesphaera hookeri	267 (215.7)							837 (575) W	W	73 (37.9)
Decapoda										
Carcinus maenas									P	
Palaeomonetes varians			W	6 (6.1)	W	W	W			
Praunus flexuosa						W				
INSECTA										
Diptera										
Chironomidae	364 (210.3)	1419 (663.4)	364 (197.6) W	97 (27.4) W	103 (48) W	188 (79.1)	1905 (761.3) W	4368 (2437.8) W	510 (211.5)	594 (342)
Diptera indet.					24					

					(24.3					
Dolichopodidae						W	6 (6.1)		6 (6.1)	
Ephydridae				12 (12.1)					6 (6.1)	
Ephydra riparia				P						
Psychodidae						W	109 (109.2)	18 (18.2)		
Stratiomyidae			18 (18.2)				6 (6.1)	W		
Coleoptera										
Berosus sp.			S							
Carabidae					6 (6.1) W					
Coleoptera indet					W			455 (434.1)		
Enochrus bicolor			6	W	24	55		18		

			(6.1)		(24.3) W	(47.9)		(18.2) W		
Ochthebius aeneas			6 (6.1)	W	103 (103.1) W	W				
Ochthebus punctatus			W		W		W	91 (91) W		
Hemiptera										
Sigara sp.	6 (6.1)				6 (6.1) W			W	P	
Sigara selecta			S							
Sigara stagnalis			S							
MOLLUSCA										
Abra tenuis	12 (7.8)	73 (47.9)	6 (6.1)	30 (30.3)	91 (91) W	206 (135.1)	18 (12.6)	346 (235.4)		133 (60.4)
Cerastoderma glaucum	6	30	109	W	24	12	6	91		425

	(6.1)	(17.9)	(76.3) W		(15.7) W	(7.8) W	(6.1) W	(91) W		(190.4)
Ecrobia ventrosa	6 (6.1)	1438 (814)	121 (69.6) W	140 (93.3)	12 (7.8) W	85 (71.8) W	1802 (177.3) W			
Haminoea navicula					12 (12.1) W	W				
Peringia ulvae	6 (6.1)	30 (24)			W	534 (434.4) W				
Politapes rhomboides										6 (6.1)
Rissostomia membranacea							W			
Ruditapes philippinarum		P								
BRYOZOA										
Conopeum seurati	P									
PICES										
Liza sp.(juv)								W		

Pomatoschistus microps		P			P	W				
Syngnatus rostellatus (juv)						W				

Table 4.

Permutational analysis of variance (PERMANOVA) using the 'adonis' function in R-package "vegan" performed on sampling sites (i.e. individual water bodies, n=70) across regions to partition the variation in community structure (based on Bray-Curtis dissimilarity index using sqrt transformed data). Salinity was removed from this analysis because it was strongly correlated with Latitude (r=-0.65, p<0.01).No. of permutations: 999. Sig. *≤ 0.05, **≤ 0.01, ***≤ 0.001

	Df	SS	MS	F	R^2	Pr (>F)	
Region	4	4.46	1.11	4.74	0.18	0.001	***
Water body Type	3	1.41	0.47	2.01	0.06	0.01	**
Latitude	6	2.45	0.41	1.74	0.10	0.021	*
Water Temperature	47	15.34	0.33	1.39	0.60	0.049	*
% Sand	1	0.03	0.03	0.13	0.001	0.996	
% Organic	1	0.04	0.04	0.15	0.001	0.995	
% Macrophyte	1	0.28	0.28	1.21	0.01	0.313	
Depth (cm)	1	0.25	0.25	1.05	0.01	0.471	
Residuals	5	1.17	0.23		0.05		
Total	69	25.43			1.00		

Table 5. Potential avian connectivity matrix within and between salt-working regions and natural lagoons on the Atlantic coast of Europe. EURING data for combined species: Eurasian spoonbill, Black-tailed godwit, Greater flamingo, Pied avocet, Black-winged stilt and Common redshank. Values are total numbers of initial and subsequent sightings of birds. Inter-regional sightings are in bold. The name of each region is preceded by the EURING code. EURING locations are shown in Fig 5.

			SUBSEQUENT SIGHTING															
			UK			**France (North)**		**France (South)**			**Iberia (North)**				**Iberia (South)**			
			GBDO Dorset	GBHA Hampshire	GB1W Isle of Wight	FR38 Morbihan	FR37 Loire -Atlantique	FR39 Vendee	FR31 Charente-Maritime	FR34 Gironde	PO01 Aveiro	PO10 Leiria	PO11 Lisbon	PO15 Setúbal	PO08 Faro	ES60 Cádiz	ES63 Huelva	ES66 Sevilla
INITIAL SIGHTING	**UK**	GBDO Dorset		5														
		GBHA Hampshire	15		4	**2**		**1**	**1**							**1**		
		GBIW Isle of Wight																
	France (North)	FR38 Morbihan					10	**6**	**23**	**7**	**1**						**8**	**3**
		FR37 Loire -Atlantique				7		**6**	**2**	**5**						**1**	**2**	**3**
	France (South)	FR39 Vendee				**11**	**6**		35	19			**3**		**1**	**6**	**10**	**4**
		FR31 Charente-Maritime				**20**	**3**	37		25						**2**	**11**	**4**
		FR34 Gironde				**28**	**1**	13	15									
	Iberia (North)	PO01 Aveiro				**1**								1				
		PO10 Leiria																
		PO11 Lisbon																
		PO15 Setúbal									1		5		**2**		**7**	**4**
	Iberia (South)	PO08 Faro						**1**								1	9	6
		ES60 Cádiz						**2**	**3**	**7**							14	13
		ES63 Huelva				**19**	**3**	**21**	**14**	**23**				**7**	4	46		157
		ES66 Sevilla				**5**	**2**		**4**	**6**				**1**		22	125	

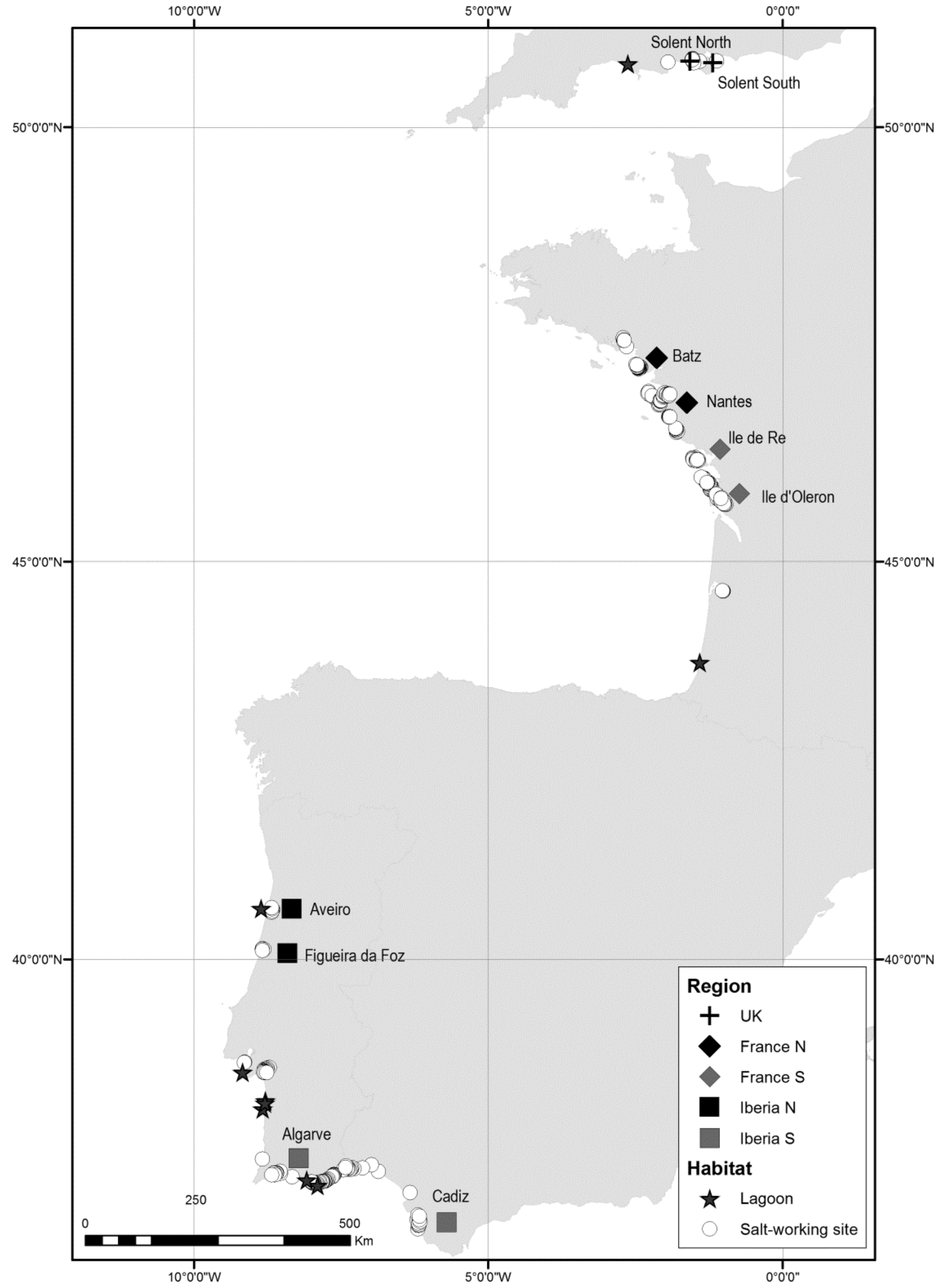

Figure 1. Location of salt-working areas, major natural lagoons and sampling locations within study regions.

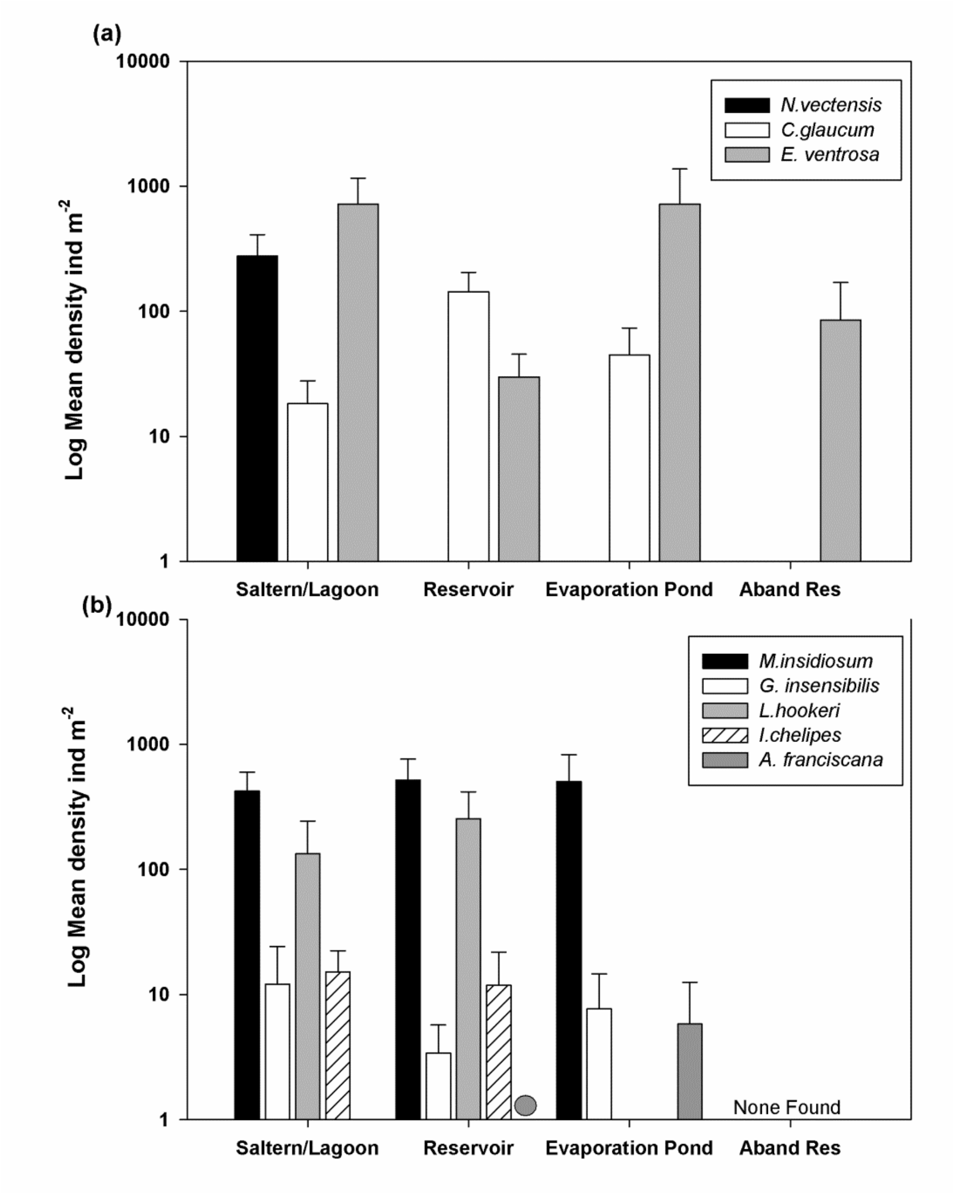

Figure 2. Mean density of selected lagoon specialist invertebrate species by water body 'Type' found in cores. ANOVA showed there were significant differences in the number of lagoon specialist species found within each water body type (F (5,59) 6.41, p<0.001). Error bars show SE. Circle symbol indicates presence in macrophtye sample only. Note: *Artemia franciscana* is non-native. See Table 3 for further information.

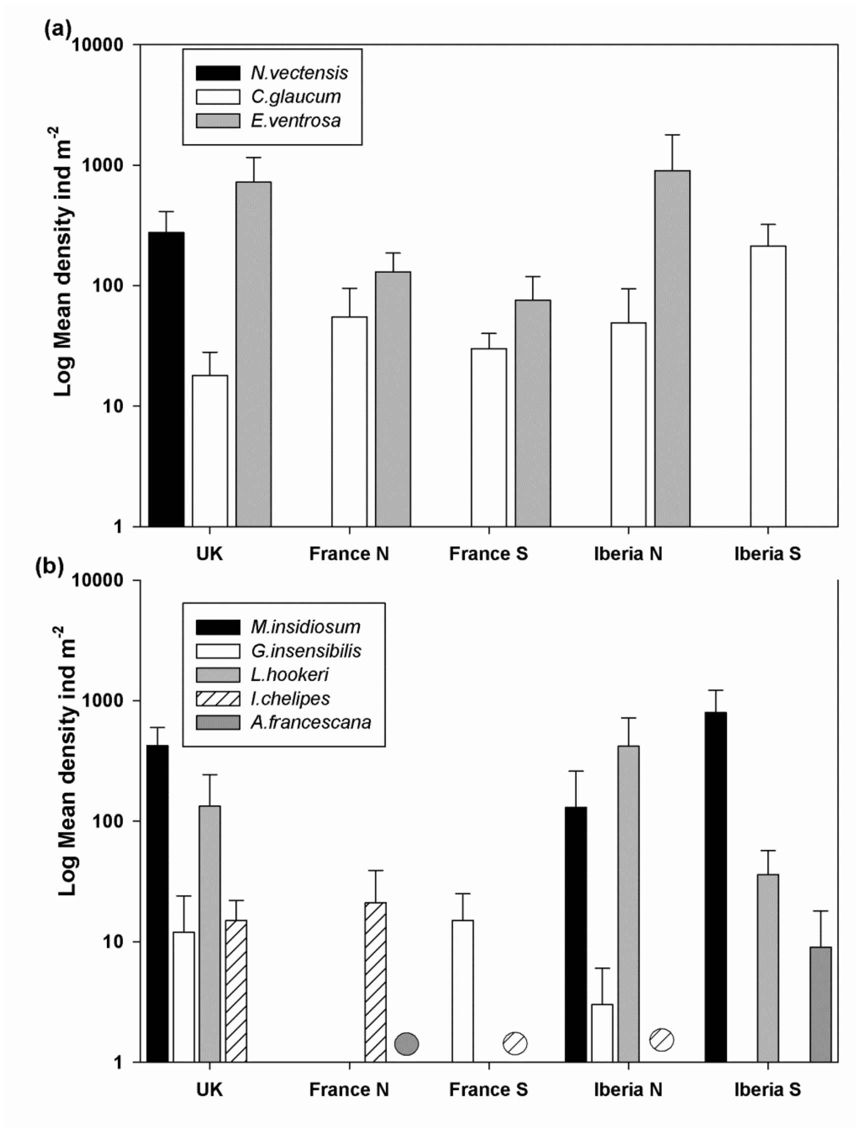

Figure 3. Mean regional density of selected specialist lagoon invertebrate species at salt-working sites. Error bars show SE. Circles indicate presence within macrophytes only. Note: *Artemia franciscana* is non-native. See Table 3 for further information.

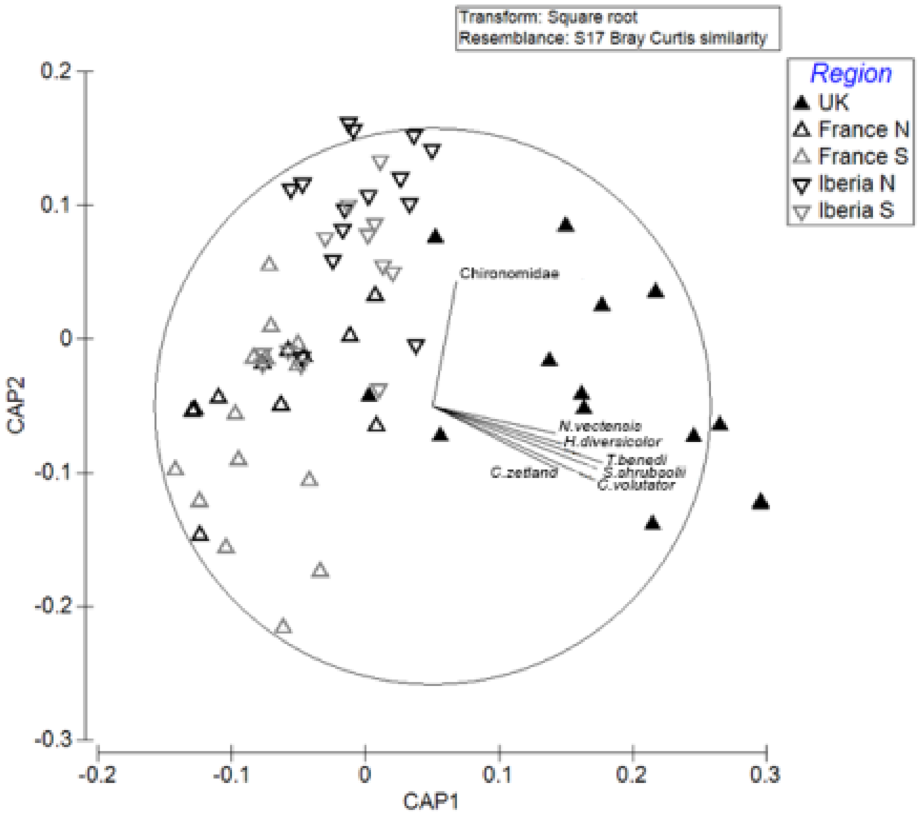

Figure 4. Canonical Analysis of Principal Coordinates (CAP) to discriminate samples between locations and regions, with overlaid Pearson rank correlated species vectors (r >0.5).

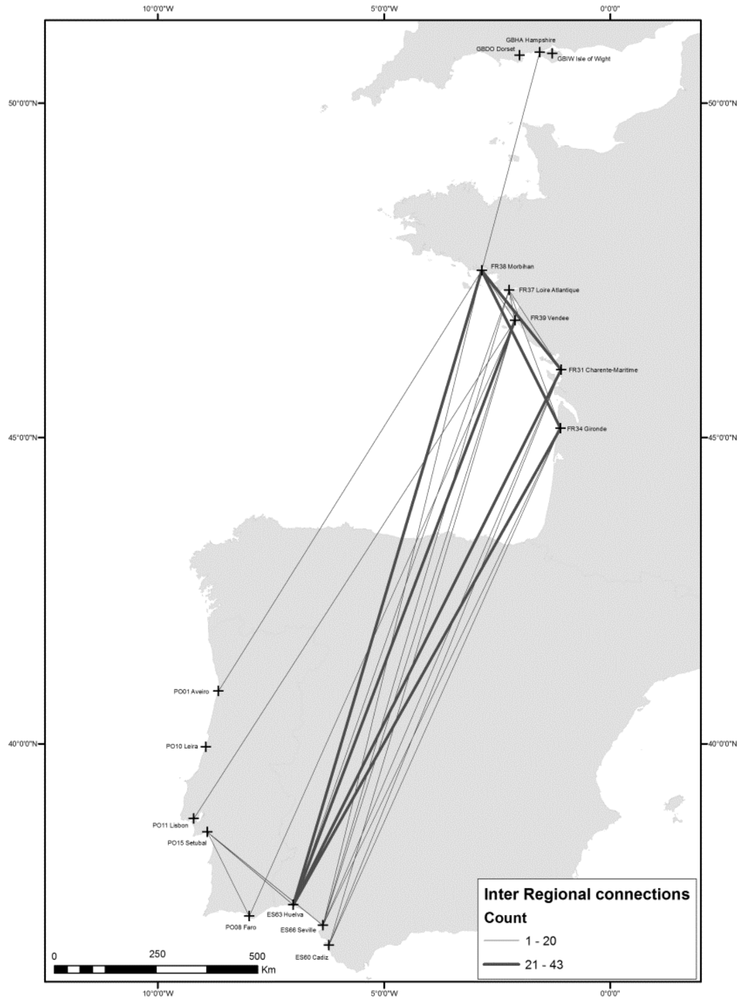

Figure 5. Inter-regional connections between salt-working sites through migratory bird movements. Locations shown are EURING place names and codes. Data shown is sum of all movements between sites from EURING data placed in two categories (1-20 movements; 21-43 movements) for clarity. See text and Table 5 for more information.