

# **Quantifying salinity-induced changes on estuarine benthic fauna: The potential implications of climate change**

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## **Abstract**

Coastal and estuarine systems worldwide are under threat from global climate change, with potential consequences including an increase in salinities and incursion of saltwater into areas currently subject to tidal and non-tidal freshwater regimes. It is commonly assumed that climate-driven increases in estuarine salinities and saline incursion will be directly reflected in an upstream shift in species distributions and patterns of community composition based on salinity tolerance. This study examined the responses of benthos to medium-term salinity changes in two macrotidal river-estuary systems in SE England to test whether these responses may be representative of climate-induced salinity changes over the long-term. The study reinforced the effect of salinity, related to tidal incursion, as the primary environmental driver of benthic species distribution and community composition. Salinity, however, acted within a hierarchy of factors followed by substratum type, with biotic competition and predator-prey relationships superimposed on these. The assumption that increasing salinities will be directly reflected in a shift in species distributions and patterns of community composition upstream over the long-term was shown to be over simplistic and not representative of a complex and highly variable system. Relative Sea Level Rise (RSLR) projections were predicted to increase estuarine salinities and

saline incursion in the study estuaries, which together with projected reductions in river flow will have important consequences for estuarine structure and function, particularly in tidal limnetic zones, despite estuarine communities being pre-adapted to cope with fluctuating salinities. The study identified, however, that limnic-derived fauna inhabiting these zones may demonstrate greater tolerance to salinity change than is currently recognised, and may persist where salinity increases are gradual and zones unbounded.

**Keywords:** saline incursion; benthic macroinvertebrates; relative sea level rise; estuary; tidal freshwater zones; freshwater-seawater interface

## 1. Introduction

Global climate change effects, including eustatic sea level rise, increased temperatures, changing precipitation patterns and increased storminess, and catchment land use (e.g. increased freshwater abstraction and channel modification) are predicted to result in an increase in salinities and saline incursion into estuaries and adjoining freshwater rivers, through reductions in summer river flows and relative sea level rise (RSLR) (Elliott et al., 2015; Prandle and Lane, 2015). Climate change research has largely neglected this in terms of its impact on coastal ecology (Peterson et al., 2010; Robins et al., 2016), despite episodic increases in salinity (often driven by prolonged drought periods) negatively affecting upper estuarine and riverine ecosystems globally (Attrill et al., 1996; Herbert et al., 2015; Kingsford et al., 2011; Turak et al., 2011).

Salinity is the primary environmental variable determining benthic macroinvertebrate community composition and structure in estuaries (Attrill, 2002; Telesh and Khlebovich, 2010). Hence the distribution and community composition of benthic fauna along the salinity gradient (from marine to freshwater) is primarily based on species salinity tolerances, *sensu* the classic study of Remane (1934). The latter describes a decreasing number of freshwater and marine species from the river and sea respectively towards the low salinity (5-7) inner estuary, which is in turn dominated by a few true estuarine/brackish species that excel in highly dynamic environments (i.e. the zone of lowest diversity and highest dominance; Whitfield et al., 2012). In macrotidal estuaries, the distribution and

composition of species integrates short-term (e.g. diurnal, weekly and lunar) changes in salinity to maintain a stable community under varying salinity changes (Elliott and Whitfield, 2011). Medium-term spatial and temporal variations in salinities and saline incursion extent (e.g. seasonal and interannual), however, are assumed to be directly reflected in a shift in species distributions and community composition indices in response to salinity tolerances *sensu* the Remane curve (Remane, 1934). As such, it is assumed that increases in salinity and extent of saline incursion driven by net changes in sea level, land level and reduced river flows over the long-term will reflect these patterns and result in a landward migration of estuarine benthic communities and associated patterns of community composition based on salinity tolerance (Little, 2012; Smyth and Elliott 2016).

Freshwater species are generally assumed to be intolerant of any increase in environmental salinity (Williams and Williams, 1998a) and thus those that inhabit lower river and upper estuarine areas (i.e. tidal freshwater zones; TFZs) are predicted to be most at risk from future increases in saline incursion (Little, 2012). This is corroborated by studies undertaken in upper estuarine areas following prolonged drought-driven saline incursion events, where notable reductions in the diversity and richness of the freshwater fauna have been recorded, together with the upstream migration of brackish and marine taxa (Attrill and Power, 2000; Attrill et al., 1996; Kingsford et al., 2011). TFZs are, however, poorly-studied compared to their non-tidal freshwater and tidal brackish and marine counterparts (Rundle et al., 1998; Sousa et al., 2007). As such, relatively little is known regarding the community composition of these areas or the response of the limnic-derived fauna to medium and long-term variations in salinity and saline incursion extents (Rundle et al., 1998; Williams and Williams, 1998a, b).

Our lack of knowledge regarding the response of estuarine benthic fauna to medium-term fluctuations in salinity over the full marine to freshwater transition, limits our potential to confirm assumptions and predict the effect of climate-driven increases in salinity on estuarine function over the long-term with confidence. This study examines the responses of estuarine benthic communities to salinity changes due to seasonal river flow in two macrotidal river-estuary systems in SE England. It tests the hypothesis that the responses of the benthos to medium-term salinity variations can be used to predict the impact

of climate-induced salinity changes over the long-term. The study also tests the current assumptions regarding the impacts of climate change on benthic estuarine communities (particularly in TFZs).

## **2 Materials and methods**

### **2.1 Study area and site selection**

The River Ouse and River Adur, (Southern England; Figure 1), rise on Gault and Weald clay and cut through alluvial valleys of the Sussex chalk, running over alluvial floodplains to enter the English Channel at Newhaven and Shoreham-by-sea respectively (Environment Agency, 2011; Buck, 1997). The adjacent catchments cover a combined area of 1073 km<sup>2</sup> and are bordered by 40.2 km of coastline, most of which has been urbanised, including the city of Brighton and Hove and the large ports of Shoreham and Newhaven (Figure 1; Environment Agency, 2010). The River Ouse estuary extends 21.8 km from Newhaven to the artificial tidal limit (marked by a series of weirs at Barcombe Mills) and has a Mean High Water Spring (MHWS) and Mean Low Water Spring height (MLWS) of 6.69 m and 0.77 m respectively. The River Adur estuary is tidal for 21 km to the normal tidal limit (NTL) on the eastern branch and 18.9 km on the western branch, with a MHWS and MLWS of 6.3 m and 0.6 m respectively (Buck, 1997). The estuary channels have been anthropogenically narrowed, deepened and constrained for navigation and flood defence, with flood storage areas removed (i.e. intertidal areas and flood plains). In the convergent Adur and Ouse estuaries, this artificial manipulation exacerbates incursion of the tidal wave by decreasing frictional drag and increasing tidal flow velocity, funnelling and propagating tidal amplitude upstream (Savenije and Veling, 2005).

The rivers have similar hydrological regimes, with the impermeable clays in the upper catchments making the rivers highly ‘flashy’ (i.e. responds very quickly to rainfall, with water flow rising rapidly to a peak before receding) in nature, with naturally low summer flows (Environment Agency, 2005a; Burrin and Jones, 1991). SE England is one of the most densely populated and driest regions in the UK and, as such, surface (and ground) water resources suffer from unsustainable abstraction during summer months, with river flow rates even in winter months deemed ‘unacceptable’ for large parts of the region (Environment Agency, 2007; Rodda, 2006). Concerns regarding increased saline incursion

(due to increased freshwater abstraction) have been raised during drought years, particularly on the River Ouse, due to a large public water supply (PWS) abstraction site located just above the tidal limits (Barcombe Mills; Figure 1; Environment Agency, 2005a, b).

Short- and long-term climate change projections for SE England are likely to exacerbate saline incursion within these estuaries (i.e. reductions in summer river flow, high RSLR exaggerated by isostatic land subsidence and potential for increased storminess; IPCC, 2014; Jenkins et al., 2009; Robins et al., 2016). In addition the South East Plan (prepared by the then South East England Regional Assembly) aims to accommodate up to one million more people by 2026, raising concerns that the already over-exploited freshwater resource will be further stressed by increasing population demands (Rodda, 2006).

These estuaries are representative of a large number of macrotidal, anthropogenically modified coastal plain estuaries of North-West Europe (Prandle and Lane, 2015) with growing catchment and coastal populations. Hence the results of this study are applicable to other similar European systems.

## **2.2 Macroinvertebrate sample collection and processing**

Macroinvertebrate sampling occurred during August 2008 and February 2009 to coincide with low summer and high winter river flows, indicative of high and low salinities and degree of tidal saline incursion respectively. Macroinvertebrate sampling at 12 and 15 sites in the River Adur and River Ouse respectively covered the complete marine to freshwater transition (Figure 1). Due to the perceived susceptibility of TFZs to future increases in salinity, more emphasis was given to these areas (Figure 1). Sites O4 and O5 were added in February 2009 to address a sampling gap.

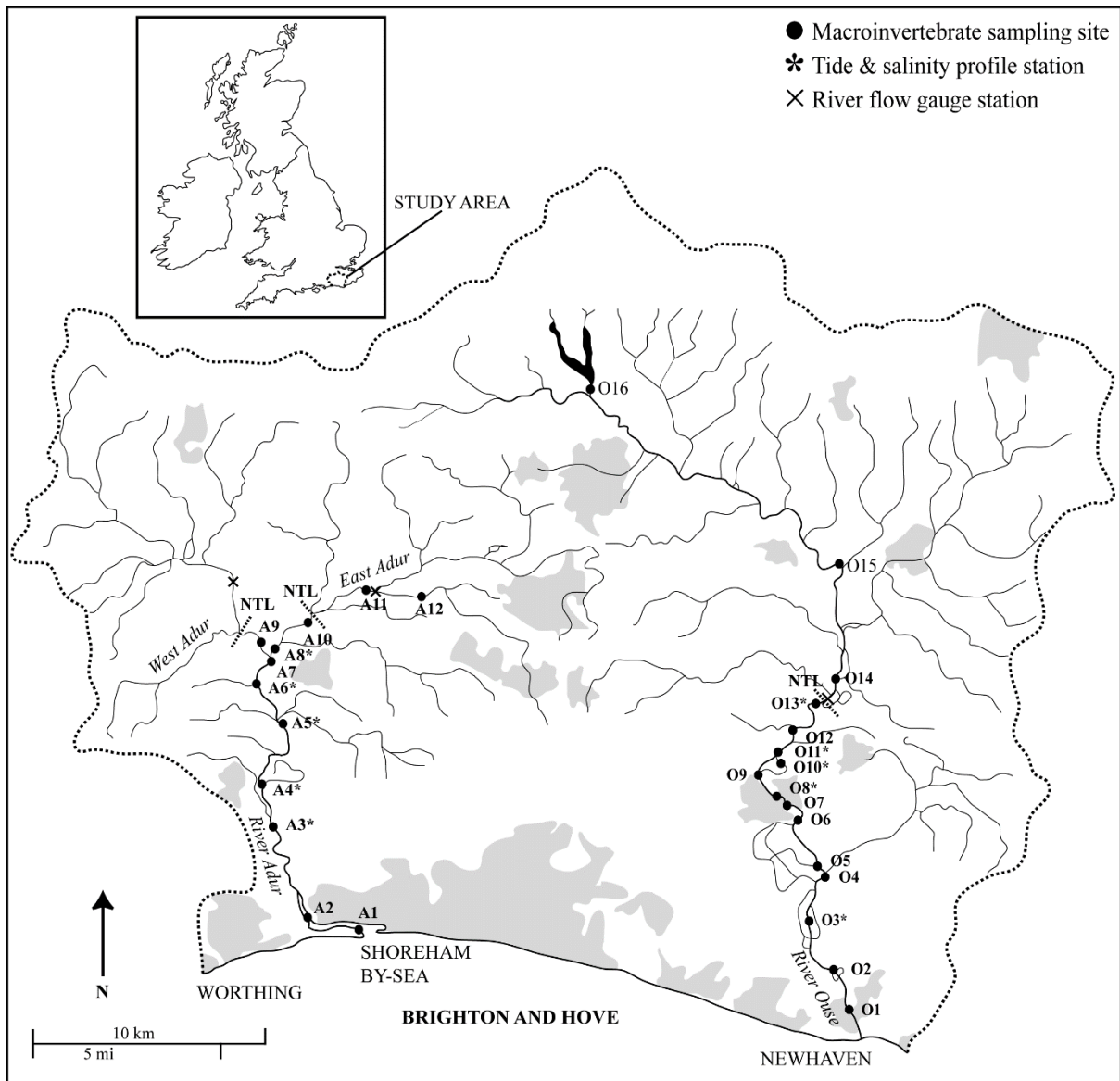


Figure 1. River Adur and River Ouse catchment showing sampling sites, normal tidal limits (NTL), tide and salinity profile stations and river flow gauging stations.

Benthic macrofaunal samples were obtained at each site, in each year, through one standard three-minute kick-sweep sample in the marginal area of the channel at low tide (Murray-Bligh, 1999). In total, 48 kick samples were collected. All samples were preserved in 10% formaldehyde and identified to species level where possible. All recorded macroinvertebrate species were assigned a salinity tolerance grouping (Table 1; adapted from Wolf et al., 2009) based on the analysis of published

literature sources (see supplementary material Table 1). These groupings were developed as part of a classification approach to meet the dynamic salinity conditions experienced by macroinvertebrates in tidal streams, and have been adopted here due to similarities in conditions (Wolf et al., 2009).

Table 1. Summary table of salinity tolerance groupings (derived from Wolf et al., 2009) with number of species allocated to each grouping.

Salinity tolerance	Salinity range	Description	Number of species
Holeuryhaline (he)	0 - 35	Marine derived taxa that tolerate the entire range of salinity from limnic to marine	4
Euryhaline-marine (em)	0.5 - 35	Marine taxa that tolerate a range of salinities between 0.5 and 35	16
Brackish (b)	0.5 - 30	Brackish water taxa that live and reproduce in brackish waters and tolerate varying salinity between 0.5 and 30	5
Euryhaline-limnic (el)	0 - 10	Freshwater taxa that tolerate salinity up to 10 (and higher for a short time)	9
Limnic, tolerates salt (l (el))	0 - <5	Freshwater taxa that tolerate salinities below 5	33
Limnic (l)	<0.5	Freshwater taxa that do not tolerate even low salinities	24

### 2.3 Environmental parameters

Tide and salinity profiles of the study estuaries were recorded at five stations (Figure 1) over four consecutive days (during the macroinvertebrate sampling period) in both years. In addition, spot samples of a number of physico-chemical parameters were recorded at each macroinvertebrate sample site, including water temperature (°C), pH, dissolved oxygen concentration (DO %), conductivity ( $\mu\text{S cm}^{-1}$ ) and salinity (psu) using a hand-held WinLab®Data-Line Conductivity Meter (with automatic calibration and temperature compensation) and additional standard meters (Hanna Instruments, Leighton Buzzard, UK).

Surface sediment was collected from three 0.2 x 0.3 m grids at each sample site using a trowel. Sediment classification (Wentworth grain size, particle roundness, sphericity; Gordon et al., 2004; Krumbein, 1941) and organic carbon, calcium carbonate and minerogenic content were determined following Dean (1974). Sediment samples were dry sieved through a sieve nest, with particles >60  $\mu\text{m}$  removed prior to the dry sieving process. The average grain size was taken as the mean interquartile (25% - 75%)

range. For sites with visible coarse material (i.e. >4mm including granules, pebbles and cobbles) the length of the b-axis was used to allocate randomly selected particles into a Wentworth size class category.

## **2.4 River Flow Gauging**

Mean daily discharge ( $\text{m}^3 \text{s}^{-1}$ ) data in August 2008 and February 2009 were provided by the Environment Agency through gauging stations on the lower River Ouse and the eastern and western branches of the lower River Adur (Figure 1). Mean daily discharge for the four-day salinity sampling periods were  $0.72 \text{ m}^3 \text{ s}^{-1}$  and  $0.73 \text{ m}^3 \text{ s}^{-1}$  in August 2008 and  $1.24 \text{ m}^3 \text{ s}^{-1}$  and  $1.43 \text{ m}^3 \text{ s}^{-1}$  in February 2009 for the Adur and Ouse respectively. The winter sampling period did not coincide with the peak discharges recorded during February 2009 (mean monthly discharges of  $4.13 \text{ m}^3 \text{ s}^{-1}$  and  $2.9 \text{ m}^3 \text{ s}^{-1}$  on the Rivers Adur and Ouse respectively), but followed an event of high river discharge. The summer sampling in August 2008 coincided with higher than average river flows, but was preceded by base-flow conditions (mean monthly discharges of  $0.66 \text{ m}^3 \text{ s}^{-1}$  and  $0.47 \text{ m}^3 \text{ s}^{-1}$  on the Rivers Ouse and Adur respectively).

## **2.5 Tide and salinity profiling – contemporary and projected future profiles**

Tide and salinity profiles were recorded using two SEBA-TEC in-situ data logging sondes, which recorded water level (m), salinity (psu) and temperature ( $^{\circ}\text{C}$ ) every 2 minutes over consecutive 24 hour periods at four stations along both estuaries (Figure 1). In order to produce interpolated, standardised tide and salinity profiles under low and high discharge conditions, the profiles at each site were standardised to the MHWS and MLWS tide height recorded at the river mouths (6.3 – 0.6 m at Shoreham and 6.69 – 0.77 m at Newhaven; Buck, 1997). Tide heights recorded at Newhaven (and applied to Shoreham) during the profiling were available through the UK National Tide Gauge Network logged at 10 minute intervals (accessed at: <http://www.ntsfl.org/data/realtime?port=Newhaven>)

### **2.5.1 Tide and salinity profile standardisation**



Each site recorded a lag between highest tide (m) and maximum salinity which differed between stations, increasing up to 62 minutes after the high tide at station A1. Maximum and minimum salinity related to high tide height at each station (in order to produce current and predicted salinity profiles) were obtained by synchronising the tide height and salinity profiles, so that highest tide level (m) matched maximum salinity and low tide level (m) matched minimum salinity. A ratio of the height of tide at each station and the height of the associated tide at the river mouth was determined. The ratio, multiplied by the MHWS and MLWS tide heights, produced a corrected vertical high and low tide height (m) for each station.

The corrected salinity and estuary level (m) relationships for the rising and falling tide profiles at each station and flow regime were plotted and the salinity associated with the corrected vertical height (m) determined. This assumes that the profiles at each station were consistent over varying tide heights. This was corroborated by comparing control tidal profile forms obtained at each salinity station during the sampling periods (August 2008 and February 2009).

This study regarded the 0.5 salt concentration as the upstream limit of saline incursion, the established Venice System oligohaline/limnetic boundary (McLusky, 1993). Alternative salt concentrations have also been used, with 1 as a typical agricultural/industrial limit and 2-4 as being biologically significant as the upstream extent of saline incursion in estuarine studies (Bulger et al., 1993; Deaton and Greenberg, 1986; Gordon et al., 2004; Kimmerer et al., 1998; Telesh et al., 2011).

### **2.5.2 Predicted future tide and salinity profiles**

Predicted future tide and salinity profiles were determined under the UK climate projection scenario (UKCP09) for high greenhouse gas emissions (Special Report on Emissions Scenarios (SRES) A1FI; Nakicenovic et al., 2000), for three time periods (2020s, 2050s and 2080s; IPCC, 2007; Lowe et al., 2009; Murphy et al., 2009). The IPCC replaced the SRES scenarios with Representative Concentration Pathways (RCPs) for its fifth Assessment Report (AR5; IPCC, 2013). SRES scenarios are however still used as the basis for UK climate projections and, as such, have been employed here (Murphy et al., 2009). SRES A1FI was selected as a predictive basis for the most extreme case scenario (within the

IPCC (2007) uncertainty range), based upon climate modelling (IPCC, 2007; Lowe et al., 2009; Nakicenovic et al., 2000).

SRES A1FI RSLR projections were selected for 12 km coastal grid squares at Newhaven and Shoreham (ID 25360 and 25151 respectively) using the UKCP09 User Interface (v1.0) (accessed at: <http://ukclimateprojections-ui.defra.gov.uk>). The estimated 5th and 95th percentile range of RSLR projections provided a range of 90% of the modelled results (Lowe et al., 2009). The projected RSLR for the three time periods, were separately combined with MHWS and MLWS tide heights for the study estuaries and multiplied by the tide height ratios (determined for the current profiles), to produce corrected MHWS and MLWS tide heights for each station and discharge regime. The maximum and minimum salinities that corresponded to the corrected MHWS and MLWS vertical tide heights (using the corrected salinity and tide level relationship plots of Section 2.5.1) were determined.

## **2.6 Statistical analyses**

Trends in the species, samples and environmental datasets were explored using multivariate techniques in Canoco v. 4.54 (ter Braak and Šmilauer, 2006). In all cases, preliminary detrended correspondence analysis (DCA) indicated a strongly unimodal pattern (DCA axis 1 gradient length >7), and subsequently the unimodal technique of detrended canonical correspondence analysis (DCCA) was employed to investigate environmental-species relationships under each flow regime, both within and between the two river systems. In all cases species data were converted to percentages and rare species were down-weighted. In order to explore trends longitudinally, sites A9 and O10 were removed from the statistical analyses due to their location on parallel/bypass channels.

Community composition indices including species richness, relative abundance (RA), Shannon-Wiener diversity index ( $H'$ ) and Berger-Parker dominance index (BP; Berger and Parker, 1970) were calculated within the  $\alpha$  Species Diversity and Richness software v.3.03 (Henderson and Seaby, 2002). To determine faunal zones of similarity between river and flow regime, faunal assemblages were compared by multivariate analyses via hierarchical clustering using Bray-Curtis similarity in PRIMER 6 (PrimerE Ltd: Plymouth Routines in Multivariate Ecological Research, Version 6). The statistical significance of

these clusters ( $p < 0.05$ ) were evaluated using similarity profile (SIMPROF) random permutation tests. The individual species responsible for the similarity and dissimilarity within and between the zones were assessed using SIMPER.

Species distribution plots were produced using the visualisation program C2 V.1.6.3 (Juggins, 2007) to sequence species distributions into salinity tolerance groupings relative to sampling point, distances from river mouths, discharge regime and species abundance. In comparing sites between discharge regimes, sites O4 and O5 were not included in the DCCA or faunal zone analysis, as these sites were only sampled under high discharge conditions (Feb 09).

### **3 Results**

#### **3.1 Species distributions and assemblage composition**

A total of 91 macroinvertebrate taxa from 18 orders (divided into the six salinity groupings; Table 1) were recorded in the River Ouse and River Adur over the sampling period, with 47 species common to both. Hierarchical similarity clustering of the faunal data identified three (A-C) and four (A1-D1) significant ( $p < 0.05$ ) longitudinal clusters of sites in the River Ouse and five (A2-E2) and three (A3-C3) significant ( $p < 0.05$ ) clusters in the River Adur under low and high discharge conditions respectively (Figures 2-4). Under both discharge regimes, diversity (Shannon-Wiener  $H'$  index) generally decreased from the head of both estuaries downstream and from the river mouth upstream (Figure 4). This was coupled with an increase in species dominance (Berger-Parker index), peaking in the upper estuary (Figure 4). A modified Remane diagram for these estuaries is provided in Figure 5.

##### **3.1.1. River Ouse**

In the River Ouse, the first clusters (A & A1) under both discharge conditions were characterised by a diverse and abundant marine dominated fauna, composed of euryhaline-marine (63.6 % & 77.9 %), brackish (29 % & 16.3 %) and holeuryhaline (7.5 % & 5.9 %) species (average dissimilarity between clusters of 61.5%) (See supplementary material Table 2 for clusters and species summary). Under low discharge conditions, cluster A (sites O1-O7) extended up to 12.8 km upstream (over max and min salinity gradients of 35-10.3 and 25.8-0.2 respectively), compared to 6.35 km upstream for cluster A1

(sites O1-O3) under high discharge conditions (max salinity of 35 and min salinity gradient of 0.2 to 25.8), a reduction in upstream extent of 6.4 km. The downstream shifts in these clusters reflect changes in the faunal data (Figures 2 and 4). Under low discharge conditions, euryhaline-marine species (e.g. *Carcinus maenas*, *Gammarus salinus* and *Melita palmata*) were recorded up to 12.8 km (O7) from the estuary mouth, and together with brackish species (e.g. *Cyathura carinata*, *Leptocheirus pilosus*), dominated the faunal community over a maximum salinity gradient of 10.3 to 35 (Figure 2). In contrast, under high discharge conditions, this community (A1) migrated downstream. A single euryhaline-marine amphipod *Corophium arenarium* was recorded at 13.44 km (O8), but was an outlier from the general trend.

The second set of clusters under both low and high discharge conditions (B & B1) were characterised by a species-poor, mixed transitional fauna, which were composed of holeuryhaline (57 & 41.2 %), brackish water (6.7 & 37.9 %) and euryhaline-limnic species (32.7 & 9.3 %), together with small numbers of limnic-derived species (3.5 & 10.1 %) (Figures 2 and 4). These clusters were dominated by the holeuryhaline amphipod *Gammarus zaddachi*, the brackish water isopod *Cyathura carinata* and the euryhaline-limnic gastropod *Potamopyrgus antipodarum* (Figure 2). Under low discharge conditions, cluster B (O8-O13) extended from 13.4 km to just below the NTL at 20.4 km upstream (over a 7.9-0.1 max salinity range), but retracted downstream by 2.9 km (11.3 km to 17.5 km) under high discharge conditions (B1; O6-O12, over a 12-0.2 max salinity range; Figure 2). This was represented by a downstream migration in the distribution of *G. zaddachi* and *C. carinata* and limnic-derived fauna *Erpobdella octoculata* and *Asellus aquaticus*. This shift in fauna was reflected in a downstream shift in the zone of lowest species diversity and highest dominance, which was recorded around the Freshwater Seawater Interface (FSI) under both discharge conditions. This general pattern was altered by site O4 (8.7 km) under high discharge conditions, which had high abundances of *G. zaddachi* (520 individuals). This zone of highest dominance and lowest diversity shifted downstream by approximately 2 km (15 km to 12.8 km) over salinity gradients of 3.3-0.2 and 10.3-0.2 respectively, demonstrating that salinity is the primary environmental variable dictating the location of this zone in the Ouse estuary.

The third set of clusters (C & C1) were characterised by an increasingly diverse and abundant limnic-derived fauna, composed of limnic salt-tolerating (36.6 & 77 %) and limnic (63.3 & 22.2 %) species (Figures 2 and 4). Under low discharge conditions, cluster C (O14-O16) extended from above the NTL at 22.37 to 47.16 km upstream (in non-tidal limnetic salinities) compared to 20.39 to 28.22 km (in tidal (O13) and non-tidal (O14-O15) limnetic salinities) under high discharge conditions (C1). This was represented by a downstream shift in the distribution of limnic salt-tolerating fauna (i.e. *Gammarus pulex* and *A. aquaticus*) of approximately 2 km from the non-tidal river into the tidal limnetic estuary (Figures 2 and 4). This reflected an increase in the overall proportion of limnic-derived species in the total and upper estuarine fauna between low and high discharge conditions (1.3 % to 5.7 % and 4 % to 32 % respectively). The downstream shift of *G. pulex* was mirrored in the downstream shift in the holeuryhaline and euryhaline-marine congeners *G. zaddachi* and *G. salinus* (Figure 2).

In contrast to the euryhaline-limnic and limnic, salt-tolerant species, most limnic species recorded did not exhibit a downstream shift in distribution between discharge conditions, with the exception of a single trichopteran *Limnephilus flavicornis* recorded at 16.1 km (O11) under high discharge conditions compared to 22.37 km (O14) under low (

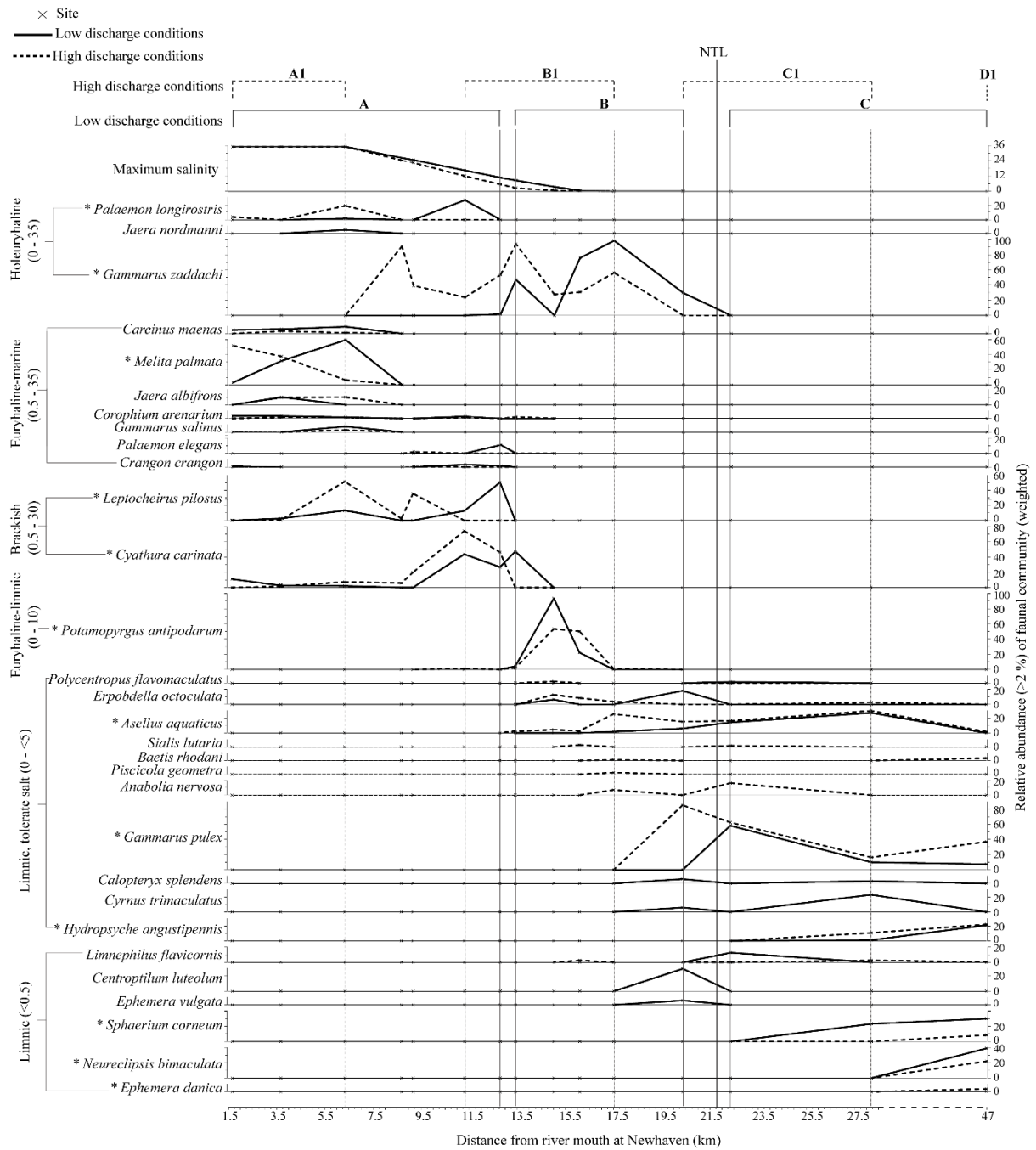


Figure 2). Several limnic species were recorded in the upper estuary (O13) in low abundances under low discharge conditions, however due to the low numbers recorded, these may have drifted downstream from the non-tidal river, rather than constituting part of a tidal limnetic community.

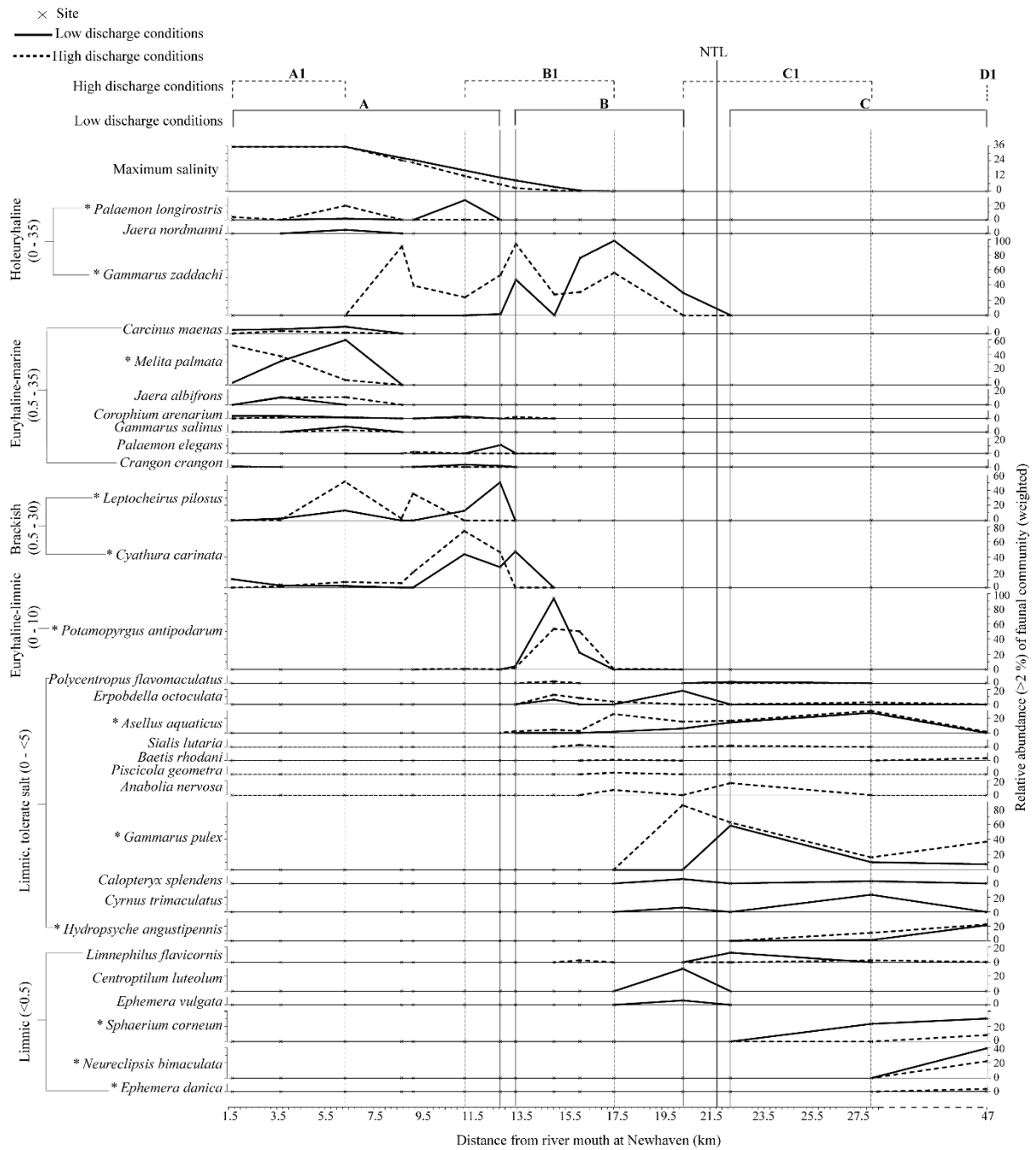


Figure 2. River Ouse summary diagram of species distributions, maximum salinity and significant site clusters ( $p < 0.05$ ) under high and low discharge conditions with distance from the river mouth. Species shown occur at  $>2\%$  abundance in one or more samples and are separated into salinity tolerance groupings. \*Species which contributed to the greatest dissimilarity ( $<7\%$ ) between clusters.

### 3.1.2 River Adur

As in the Ouse estuary, under both discharge conditions the first clusters in the Adur estuary (A2 & A3) were characterised by a diverse and abundant marine dominated fauna, composed of euryhaline-marine (75.3% & 88.1%) and brackish water (24.7% & 11.2%) species (average dissimilarity 60 %) (See supplementary material Table 3 for clusters and species summary). Under low discharge conditions, cluster A2 extended from 0.32 to 8.3 km from the river mouth (max salinities of 35 and min salinity gradient of 33.7-0.2), compared to 0.32 to 3.8 km under high discharge conditions (over max salinities of 35 and min salinity gradient of 33.7-19.2), a reduction in extent of 4.5 km (Figure 4). However, in contrast to the Ouse estuary, this downstream shift in clusters was not reflected in the distributions of euryhaline-marine (e.g. *C. arenarium*, *Hediste diversicolor*) and brackish water species (e.g. *C. carinata*, *Hydrobia ulvae*), which dominated the faunal community from 0.32 to 8.27 km (over maximum salinities of 35) under both low and high discharge conditions (Figures 3 and 4).

Under both discharge conditions, the second set of clusters (B2 and B3; average dissimilarity 63.8%) were characterised by a species-poor mixed transitional fauna, composed of holeuryhaline (5.8 % & 11.2%), brackish (79.4% & 71.5%) and euryhaline-limnic (11.2% & 11.4%) species, with small numbers of limnic-derived (0.24% & 3.9%) species (Figure 4). These clusters were dominated by *C. multisetosum* and *G. zaddachi* (Figure 3). Under low discharge conditions cluster B2 extended from 10.6 to 17.9 km upstream (over a max salinity gradient of 20-0.4 and 0.2 min salinities). However, under high discharge conditions, cluster B3 extended from 8.3 to 17.9 km (35-0.27 salinity range), which is reflected in the faunal data with reductions in brackish species and an increase in limnic-derived species downstream (Figures 3 and 4). This faunal assemblage represented the zone of lowest diversity and highest dominance in the Adur estuary. However, in contrast to the Ouse estuary, this zone stayed at 14-17.8 km from the river mouth between discharge regimes, indicating that salinity may not be the dominant environmental variable dictating the location of this zone in the Adur estuary (Figure 4). This zone is immediately upstream of the transition in environmental parameters from lower to upper estuary (see supplementary material Figure 1). Diversity ( $H'$ ) and dominance (BP) indices were significantly correlated with sediment grain size parameters (under high discharge conditions), indicating that the transition from muddy sands and gravel to fine grained mud (perhaps in addition to



additional environmental variables) may limit the upstream migration of some euryhaline-marine and brackish species. This is supported by the stationary distributions of most euryhaline-marine and brackish water species at 10.6 km upstream despite tolerable maximum salinity conditions continuing for a further 8.7 and 4.9 km upstream (low and high discharge conditions respectively). The anthropogenic extension of coarse grained sediment for bank stabilisation may explain why this pattern was not recorded in the Ouse estuary.

Under low discharge conditions, the third cluster (C2) was again characterised by a transitional fauna, but in contrast to cluster B2, was composed of holeuryhaline and limnic-derived species, rather than a transitional brackish community. This cluster had relatively high and increasing (towards the NTL) levels of diversity, abundances and richness of holeuryhaline (74.1%), euryhaline-limic (10.7%), limnic salt-tolerating (13.7%) and limnic (1.4%) species, however was dominated by high numbers *G. zaddachi* (74.2%), particularly in the tidal limnetic reaches (69% in site A8 and 77% in site A10; Figures 3 and 4). This cluster extended from 17 to 20.5 km upstream, over tidal limnetic maximum and minimum salinities (0.39 - 0.2). The non-tidal (above the NTL) River Adur was characterised by a generally diverse and abundant limnic-derived fauna (Figures 3 and 4).

In contrast to low discharge conditions, under high discharge conditions, cluster C3 extended from 18 km to above the tidal limits at 26.5 km (encompassing sites A8-A12) over tidal and non-tidal limnetic conditions (<0.5; Figure 4). Cluster C3 was characterised by increasing diversity, abundances and numbers of limnic-derived species (99.8%) and was similar in faunal composition (average dissimilarity 61.9%) to the abundant and diverse non-tidal limnic community which constituted the fourth cluster (D2) under low discharge conditions (above the NTL at 24 km). In contrast to the distributions of euryhaline-marine and brackish species, this downstream shift in limnic-composed faunal clusters under high discharge conditions, was recorded in the distributions of some species, with a number of euryhaline-limnic species (i.e. *I. elegans*) extending their range downstream by 2.44 km (after the removal of *P. antipodarum*) and limnic salt-tolerating species (e.g. *A. aquaticus*, *E. octoculata*, *Gammarus pulex*, *H. sahlbergi*, *Potamopyrgus geometra* & *S. lutaria*) by 1.96 km under high discharge

conditions (Figures 3 and 4). This is reflected in the proportion of limnic-derived fauna recorded in the total and upper estuary between low and high discharge conditions (4.3 % to 21.4 % and 11.2 % and 72 % respectively). As in the Ouse estuary, the downstream shift of *G. pulex* was mirrored in the downstream shift of *G. zaddachi* (Figure 3).

In contrast to the euryhaline-limnic and limnic, salt-tolerating species, the downstream distribution of limnic classified species remained static at 18.01 km (although within the tidal limits) as in the Ouse estuary.

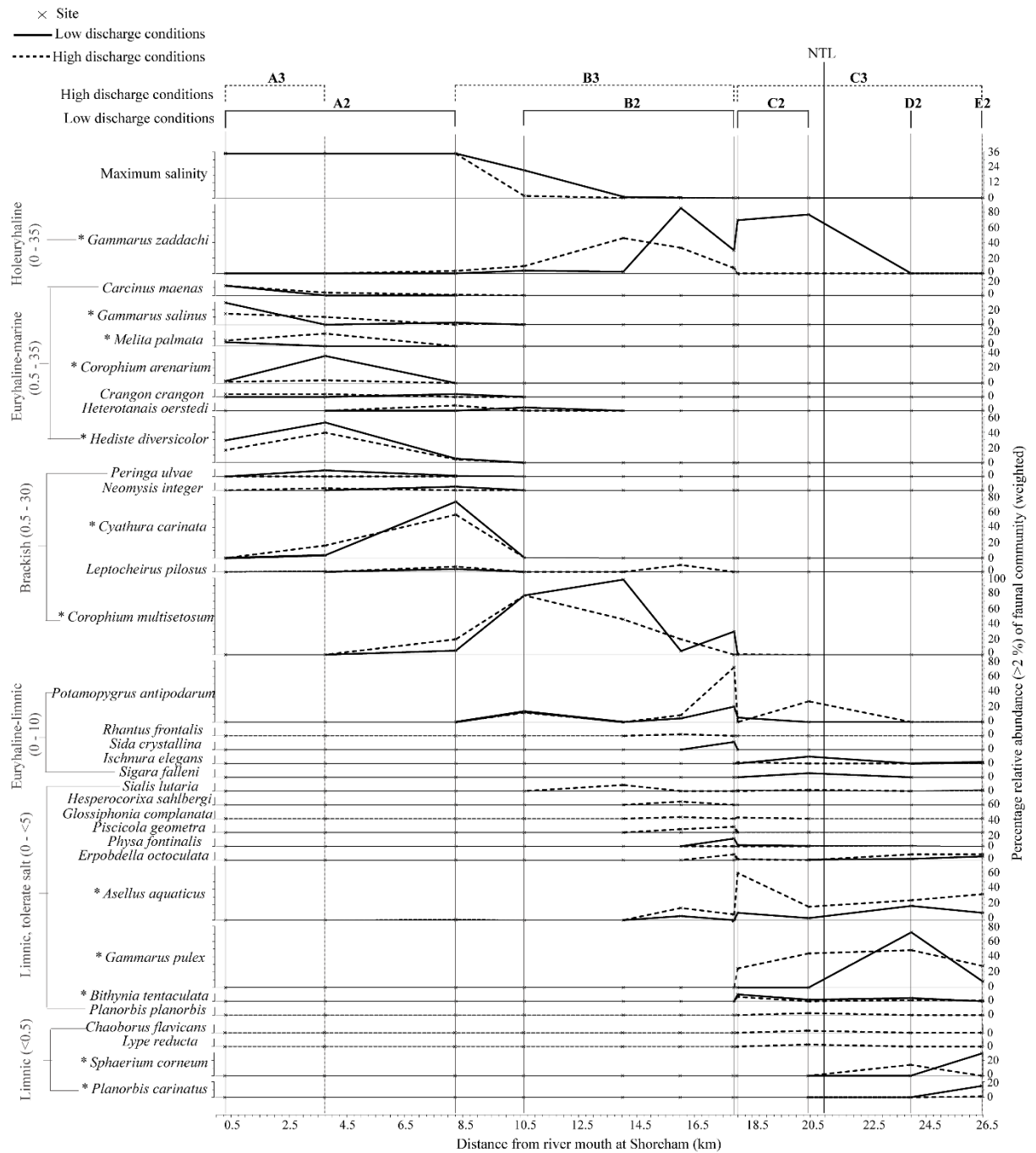


Figure 3. River Adur summary diagram of species distributions, maximum salinity and significant site clusters ( $p < 0.05$ ) under high and low discharge conditions with distance from the river mouth. Species shown occur at  $>2\%$  abundance in one or more samples and are separated into salinity tolerance groupings. \*Species which contributed to the greatest dissimilarity ( $<7\%$ ) between clusters.

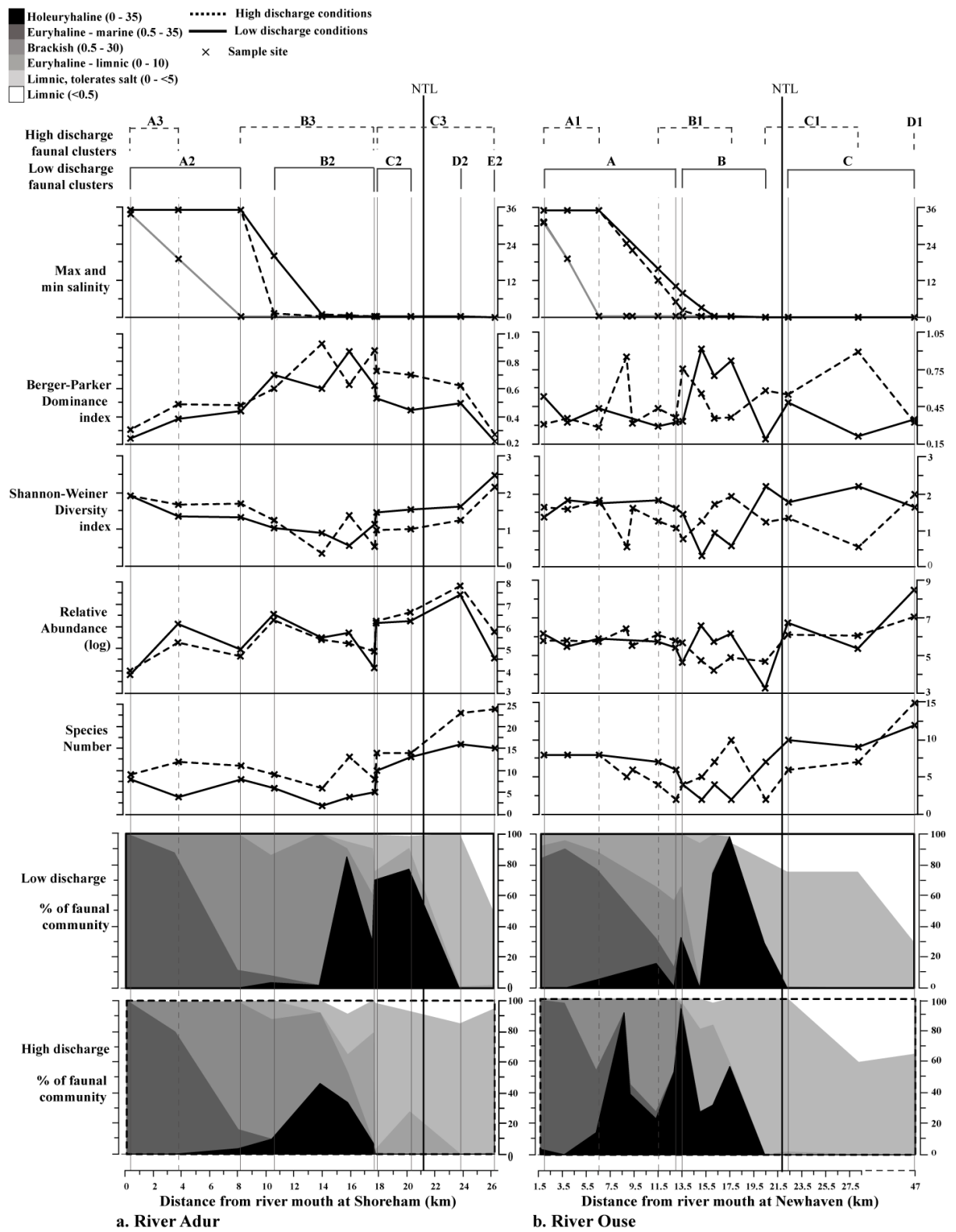


Figure 4. Summary diagrams of salinity parameters, significant site clusters ( $p < 0.05$ ), community composition indices and relative abundance of salinity tolerance groups with distance from the river

mouth under low and high discharge conditions (i.e. high and low saline incursion extents) for the River Adur (a) and River Ouse (b).

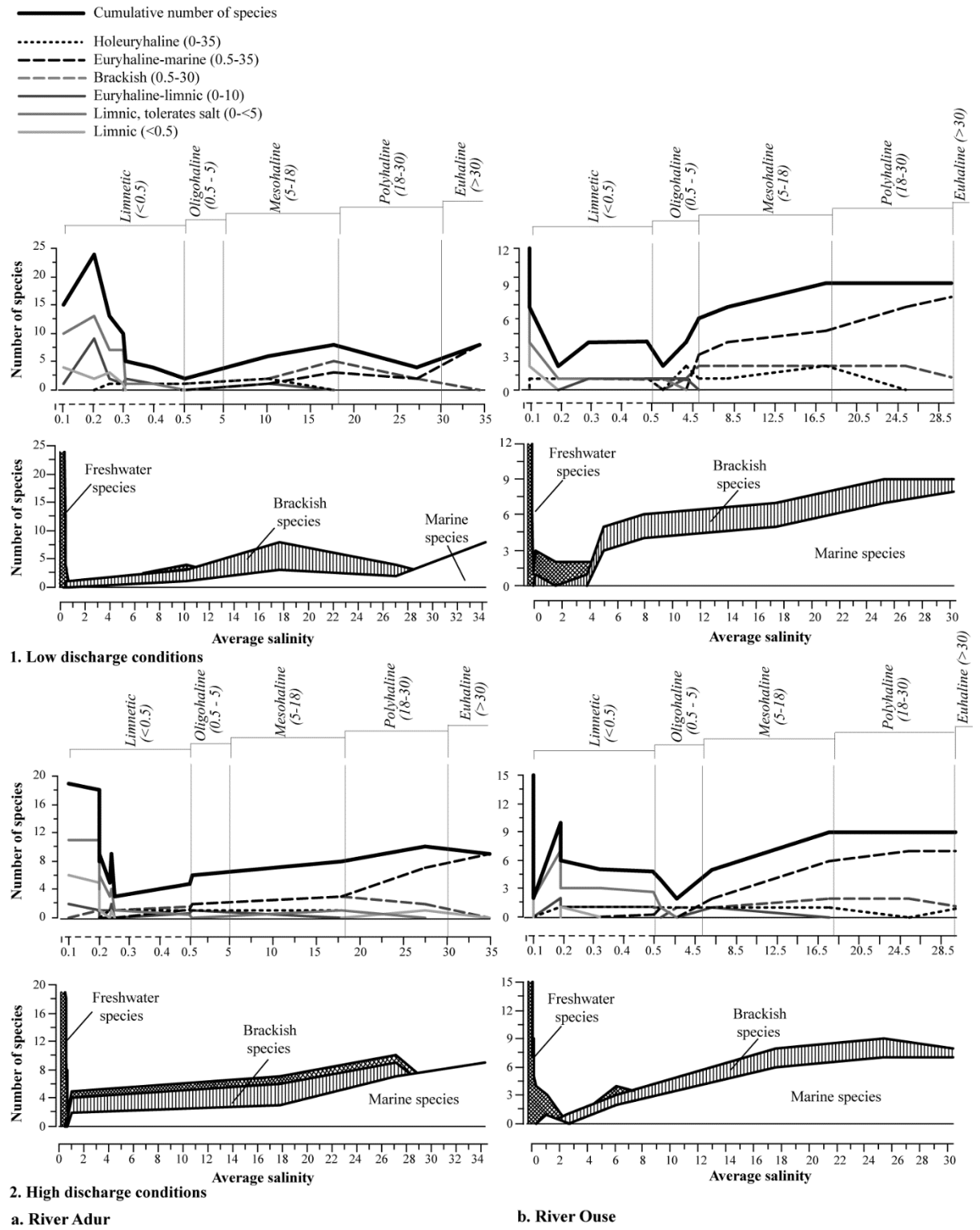


Figure 5. Modified Remane diagrams showing number of species per salinity tolerance grouping along the average salinity gradient of the River Adur (a) and River Ouse (b) under low (1) and high (2) discharge conditions.

### 3.2 Environment-species relationships

Under low and high discharge conditions, saltwater penetrated 16.98 km and 13.25 km into the Adur estuary and 16.06 km and 14.91 km into the River Ouse estuary respectively; a reduction in incursion extent of 3.73 km for a  $0.52 \text{ m}^3 \text{ s}^{-1}$  reduction in river discharge in the Adur and 1.15 km for a  $0.7 \text{ m}^3 \text{ s}^{-1}$  reduction in the Ouse (Table 2). A corresponding reduction in the maximum (high tide) salinity gradient was also recorded.

In the Adur and Ouse estuaries there was a clear division into lower and upper estuarine zones (at 14.06 km and 13.44 km respectively). The lower estuaries were characterised by high maximum salinities, macroalgal cover, high dissolved oxygen concentration (63–91%) and poorly sorted sediment (silty mud with sand containing shells and gravel) with a high calcium carbonate (up to 72%) and low organic content (2–5%). At sites O2–O5 on the lower Ouse estuary, a surface layer of coarse sediment (chalk or limestone riprap) had been used to stabilise the channel banks (Environment Agency, 2010). In contrast, the upper Adur and Ouse estuaries were characterised by low maximum salinity (3.3) to tidal limnetic (<0.5) conditions, a shift from saltmarsh vegetation to emergent macrophytes, relatively low dissolved oxygen concentration (6–67%) and fine grained sediments (silty mud) with decreasing calcium carbonate content (17–3%) and increasing organic content (2–21%) (See supplementary material Figure 1 for summary of environmental variables).

A DCCA of the combined macrofaunal and environmental data showed a distinct clustering of samples within the biplot and the location of major faunal changes within and between and the Adur and Ouse under both discharge conditions (Figure 6). The pattern of species distributions indicates a strong salinity signal over the marine to freshwater transition, with the transition from euryhaline-marine to brackish to limnic species identifiable from left to right within the biplot, with holeuryhaline (i.e. *Gammarus zaddachi*) and euryhaline-limnic (i.e. *Potamopyrgus antipodarum*) species occupying

central positions (Figure 6). The biplot indicates spatial and temporal shifts in faunal assemblages between discharge conditions. This is most clear (based on biplot position) in the mid to upper-estuary sites (O6-O12 & A4-A10), with lower estuary sites showing less difference between discharge regimes (Figure 6). The general pattern of faunal distributions suggested that these two rivers were broadly comparable in terms of the resident macroinvertebrate species recorded and their relationships with environmental variables.

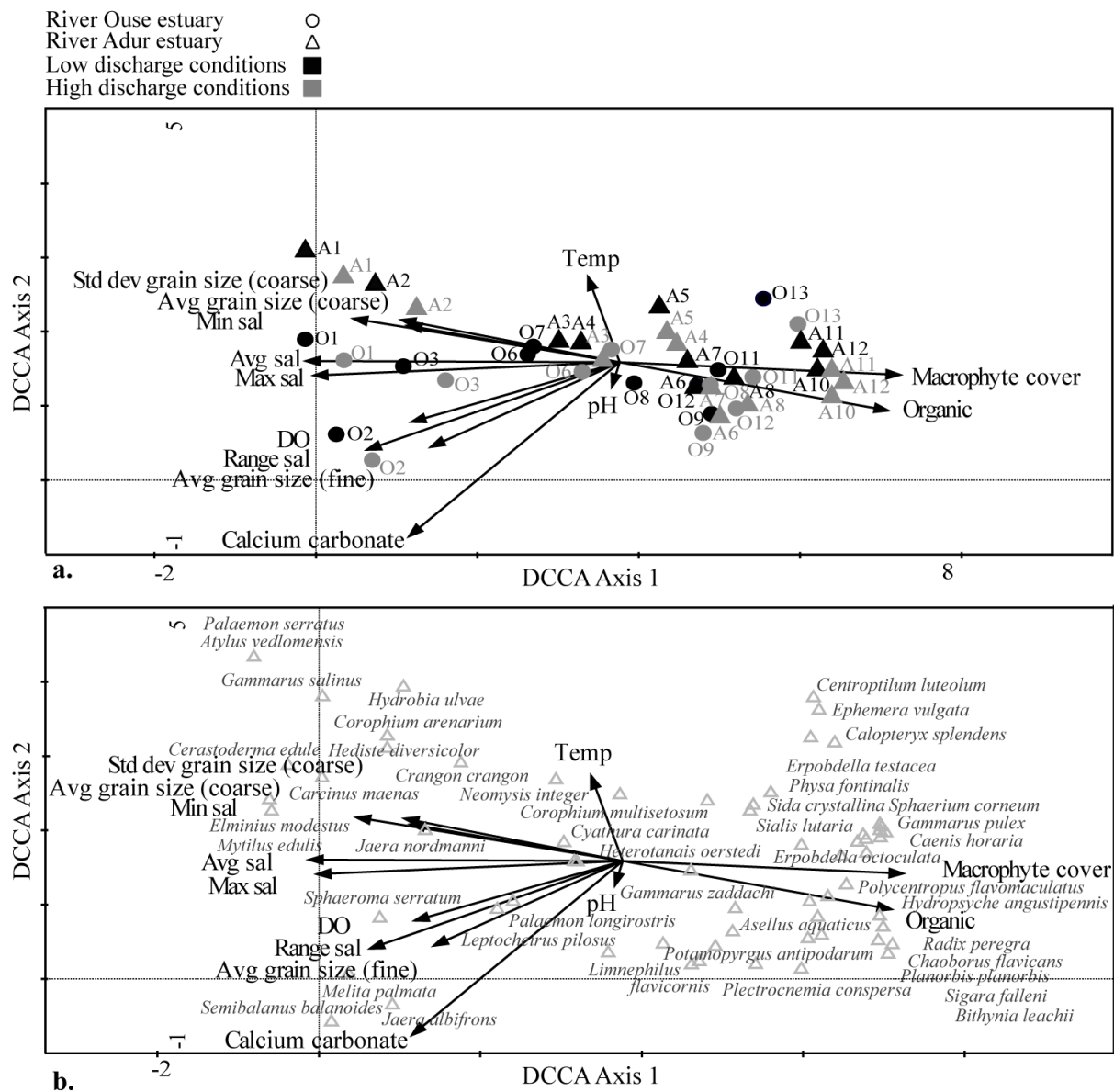


Figure 6. Detrended Canonical Correspondence Analysis (DCCA) triplot for the combined faunal dataset of the River Adur and River Ouse (sites O1 – O13), under low and high discharge conditions, showing selected environmental variables with sites (a.) and most abundant species (b.).

DCCAs performed on the Adur and Ouse datasets independently under both low and high discharge conditions, suggested that the variance explained by axis 1 was strongly driven by salinity, although co-variation was observed with macrophyte cover and organic content and sediment grain size in the Ouse estuary (Figures 7 and 8). Faunal changes were clearly identifiable along the salinity gradient (35 – 0.1) and in response to salinity differences at sites along both estuaries, although these were most pronounced in the lower zones, where the largest changes in average, maximum and minimum salinity occurred (Figures 7 and 8). A significant negative ( $p < 0.01$ ) relationship existed for all salinity parameters in both estuaries when plotted against DCA axis 1 sample scores, emphasising the importance of salinity influencing species distributions. As the lower catchment area for both rivers is situated on chalk, it is expected that calcium carbonate covaried with these salinity parameters. Whilst this might be largely coincidental, sites O2 and O3 on the Ouse estuary appeared more strongly associated with  $\text{CaCO}_3$  content and coarse grain size parameters, which may be the result of shell deposits and/or human modification of the channel at these sites (i.e. addition of chalk cobbles for bank stabilisation; see supplementary material Figure 1). Salinity was inversely related to organic content and macrophyte cover, which were important parameters in the upper estuary and above the NTL (Figures 7 and 8).



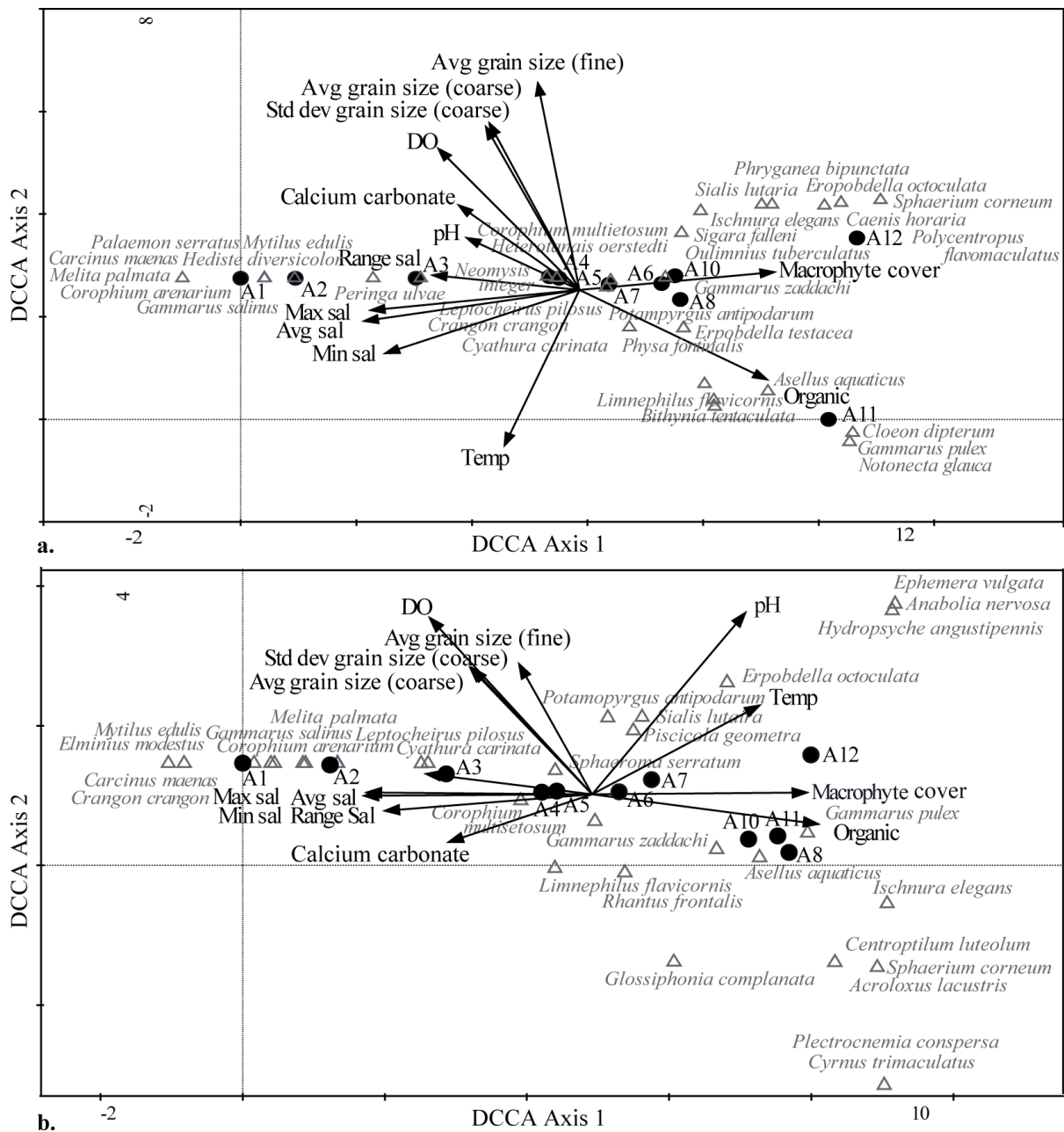


Figure 7. Detrended Canonical Correspondence Analysis (DCCA) triplot of the River Adur under low (a) and high (b) discharge conditions, showing selected environmental variables and selected most abundant macroinvertebrate species.

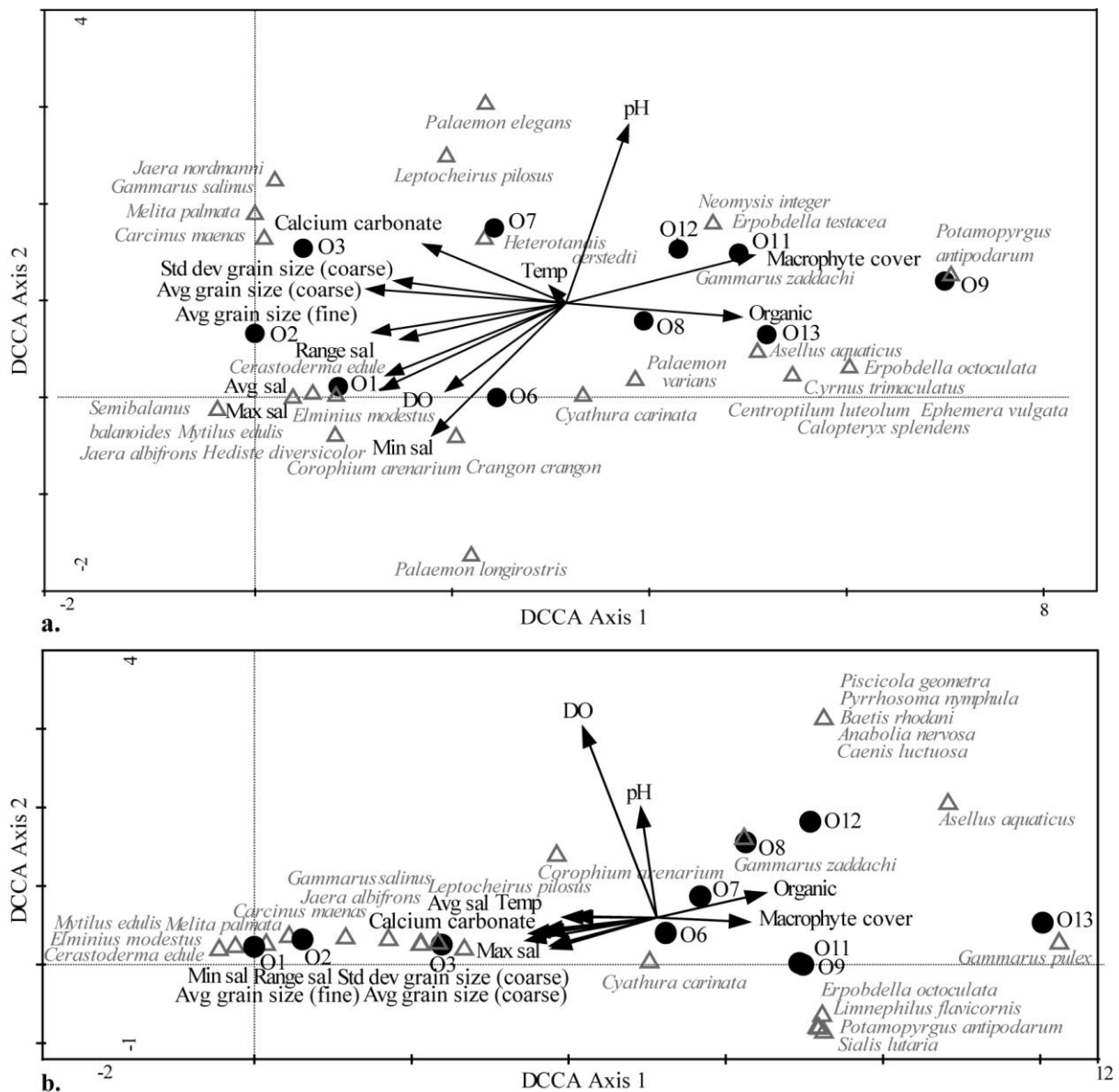


Figure 8. Detrended Canonical Correspondence Analysis (DCCA) triplot of the River Ouse estuary (sites O1 – O13) under low (a) and high (b) discharge conditions, showing selected environmental variables and selected most abundant macroinvertebrate species.

### 3.3 Future saline incursion projections

Projected RSLR under the SRES A1FI scenario for the years 2020, 2050 and 2080 resulted in an increase in salinities and the upstream extent of saline incursion in the Adur and Ouse estuaries when compared to current salinity profiles (Table 2). However, these increases were relatively small, even for the greatest projected RSLR (0.677 m; 95<sup>th</sup> %ile for 2080) under low discharge conditions. In the

Adur estuary this RSLR resulted in a 0.32 km and 0.78 km increase in saline incursion between low and high discharge conditions respectively, compared to 0.15 km and 0.89 km in the Ouse estuary (Table 2). The small increases predicted for both estuaries under low discharge conditions (compared to high) is probably due to the influence of increasing bed gradient in the upper estuary. This is reflected in the Ouse estuary where an artificial increase in gradient at a cut-through channel acts as a partial barrier to the upstream ingress of saline water (Figure 1). The differences in salinity and saline incursion extent recorded between discharge conditions highlight the importance of river flow in determining salinities in these estuaries (Table 2). It is important to note, however, that neither projected increases in tidal amplitude (related to RSLR) or extreme tide height events (i.e. storm surges) were included in these projections, which are likely to increase salinity and saline incursion extents projected for these estuaries.

Table 2. Recorded and predicted saline incursion extents in the River Ouse and Adur estuaries under low and high discharge conditions for the SRES: A1FI RSLR scenarios for the years 2020, 2050 and 2080.

			Saline incursion extent (95 <sup>th</sup> %ile, km)	
River Ouse estuary	Year	RSLR (5 <sup>th</sup> -95 <sup>th</sup> %ile, m)	Low discharge conditions (0.72 m <sup>3</sup> s <sup>-1</sup> ) (km)	High discharge conditions (1.43 m <sup>3</sup> s <sup>-1</sup> ) (km)
	2008	-	16.06	-
	2009	-	-	14.91
	2020	0.53 – 0.176	16.11	15.3
	2050	0.116 – 0.402	16.17	15.6
	2080	0.188 – 0.677	16.21	15.8
River Adur estuary	Year	RSLR (5 <sup>th</sup> -95 <sup>th</sup> %ile, m)	Low discharge conditions (0.73 m <sup>3</sup> s <sup>-1</sup> ) (km)	High discharge conditions (1.24 m <sup>3</sup> s <sup>-1</sup> ) (km)
	2008	-	16.98	-
	2009	-	-	13.25
	2020	0.53 – 0.176	16.99	13.79
	2050	0.116 – 0.402	17.07	13.94
	2080	0.188 – 0.677	17.30	14.03

#### 4 Discussion

Salinity is the primary environmental variable driving species distributions and community composition in estuaries (Attrill, 2002; Bulger et al., 1993; Elliott and Whitfield, 2011; Remane and Schlieper, 1971;

Whitfield et al., 2012) and large increases in salinities (in response to reductions in river discharge) have resulted in upstream shifts in the distributions of brackish and marine species and the local loss of freshwater-derived species (Attrill et al., 1996; Bessa et al., 2010; Herborg et al., 2005; Kingsford et al., 2011). As shown here, once river flows increase and salinities subsequently decrease, euryhaline-limnic and limnic salt-tolerating freshwater species repopulate these upper estuarine areas via downstream drift (Attrill et al., 1996). In the Adur and Ouse estuaries the decrease in salinities and saline incursion between low and high discharge conditions resulted in a downstream shift in the distribution of some species thus changing community composition indices. The extent of these changes, however, differed within and between the Adur and Ouse estuaries, indicating a hierarchical response of the benthos to both environmental and biological variables to varying degrees (Ferraro and Cole, 2012).

In the lower to mid zones of both estuaries, the distributions of most euryhaline-marine and brackish species were closely associated with coarse grained sediment (i.e. >4mm; i.e. granules, pebbles and cobbles) with the transition from sandy mud with gravel to fine grained silty mud apparently a barrier to the upstream distributions of some of these species, particularly in the Adur estuary, where the effect may have been observed on the community composition (low diversity, high dominance zone; Remane 1934), usually linked to salinity (Whitfield et al., 2012). This sediment boundary 'effect' was less apparent in the Ouse estuary, where anthropogenic modification of the estuary banks extended coarse grained sediment (i.e. chalk cobbles) further upstream. The observed association between grain size and the distribution of euryhaline-marine and brackish water species may be related to habitat heterogeneity, food retention and the refuge potential of pebbles and cobbles, providing protection against aerial exposure (desiccation), predation and access to higher interstitial salinities in the estuary at low tide (Fischenich, 2003; Gray and Elliott, 2009; Hayward and Ryland, 1995; Lincoln, 1979; Williams and Hamm, 2002). This refuge function may extend the upstream range of euryhaline-marine and brackish species into areas of the estuary which would otherwise be outside their tolerance range (e.g. *G. salinus*, *M. palmata*, *C. maenas* and *L. pilosus* were observed partially buried in the sediment under stones and cobbles in sites with tidal limnetic salinities at low tide). The interstitial salinity of intertidal sediments

varies with season and large-scale changes in river flow (Chapman and Brinkhurst, 1981; Wolff, 1973). The downstream shift in these species recorded in the River Ouse under high discharge conditions, could therefore indicate a reduction in both the maximum salinity of the overlying water at high tide, and the sediment interstitial salinity at low tide.

This sediment boundary may limit future upstream migration of these species in response to predicted increases in salinity and saline incursion. In both estuaries, the low diversity, high dominance, mid to upper estuarine zones were inhabited by species that can cross these sediment habitat boundaries (i.e. inhabit both mixed and fine grained sediments) and can tolerate the physiologically challenging mid to low maximum salinities (0.41 - 8) experienced at these sites (e.g. the estuarine ‘specialists’ *G. zaddachi*, *C. carinata*, *C. multisetosum* and *P. antipodarum*; Alonso and Castro-Díez, 2008; Barnes, 1994; Gérard et al., 2003; Lincoln, 1979). As such, rather than increasing salinities directly reflecting a shift in species distributions and community composition indices as per species salinity tolerances (as per Remane, 1934); these low diversity, high dominance mid to upper estuarine zones may extend upstream.

In the Ouse estuary, the zone of lowest faunal diversity and highest dominance was located around the freshwater-seawater interface (FSI), which shifted downstream between low and high discharge conditions. The FSI has been highlighted as a key site for physical, chemical and biological interactions within the water column, but is not typically associated with zones of lowest diversity (Deaton and Greenberg, 1986; McLusky and Elliott, 2004; Rundle et al., 1998; Uncles, 2003). These zones have been predicted to exist from 5 to 8 (often termed the area of ‘critical salinity’ or horohalnicum), which is believed to represent an ecophysiological boundary at the point at which limnic species become intolerant to increases in salinity and only a few euryhaline-marine and brackish species can survive (Deaton and Greenberg, 1986; Remane and Schlieper, 1971; Telesh and Khlebovich, 2010; Wolff, 1973). With the exception of *P. antipodarum*, no euryhaline-limnic and only a small number of limnic salt-tolerating species (i.e. *Eropbdella testacea*, *E. octoculata*, *A. aquaticus*, *Potamopyrgus flavomaculatus* and *S. lutaria*) were recorded in the FSI zones, despite being within these species reported salinity tolerances. This may be due to the fluctuating

physiochemical conditions (in addition to salinity) experienced at the FSI over a tidal cycle (i.e. increased turbidity, decreased oxygen content and the biogeochemical processes at salinities of around 1 – 2; McLusky, 1993; Uncles, 2003), compared to the comparatively stable tidal limnetic sites in the upper estuary (Uncles and Stephens, 1993).

The ability of limnic-derived species to inhabit the FSI and tidal limnetic zones potentially indicates a degree of tolerance and/or adaptability to fluctuating physiochemical tidal conditions (e.g. increased turbidity, oscillating water levels, decreased oxygen content and changing current velocities and directions; Rundle et al., 1998; Schuchardt et al., 1993a) and low salinities that are currently not widely recognised (Williams and Williams, 1998b). In the absence of extreme salinity increases (e.g. driven by droughts and storm surges) or ‘squeezing’ of the tidal limnetic zone (i.e. against in-stream engineering structures such as weirs/ dams), some of these species may persist in tidal conditions where salinity increases are gradual, particularly in estuaries and rivers where abiotic environmental factors (such as substratum composition) provide suitable habitat and refuges for these species (Williams and Hamm, 2002). For example, some studies have shown that limnic macroinvertebrate species have considerable physiological capacities to tolerate saline conditions (Berezina, 2003; Chadwick and Feminella, 2001; Chadwick et al., 2002; Kefford et al., 2007), particularly aquatic insects, which have traditionally been viewed as the most sensitive to increases in salinity, but most frequently overlooked in estuaries (Williams, 2009). Several of these taxa have been shown to function normally in brackish estuarine environments (Blinn and Ruiter, 2006; Müller, 1980; Piscart et al., 2005; Williams, 2009; Williams and Hamm, 2002; Williams and Williams, 1998a). As such, the response of these fauna may be more complex and occur over longer time periods than is currently assumed, particularly as the physiological mechanisms that allow species and populations to survive saltwater incursion (and other climate stressors, such as temperature, which may act synergistically) are still not fully understood and neither are the time-scales on which different physiological and evolutionary mechanisms could operate (Tills et al., 2010). The role of TFZs (and resident limnic-derived fauna) on the structure and functioning of estuaries has not been quantified, however any loss or change in these areas is likely to be detrimental to estuarine food-web function (Williams and

Williams, 1998b) and physical, chemical and biological processes essential to ecosystem health and the continued provision of ecosystem services (Schuchardt et al., 1993b).

The current study has emphasised the effect of salinity, related to tidal incursion, as the primary environmental driver within estuaries. However, salinity clearly acts in a hierarchy with substratum type; the latter being of importance due to its role in providing habitat diversity, acting as a refuge and retaining food. Superimposed on these factors are biotic relationships of competition and predator-prey relationships. For example, the observed downstream shift of the limnic-derived *G. pulex* in both estuaries under high discharge conditions may explain the downstream migration of the holeuryhaline *G. zaddachi* (and subsequently the distribution of the euryhaline-marine *G. salinus* in the Ouse estuary) due to interspecific competition forced by the downstream migration of competing congeners (Kolding, 1986; Korpinen and Westerbom, 2009; Lincoln, 1979). These follow the scheme outlined by Wolanski & Elliott (2015) whereby the environment-biology relationships create and fill the set of niches in both the water column and benthic substrata and then the biology-biology relationships modify the resultant community. This complex set of relationships challenges the use of, and assumption that, species salinity tolerances alone will determine species distributions and community compositional change associated with future climate-driven increases in salinity and saline incursion. This is supported by the disparity between recorded species distributions and projected distributions based on salinity tolerance ranges. This may also reflect the current poor knowledge regarding the salinity tolerances of estuarine (particularly limnic-derived) species.

RSLR projections increased salinities and the extent of saline incursion in the Adur and Ouse and similar estuaries but these increases were moderate, even when based on the greatest projection of RSLR and low summer discharge conditions. However, in estuaries where river flow mainly determines salinity, reductions in river flow may be more critical than projected increases in relative sea level in determining future saline incursion extents, with only small differences between summer and winter discharges in the Adur and Ouse estuaries ( $0.52 \text{ m}^3 \text{ s}^{-1}$  and  $0.7 \text{ m}^3 \text{ s}^{-1}$ ), resulting in large differences in salinities and saline incursion (3.73 km and 1.15 km). Under future climate change, summers are projected to be warmer and drier, resulting in reductions in river discharge both directly and indirectly

through reductions in reservoir levels (through increases in evaporation), increased abstraction (for domestic, agricultural and urban use) and an increase in evapotranspiration and soil moisture deficits, reducing the volume and distribution of water to groundwater recharge and run-off to river systems (Herrera-Pantoja and Hiscock, 2008; IPCC, 2013; Murphy et al., 2009; Robins et al., 2016; Wilby et al., 2010). In the 2080s (under high emissions), long term mean annual potential groundwater recharge in SE England (the study area) is predicted to decrease by 40% (with decreases from 2011 to 2100 in summer and winter) together with a marked decrease in summer river flows (Herrera-Pantoja and Hiscock, 2008). In contrast warmer and wetter winters (Murphy et al., 2009; Telesh et al., 2011) may increase river discharge (and groundwater recharge), which would act to reduce salinities and result in extreme seasonal differences in saline incursion extents between summer and winter (Robins et al., 2016). These changes may both reflect and be caused by changes to the North Atlantic oscillation (NAO) patterns (Attrill and Power, 2002). This may increase flash floods but as yet the influence of high-intensity, episodic events rather than chronic salinity changes on the fauna is as yet not known. Seasonal differences in saline incursion extents may make the distributions of mobile estuarine benthic species more variable and unable to progress beyond early benthic community succession as favourable conditions extend and contract (Santos et al., 1996; Ysebaert et al., 2005).

Despite the above, the effect of changing climate on increased winter river flows might be negated by future increased abstraction of freshwater to support growing coastal populations (particularly in SE England), which has been estimated to considerably exceed any future effects of climate change on river flow regimes (Lester et al., 2011; Vorosmarty et al., 2000; Vorosmarty et al., 2010). For example, applying projected modelled reductions of 32 % (as per Romanowicz et al., 2006) to the summer river discharge of the River Adur, results in over five times the increase in saline incursion predicted for RSLR alone (from 0.32 km to 2 km for a 67 cm RSLR). It is also of note that these tide and salinity profiles have been determined under reference conditions (MHWS/MLWS tide heights and moderate low and high freshwater discharge regimes) and as such do not factor in extreme events (e.g. highest tides, storm surges, drought and flood). These profiles are therefore likely to underestimate the full extent of saline incursion under an extreme combination of these conditions.



## **5 Conclusions**

This research clearly indicates that salinity is the primary environmental driver of benthos composition in the Adur and Ouse estuaries. However, the response of estuarine benthic communities to climate-driven increases in saline incursion over the long-term should not be assumed to simply follow patterns of species salinity tolerances. We clearly illustrate that this assumption is oversimplistic and fails to represent the complex variability of estuarine ecosystems and hierarchical relationships between the fauna and environmental (e.g., substratum) and biological drivers (e.g., competition).

Tidal freshwater zones and their associated fauna are vulnerable to future increases in salinity and its incursion upstream; although the fauna probably possess greater tolerances to salinity variability than has previously been recognised and may persist, particularly where changes are gradual and the zones within the estuary are unbounded. The long-term repercussions of future climate driven changes in salinity and saline incursion on the structure and function of estuaries are largely unknown but requires much greater attention to enable the development of sustainable management strategies to safeguard estuarine ecosystem health and resilience into the future.

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## Appendix A. Supplementary data

Table 1. Macroinvertebrate species recorded in the River Ouse and River Adur under high and low discharge conditions. Species listed with their allocated salinity tolerance grouping and primary literature sources.

Species	Order	Class	Source	Species	Order	Class	Source
<i>Acroloxus lacustris</i>	Gastropoda	l(el)	Macan & Cooper, 1977; Kerney, 1999; Carlsson, 2006.	<i>Peringa ulvae</i>	Gastropoda	b	Barnes, 1994; Hayward & Ryland, 1995; Kerney, 1999.
<i>Agabus bipustulatus</i>	Coleoptera	l(el)	Nicol, 1935; Friday, 1988; Sutcliffe, 1961b; Barnes <i>et al.</i> , 1971; 1994.	<i>Hydropsyche angustipennis</i>	Trichoptera	l(el)	Edington & Hildrew, 2005; Bätthe & Coring, 2010.
<i>Anabolia nervosa</i>	Trichoptera	l(el)	Sutcliffe, 1961(2); Blasius & Merritt, 2002; Wallace <i>et al.</i> , 2003.	<i>Hydropsyche pellucidula</i>	Trichoptera	l(el)	Edington & Hildrew, 2005; Piscart <i>et al.</i> , 2005.
<i>Anacaena globulus</i>	Coleoptera	l	Friday, 1988.	<i>Ischmura elegans</i>	Odonata	el	Ward, 1992; Barnes, 1994; Merritt <i>et al.</i> , 1996.
<i>Asellus aquaticus</i>	Isopoda	l(el)	Lagerspetz & Mattila, 1961; Williams, 1962a; Sutcliffe, 1974; Moon & Harding 1982; Gledhill <i>et al.</i> , 1993; Barnes, 1994; Piscart <i>et al.</i> , 2010.	<i>Jaera albifrons</i>	Isopoda	em	Jones, 1972; Naylor, 1972; Barnes, 1994; Hayward & Ryland, 1995.
<i>Athripsodes cinereus</i>	Trichoptera	l	Wallace <i>et al.</i> , 2003.	<i>Jaera nordmanni</i>	Isopoda	he	Barnes, 1994. Naylor, 1972. Hayward & Ryland, 1995, Naylor & Slinn, 1958.
<i>Atylus vedlomensis</i>	Amphipoda	em	Barnes, 1994; Hayward & Ryland, 1995.	<i>Leptocheirus pilosus</i>	Amphipoda	b	Lincoln, 1979; Barnes, 1994; Wolf <i>et al.</i> , 2009.
<i>Baetis rhodani</i>	Ephemeroptera	l(el)	Macan, 1979; Galardo-Mayenco, 1994; Williams & Williams 1998b; Rundle <i>et al.</i> , 1998.	<i>Libella fulva</i>	Odonata	l	Merritt <i>et al.</i> , 1996.
<i>Bithynia leachii</i>	Gastropoda	l	Macan & Cooper, 1977; Kerney, 1999; Wolf <i>et al.</i> , 2009.	<i>Limnephilus flavicornis</i>	Trichoptera	l	Wallace <i>et al.</i> , 2003.
<i>Bithynia tentaculata</i>	Gastropoda	l(el)	Klekowski, 1961; Kerney, 1999; Costil <i>et al.</i> , 2001; Berezina, 2003; Sousa <i>et al.</i> , 2005.	<i>Limnephilus lunatus</i>	Trichoptera	l(el)	Vierssen & Verhoeven, 1983; Wallace <i>et al.</i> , 2003.
<i>Brachycentrus subnubilus</i>	Trichoptera	l	Edington & Hildrew, 2005.	<i>Limnius volckmari</i>	Coleoptera	l	Friday, 1988.
<i>Caenis horaria</i>	Ephemeroptera	l(el)	Lingdell & Müller, 1982; Macan, 1979; Wolf <i>et al.</i> , 2009.	<i>Omphiscola glabra</i>	Gastropoda	l	Macan & Cooper, 1977; Kerney, 1999; Costil <i>et al.</i> , 2001.
<i>Caenis luctuosa</i>	Ephemeroptera	l(el)	Attrill, 1998; Macan, 1979; Galardo-Mayenco, 1994.	<i>Radix peregra</i>	Gastropoda	l(el)	Nicol 1938; Kerney, 1999; Costil <i>et al.</i> , 2001.
<i>Calopteryx splendens</i>	Odonata	l(el)	Merritt <i>et al.</i> , 1996; Wolf <i>et al.</i> , 2009; Bätthe & Coring, 2010; Piscart <i>et al.</i> , 2011.	<i>Lype reducta</i>	Trichoptera	l	Edington & Hildrew, 2005.
<i>Carcinus maenas</i>	Decapoda	em	Crothers, 1988; Barnes, 1994; Hayward & Ryland, 1995.	<i>Melita palmata</i>	Amphipoda	em	Lincoln, 1979; Barnes, 1994; Hayward & Ryland, 1995.
<i>Centropilum luteolum</i>	Ephemeroptera	l	Macan, 1979; Galardo-Mayenco, 1994; Wolf <i>et al.</i> , 2009.	<i>Mytilus edulis</i>	Bivalvia	em	Hayward & Ryland, 1995.
<i>Centrostoma edule</i>	Bivalvia	em	Barnes, 1994; Hayward & Ryland, 1995.	<i>Neomysis integer</i>	Mysida	b	Tattersall & Tattersall, 1951; Barnes, 1994; Hayward & Ryland, 1995.
<i>Chaoborus flavicans</i>	Diptera	l	Smith, 1989.	<i>Neureclipsis bimaculata</i>	Trichoptera	l	Edington & Hildrew, 2006.
<i>Cloeon dipterum</i>	Ephemeroptera	l(el)	Macan, 1979; Lingdell & Müller, 1982; Barnes, 1994; Wolf <i>et al.</i> , 2009.	<i>Notonecta glauca</i>	Hemiptera	l(el)	Macan, 1965; Vierssen & Verhoeven, 1983; Barnes, 1994.
<i>Corophium arenarium</i>	Amphipoda	em	Barnes, 1994; Hayward & Ryland, 1995.	<i>Oulimnius tuberculatus</i>	Coleoptera	l(el)	Friday 1988; Bätthe & Coring, 2010.
<i>Corophium multisetosum</i>	Amphipoda	b	Queiroga, 1990; Barnes, 1994; Hayward & Ryland, 1995.	<i>Palaemon elegans</i>	Decapoda	em	Smaldon, 1993; Barnes, 1994; Hayward & Ryland, 1995.
<i>Crangon Crangon</i>	Decapoda	em	Smaldon, 1993; Barnes, 1994; Hayward & Ryland, 1995.	<i>Palaemon longirostris</i>	Decapoda	he	Hayward & Ryland, 1990; Smaldon, 1993; Galardo-Mayenco, 1994; Barnes, 1994.
<i>Cyathura carinata</i>	Isopoda	b	Naylor, 1972; Barnes, 1994; Hayward & Ryland, 1995.	<i>Palaemon serratus</i>	Decapoda	em	Hayward & Ryland, 1990; Smaldon, 1993; Barnes, 1994.
<i>Cyrnus trimaculatus</i>	Trichoptera	l(el)	Edington & Hildrew, 2005; Piscart <i>et al.</i> , 2005; Bätthe & Coring, 2010.	<i>Palaemonetes varians</i>	Decapoda	he	Lofts, 1956; Hayward & Ryland, 1990; Smaldon, 1993; Barnes, 1994.
<i>Elminius modestus</i>	Sessilia	em	Rainbow, 1984; Hayward & Ryland, 1995; Barnes, 1995.	<i>Phryganea bipunctata</i>	Trichoptera	l	Wallace <i>et al.</i> , 2003.
<i>Elmis aenea</i>	Coleoptera	l(el)	Friday 1988; Williams & Williams, 1998b.	<i>Physa fontinalis</i>	Gastropoda	l(el)	Macan & Cooper, 1977; Kerney, 1999; Costil <i>et al.</i> , 2001; Wolf <i>et al.</i> , 2009.
<i>Ephemera danica</i>	Ephemeroptera	l	Macan, 1979; Galardo-Mayenco, 1994.	<i>Piscicola geometra</i>	Hirudinea	l(el)	Mann & Watson, 1964; Hægge <i>et al.</i> , 2003; Wolf <i>et al.</i> , 2009.
<i>Ephemera vulgata</i>	Ephemeroptera	l	Macan, 1979.	<i>Planorbis carinatus</i>	Gastropoda	l	Macan & Cooper, 1977; Kerney, 1999.
<i>Erpobdella octoculata</i>	Hirudinea	l(el)	Mann & Watson, 1964; Berezina, 2003; Wolf <i>et al.</i> , 2009.	<i>Planorbis planorbis</i>	Gastropoda	l(el)	Kerney, 1999; Costil <i>et al.</i> , 2001; Berezina, 2003.
<i>Erpobdella testacea</i>	Hirudinea	l(el)	Mann & Watson, 1964; Attrill, 1998.	<i>Platycnemis pennipes</i>	Odonata	l	Merritt <i>et al.</i> , 1996.
<i>Gammarus pulex</i>	Amphipoda	l(el)	Gledhill <i>et al.</i> , 1993; Barnes, 1994; Piscart <i>et al.</i> , 2011.	<i>Plectrocnemia conspersa</i>	Trichoptera	l	Wallace <i>et al.</i> , 2003.
<i>Gammarus salinus</i>	Amphipoda	em	Lincoln, 1979; Barnes, 1994; Hayward & Ryland, 1995.	<i>Polycentropus flavomaculatus</i>	Trichoptera	l(el)	Williams & Williams, 1998b; Wolf <i>et al.</i> , 2009; Bätthe & Coring, 2010.
<i>Gammarus zaddachi</i>	Amphipoda	he	Lincoln, 1979; Gledhill <i>et al.</i> , 1993; Barnes, 1994; Hayward & Ryland, 1995.	<i>Potamopyrgus antipodarum</i>	Gastropoda	el	Winterbourn, 1970; Siegismund & Hylleberg 1987; Barnes, 1994; Kerney, 1999.
<i>Glossiphonia complanata</i>	Hirudinea	l(el)	Nicol, 1938; Mann & Watson, 1964; Barnes <i>et al.</i> , 1971.	<i>Pyrrhosoma nymphula</i>	Odonata	el	Butler & Popham, 1958; Merritt <i>et al.</i> , 1996.
<i>Gyraulus laevis</i>	Gastropoda	l(el)	Macan & Cooper, 1977; Kerney, 1999.	<i>Rhantus frontalis</i>	Coleoptera	el	Friday, 1988; Greenwood & Wood, 2003.
<i>Halesus radiatus</i>	Trichoptera	l	Wallace <i>et al.</i> , 2003.	<i>Rhyacophila dorsalis</i>	Trichoptera	l(el)	Williams & Williams, 1998b; Edington & Hildrew, 2006.
<i>Haliplus flavicollis</i>	Coleoptera	l(el)	Friday 1988; Barnes, 1994.	<i>Semibalanus balanoides</i>	Sessilia	em	Rainbow 1984; Barnes, 1994; Hayward & Ryland, 1995.
<i>Haliplus ruficollis</i>	Coleoptera	l(el)	Vierssen & Verhoeven, 1983; Friday, 1988.	<i>Sericostoma personatum</i>	Trichoptera	l(el)	Williams & Williams 1998b; Wallace <i>et al.</i> , 2003.
<i>Hediste diversicolor</i>	Polychaeta	em	Smith, 1964; Ozoh & Jones, 1990; Barnes, 1994; Hayward & Ryland, 1995; Abrantes <i>et al.</i> , 1999.	<i>Sialis lutaria</i>	Megaloptera	l(el)	Segerstråle, 1949; Shaw, 1955; Elliott, 1977.
<i>Helobdella stagnalis</i>	Hirudinea	l(el)	Nicol, 1938; Mann & Watson, 1964; Barnes, 1994; Attrill, 1998; Berezina, 2003; Wolf <i>et al.</i> , 2009.	<i>Sida crystallina</i>	Cladocera	el	Scourfield & Harding, 1966; Aladin & Potts, 1995.
<i>Helophorus dorsalis</i>	Coleoptera	l	Friday, 1988.	<i>Sigara dorsalis</i>	Hemiptera	el	Macan, 1965; Scudder, 1976.
<i>Hesperocorixa sahlbergi</i>	Hemiptera	l(el)	Scudder, 1976; Ward, 1992.	<i>Sigara falleni</i>	Hemiptera	el	Scudder, 1976; Vierssen & Verhoeven, 1983; Macan, 1965; Barnes, 1994.
<i>Heterotanais oerstedti</i>	Malacostraca	em	Hayward & Ryland, 1995.	<i>Sigara stagnalis</i>	Hemiptera	el	Macan, 1965; Scudder, 1976; Krebs, 1982; Barnes, 1994; Garrido & Munilla, 2008.
				<i>Sphaerium corneum</i>	Bivalvia	l	Killeen <i>et al.</i> , 2004.
				<i>Sphaeroma serratum</i>	Isopoda	em	Naylor, 1972; Charmantier & Charmantier-Daures, 1994; Hayward & Ryland, 1995.
				<i>Stictotarsus duodecimpustulatus</i>	Coleoptera	l	Friday, 1988.
				<i>Theodoxus fluviatilis</i>	Gastropoda	el	Barnes, 1994; Kerney, 1999; Bunje, 2005; Symanowski & Hildebrandt, 2010.
				<i>Unio pictorum</i>	Bivalvia	l	Killeen <i>et al.</i> , 2004.

**he** = marine derived taxa that tolerate the entire range of salinity from limnic to marine 0 - 35, **em** = marine taxa that tolerate a large range of salinities between 0.5 and 35, **b** = brackish water taxa that live and reproduce in brackish waters and tolerate varying salinity between 0.5 and 30, **el** = freshwater derived taxa that tolerate salinity up to 10, **l(el)** = freshwater derived taxa that tolerate salinities below 5, **l** = freshwater taxa that do not tolerate even low salinity <0.5.

Table 2. Macroinvertebrate species and relative abundances recorded in the significant ( $p < 0.05$ ) site clusters (with associated distances and maximum salinities) of the River Ouse under high and low discharge conditions. \* Limnic derived species recorded within the estuarine extent.

Low discharge conditions	High discharge conditions
<b>Cluster A (0–12.8 km, 10.3-35)</b>	<b>Cluster A1 (0–6.35 km, 35)</b>
<b>Holeuryhaline (0-35)</b> <i>Palaemon longirostris</i> (6%), <i>Jaera nordmanni</i> (1.3%), <i>Gammarus zaddachi</i> (0.2%)	<b>Holeuryhaline (0-35)</b> <i>Palaemon longirostris</i> (5.9%)
<b>Euryhaline-marine (0.5-35)</b> <i>Melita palmata</i> (22.3%), <i>Hediste diversicolor</i> (10.6%), <i>Semibalanus balanoides</i> (8%), <i>Elminius modestus</i> (5.5%), <i>Carcinus maenas</i> (3.9%), <i>Heterotanais oerstedii</i> (3.1%), <i>Gammarus salinus</i> (2%), <i>Corophium arenarium</i> (1.9%), <i>Jaera albifrons</i> (1.9%), <i>Mytilus edulis</i> (1.8%), <i>Palaemon elegans</i> (1.6%), <i>Crangon crangon</i> (1%), <i>Cerastoderma edule</i> (0.1%)	<b>Euryhaline-marine (0.5-35)</b> <i>Melita palmata</i> (30.6%), <i>Semibalanus balanoides</i> (17.2%), <i>Elminius modestus</i> (9.9%), <i>Hediste diversicolor</i> (7.8%), <i>Jaera albifrons</i> (6.2%), <i>Carcinus maenas</i> (1.5%), <i>Cerastoderma edule</i> (1.3%), <i>Corophium arenarium</i> (1%), <i>Mytilus edulis</i> (1%), <i>Gammarus salinus</i> (0.9%), <i>Sphaeroma serratum</i> (0.6%)
<b>Brackish water (0.5-30)</b> <i>Cyathura carinata</i> (15%), <i>Leptocheirus pilosus</i> (13.9%)	<b>Brackish water (0.5-30)</b> <i>Leptocheirus pilosus</i> (13.8%), <i>Cyathura carinata</i> (2.5%)
<b>Cluster B (13.4 - 20.4 km, 0.1 - 7.9)</b>	<b>Cluster B1 (11.3-17.5 km, 0.2 - 12)</b>
<b>Holeuryhaline (0-35)</b> <i>Gammarus zaddachi</i> (56.8%), <i>Palaemonetes varians</i> (0.2%)	<b>Holeuryhaline (0-35)</b> <i>Gammarus zaddachi</i> (41.2%)
<b>Brackish water (0.5-30)</b> <i>Cyathura carinata</i> (6%), <i>Neomysis integer</i> (0.7%)	<b>Euryhaline-marine (0.5-35)</b> <i>Hediste diversicolor</i> (1%), <i>Corophium arenarium</i> (0.6%)
<b>Euryhaline-limnic (0-10)</b> <i>Potamopyrgus antipodarum</i> (31%), <i>Theodoxus fluviatilis</i> (1.4%)	<b>Brackish water (0.5-30)</b> <i>Cyathura carinata</i> (37.9%)
<b>Limnic, salt tolerating (0-&lt;5)</b> <i>Erpobdella octoculata</i> * (1.2%), <i>Erpobdella testacea</i> * (0.5%), <i>Asellus aquaticus</i> * (0.4%), <i>Calopteryx splendens</i> * (0.2%), <i>Cyrrnus trimaculatus</i> * (0.2%)	<b>Euryhaline-limnic (0-10)</b> <i>Potamopyrgus antipodarum</i> * (9.2%), <i>Pyrrhosoma nymphula</i> * (0.1%)
<b>Limnic (&lt;0.5)</b> <i>Centroptilum luteolum</i> * (0.9%), <i>Ephemera vulgata</i> * (0.2%)	<b>Limnic, salt tolerating (0-&lt;5)</b> <i>Asellus aquaticus</i> * (3.7%), <i>Erpobdella octoculata</i> * (3%), <i>Anabolia nervosa</i> * (0.8%), <i>Piscicola geometra</i> * (0.3%), <i>Baetis rhodani</i> * (0.1%), <i>Caenis luctuosa</i> * (0.1%), <i>Hesperocorixa sahlbergi</i> * (0.1%), <i>Polycentropus flavomaculatus</i> * (0.1%), <i>Sialis lutaria</i> * (0.1%)
<b>Cluster C (22.37- 47.1 km, &lt;0.5)</b>	<b>Limnic (&lt;0.5)</b> <i>Succinea putris</i> * (0.1%), <i>Limnephilus flavicornis</i> * (0.1%), <i>Unio pictorum</i> * (0.1%), <i>Bithynia leachii</i> * (1.2%)
<b>Euryhaline-limnic (0-10)</b> <i>Ischnura elegans</i> (0.1%)	<b>Cluster C1 (20.39-28.22 km, &lt;0.5)</b>
<b>Limnic, salt tolerating (0-&lt;5)</b> <i>Hydropsyche angustipennis</i> (17.5%), <i>Gammarus pulex</i> (14.3%), <i>Asellus aquaticus</i> (2.8%), <i>Cyrrnus trimaculatus</i> (0.8%), <i>Bithynia tentaculata</i> (0.4%), <i>Polycentropus flavomaculatus</i> (0.2%), <i>Calopteryx splendens</i> (0.1%), <i>Erpobdella octoculata</i> (0.1%), <i>Glossiphonia complanata</i> (0.1%), <i>Helobdella stagnalis</i> (0.1%), <i>Rhyacophila dorsalis</i> (0.1%), <i>Radix peregra</i> (0.1%), <i>Gyraulus laevis</i> (0.1%), <i>Planorbis planorbis</i> (0.1%)	<b>Euryhaline-limnic (0-10)</b> <i>Ischnura elegans</i> (0.7%)
<b>Limnic (&lt;0.5)</b> <i>Neureclipsis bimaculata</i> (32.5%), <i>Sphaerium corneum</i> (26.1%), <i>Limnephilus flavicornis</i> (1.7%), <i>Ephemera danica</i> (0.5%), <i>Lype reducta</i> (0.2%), <i>Limnius volckmari</i> (0.2%), <i>Planorbis carinatus</i> (0.1%), <i>Phryganea bipunctata</i> (0.1%), <i>Bithynia leachii</i> (1.4%), <i>Athripsodes cinereus</i> (0.7%)	<b>Limnic, salt tolerating (0-&lt;5)</b> <i>Gammarus pulex</i> * (47.4%), <i>Asellus aquaticus</i> * (17.8%), <i>Anabolia nervosa</i> (6.7%), <i>Hydropsyche angustipennis</i> (3%), <i>Erpobdella octoculata</i> (1%), <i>Glossiphonia complanata</i> (1%), <i>Sialis lutaria</i> (1%)
	<b>Limnic (&lt;0.5)</b> <i>Anisus vortex</i> (11.1%), <i>Plectrocnemia conspersa</i> (3.7%), <i>Limnephilus flavicornis</i> (0.7%), <i>Brachycentrus subnubilus</i> (6.7%)
	<b>Cluster D1 (47.16 km, &lt;0.5)</b>
	<b>Limnic, salt tolerating (0-&lt;5)</b> <i>Gammarus pulex</i> (37%), <i>Hydropsyche angustipennis</i> (22%), <i>Baetis rhodani</i> (3%), <i>Asellus aquaticus</i> (1.4%), <i>Sericostoma personatum</i> (0.9%), <i>Caenis horaria</i> (0.2%), <i>Rhyacophila dorsalis</i> (0.2%), <i>Glossiphonia complanata</i> (0.1%)
	<b>Limnic (&lt;0.5)</b> <i>Neureclipsis bimaculata</i> (22.2%), <i>Sphaerium corneum</i> (8.3%), <i>Ephemera danica</i> (3.5%), <i>Limnius volckmari</i> (0.4%), <i>Halesus radiatus</i> (0.3%), <i>Limnephilus flavicornis</i> (0.3%), <i>Bithynia leachii</i> (0.1%)

Table 3. Macroinvertebrate species and relative abundances recorded in the significant ( $p < 0.05$ ) site clusters (with associated distances and maximum salinities) of the River Adur under high and low discharge conditions. \* Limnic derived species recorded within the estuarine extent.

Low discharge conditions	High discharge conditions
<b>Cluster A2 (0.32- 8.3 km, 35)</b>	<b>Cluster A3 (0.32 - 3.8 km, 35)</b>
<b>Euryhaline-marine (0.5-35)</b> <i>Hediste diversicolor</i> (42%), <i>Corophium arenarium</i> (26.3%), <i>Gammarus salinus</i> (3%), <i>Carcinus maenas</i> (1.1%), <i>Palaemon serratus</i> (0.9%), <i>Atylus vedlomensis</i> (0.7%), <i>Crangon crangon</i> (0.7%), <i>Melita palmata</i> (0.5%), <i>Mytilus edulis</i> (0.2%)	<b>Euryhaline-marine (0.5-35)</b> <i>Hediste diversicolor</i> (29.9%), <i>Elminius modestus</i> (14.2%), <i>Melita palmata</i> (12.7%), <i>Gammarus salinus</i> (12%), <i>Carcinus maenas</i> (7.5%), <i>Mytilus edulis</i> (3.7%), <i>Crangon crangon</i> (3.7%), <i>Corophium arenarium</i> (3%), <i>Cerastoderma edule</i> (1.5%)
<b>Brackish water (0.5-30)</b> <i>Cyathura carinata</i> (16%), <i>Hydrobia ulvae</i> (6.3%), <i>Neomysis integer</i> (1%), <i>Corophium multisetosum</i> (1%), <i>Leptocheirus pilosus</i> (0.7%)	<b>Brackish water (0.5-30)</b> <i>Cyathura carinata</i> (9.7%), <i>Neomysis integer</i> (1.5%)
<b>Cluster B2 (10.6-17.9 km, 0.4 - 20.2)</b>	<b>Limnic (&lt;0.5)</b> <i>Limnephilus flavicornis</i> * (0.8%)
<b>Holeuryhaline (0-35)</b> <i>Gammarus zaddachi</i> (5.6%), <i>Palaemonetes varians</i> (0.1%)	<b>Cluster B3 (8.3-17.9 km, 0.2 - 35)</b>
<b>Euryhaline-marine (0.5-35)</b> <i>Heterotanais oerstedii</i> (3.4%)	<b>Holeuryhaline (0-35)</b> <i>Gammarus zaddachi</i> (11.3%)
<b>Brackish water (0.5-30)</b> <i>Corophium multisetosum</i> (79%), <i>Cyathura carinata</i> (0.5%)	<b>Euryhaline-marine (0.5-35)</b> <i>Heterotanais oerstedii</i> (1%), <i>Hediste diversicolor</i> (0.9%), <i>Carcinus maenas</i> (0.2%)
<b>Euryhaline-limnic (0-10)</b> <i>Potamopyrgus antipodarum</i> * (11%), <i>Sida crystallina</i> * (0.1%)	<b>Brackish water (0.5-30)</b> <i>Corophium multisetosum</i> (61.3%), <i>Cyathura carinata</i> (9.2%), <i>Leptocheirus pilosus</i> (1%)
<b>Limnic, salt tolerating (0-&lt;5)</b> <i>Physa fontinalis</i> * (0.1%), <i>Asellus aquaticus</i> * (0.1%)	<b>Euryhaline-limnic (0-10)</b> <i>Potamopyrgus antipodarum</i> * (11.3%), <i>Rhantus frontalis</i> * (0.2%)
<b>Cluster C2 (17-20.5 km, &lt;0.5)</b>	<b>Limnic, salt tolerating (0-&lt;5)</b> <i>Asellus aquaticus</i> * (1.7%), <i>Piscicola geometra</i> * (0.5%), <i>Hesperocorixa sahlbergi</i> * (0.4%), <i>Glossiphonia complanata</i> * (0.2%), <i>Sialis lutaria</i> * (0.2%), <i>Erpobdella octoculata</i> * (0.2%)
<b>Holeuryhaline (0-35)</b> <i>Gammarus zaddachi</i> (74.2%),	<b>Limnic (&lt;0.5)</b> <i>Limnephilus flavicornis</i> * (0.7%), <i>Sphaeroma serratum</i> * (0.2%)
<b>Euryhaline-limnic (0-10)</b> <i>Ischnura elegans</i> (5.5%), <i>Sigara falleni</i> * (3.2%), <i>Potamopyrgus antipodarum</i> (2.1%)	<b>Cluster C3 (18-26.5 km, &lt;0.5)</b>
<b>Limnic, salt tolerating (0-&lt;5)</b> <i>Asellus aquaticus</i> * (5.3%), <i>Bithynia tentaculata</i> (4.8%), <i>Physa fontinalis</i> (1.1%), <i>Sialis lutaria</i> * (0.6%), <i>Erpobdella octoculata</i> * (0.6%), <i>Erpobdella testacea</i> * (0.4%), <i>Piscicola geometra</i> * (0.4%), <i>Oulimnius tuberculatus</i> * (0.2%), <i>Calopteryx splendens</i> * (0.2%)	<b>Brackish water (0.5-30)</b> <i>Peringa ulvae</i> (0.2%), <i>Corophium multisetosum</i> * (0.1%)
<b>Limnic (&lt;0.5)</b> <i>Phryganea bipunctata</i> * (0.6%), <i>Libella fulva</i> (0.4%), <i>Limnephilus flavicornis</i> * (0.4%)	<b>Euryhaline-limnic (0-10)</b> <i>Potamopyrgus antipodarum</i> * (6.7%), <i>Ischnura elegans</i> * (0.2%), <i>Sigara stagnalis</i> (0.1%)
<b>Cluster D2 (24 km, &lt;0.5)</b>	<b>Limnic, salt tolerating (0-&lt;5)</b> <i>Gammarus pulex</i> * (40.9%), <i>Asellus aquaticus</i> * (28.3%), <i>Erpobdella octoculata</i> * (5.8%), <i>Anabolia nervosa</i> (1.6%), <i>Bithynia tentaculata</i> * (1.6%), <i>Limnephilus lunatus</i> (1%), <i>Hydropsyche augustipennis</i> (0.4%), <i>Glossiphonia complanata</i> * (0.3%), <i>Physa fontinalis</i> (0.3%), <i>Baetis rhodani</i> (0.2%), <i>Cyrrhus trimaculatus</i> * (0.2%), <i>Hydropsyche pellucidula</i> (0.2%), <i>Planorbis planorbis</i> * (0.2%), <i>Radix peregra</i> (0.2%), <i>Sialis lutaria</i> * (0.2%), <i>Acroloxus lacustris</i> (0.1%), <i>Notonecta glauca</i> (0.1%), <i>Caenis horaria</i> (0.1%), <i>Helobdella stagnalis</i> (0.1%)
<b>Euryhaline-limnic (0-10)</b> <i>Sigara dorsalis</i> (0.8%)	<b>Limnic (&lt;0.5)</b> <i>Aplexa hypnorum</i> (0.2%), <i>Sphaerium corneum</i> (9.4%), <i>Platynemis pennipes</i> (0.4%), <i>Limnephilus flavicornis</i> (0.2%), <i>Chaoborus flavicans</i> * (0.2%), <i>Lype reducta</i> * (0.2%), <i>Anisus vortex</i> (0.2%), <i>Plectrocnemia conspersa</i> * (0.2%), <i>Planorbis carinatus</i> (0.2%), <i>Ephemera vulgata</i> (0.1%), <i>Helophorus dorsalis</i> (0.1%), <i>Limnius volckmari</i> * (0.1%), <i>Omphiscola glabra</i> (0.1%), <i>Stictotarsus duodecimpustulatus</i> (0.1%), <i>Centroptilum luteolum</i> (0.1%)
<b>Limnic, salt tolerating (0-&lt;5)</b> <i>Limnephilus flavicornis</i> (0.3%), <i>Phryganea bipuncta</i> (0.1%)	
<b>Cluster E2 (26.46 km, &lt;0.5)</b>	
<b>Limnic, salt tolerating (0-&lt;5)</b> <i>Asellus aquaticus</i> (9.7%), <i>Gammarus pulex</i> (8%), <i>Polycentropus flavomaculatus</i> (8%), <i>Erpobdella octoculata</i> (4.8%), <i>Caenis luctuosa</i> (3.2%), <i>Caenis horaria</i> (3.2%), <i>Calopteryx splendens</i> (3.2%), <i>Radix peregra</i> (3.2%), <i>Acroloxus lacustris</i> (1.6%), <i>Sialis lutaria</i> (1.6%)	
<b>Limnic (&lt;0.5)</b> <i>Sphaerium corneum</i> (29%), <i>Planorbis carinatus</i> (14.5%), <i>Bithynia leachii</i> (6.5%), <i>Ischnura elegans</i> (1.6%), <i>Phryganea bipuncta</i> (1.6%)	

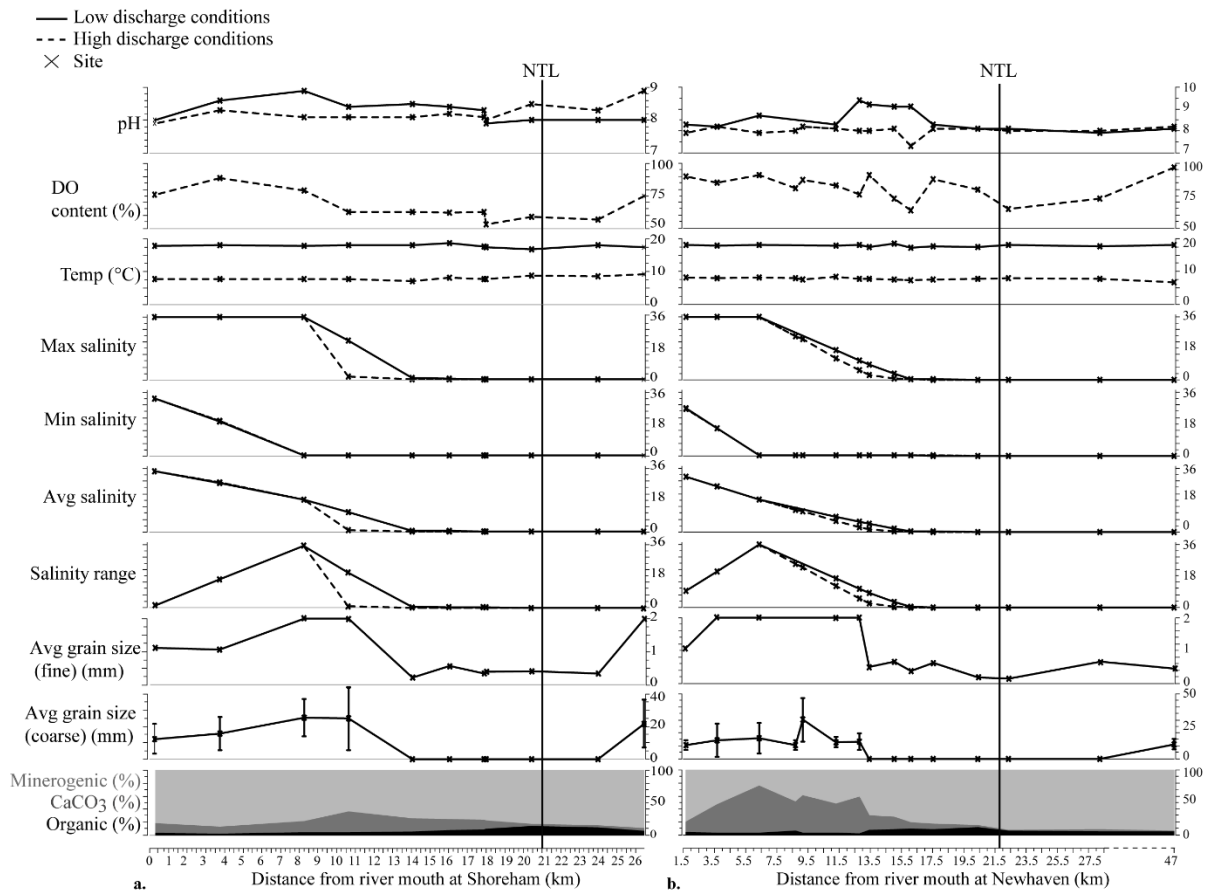


Figure 1. Summary diagram of selected environmental variables in the River Adur (a.) and River Ouse (b.).

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