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Climate variability impacts on coastal dune slack ecohydrology

Sara Varandas Martins[1], Helene Burningham[1], Carla Pinto-Cruz[2]
[1]Department of Geography, University College London, Pearson Building, Gower Street, London WC1E 6BT; [2] Departamento de Biologia, ICAAM – Instituto de Ciências Agrárias e Ambientais Mediterrânicas, Universidade de Évoraa, 7002-554 Évora, Portugal

Abstract: The hydrological regime of freshwater systems plays a crucial role in shaping the dynamics of the different biological communities that inhabit them. Climate change is expected to cause major alterations in the hydrological regime of dune slacks by producing shifts in temperature, precipitation and evapotranspiration. Across seasons, we explore the controls on common water fleas (Cladocera) and aquatic plant communities relative to water level regime, water chemistry, weather and geomorphological setting, in a slack of the Sheskinmore dune system, Co. Donegal, northwest Ireland. Cladoceran abundance and diversity peak in summer, but also vary inter-annually, and drivers for this and hydrological variability are discussed. Vegetation is likewise affected by hydrology in a spatial sense, where distribution follows wet/dry patches of water. Water chemistry is more variable within the same season than across different years, particularly related to the drying out of the slack. Rainfall through 2016-2017 was lower than average and evapotranspiration showed higher values than average for the same time period. The influence on the slack of this decreased precipitation extended across successive seasons. The water table is the most important driver of slack ecology, with incidence on biological communities expressed by the increased variability inter-annually, as opposed to seasonal variation.

Keywords: *hydrology, humid dune slacks, climate change, cladocera, aquatic vegetation, coastal sand dunes, water table*

Introduction

Seasonal and inter-annual variability of biological communities in temporary freshwater bodies in relation to hydroregime have been studied broadly as species composition varies within seasons and within a single hydrological cycle (a year), dependent on water

*h.burningham@ucl.ac.uk (Corresponding author)

permanence and duration imposed by climatic controls (Mengestou and Fernando, 1991; Brooks, 2000; Mwaluma *et al.,* 2003; Sahuquillo and Miracle, 2010). In the dune slacks of northwest Ireland, the groundwater variability seen year to year is likely imposing changes on cladocerans and other aquatic community composition.

Dunes are present throughout the coast of Ireland. However, on the west coast the influence of the strong onshore wind promotes a wider range of morphologies due to erosion, shaping the dunes in varied ways (Mckenzie and Cooper, 2001; Barrett-Mold and Burningham, 2010). Dune formation in western Ireland is still on-going but, in most cases, involves the reworking of existing sediments with limited supply of new material. In much of the west Irish coastal dunes, aquatic systems occur in lulls between dune ridges, but also develop within blowouts. Blowouts are depressions formed as a result of erosion and denudation processes (both natural and anthropogenic), and where these reach the water table, distinct isolated water ecosystems within steep-walled depressions form (Fossitt, 2000; Houston, 2008; Davy *et al.*, 2010; Semeniuk and Semeniuk, 2011; Delaney *et al.,* 2013). There is often a clear distinction between the aquatic environments of inter-dune ridges (i.e., classic 'slacks') and those found within blowouts due to the latter being more significantly topographically constrained, leading to the potential isolation of communities and species. Nevertheless, the wetlands of both inter-dune ridges and blowouts are colonised by specialised plant species and, in many cases, support rare and protected species such as Natterjack toad (*Bufo calamita*) (Houston, 2008), creating a unique biodiversity and important niche habitats within the wider dune landscape (Houston, 2008; Jones *et al.,* 2011). The vast majority of Irish coastal dune wet depressions are classified by the EU Habitats Directive as humid dune slacks (HDS; habitat code 2190) (Houston, 2008). The conservation status of HDS in Ireland has been recently assessed as Unfavourable-Inadequate (deteriorating), with an increasing rate of habitat loss over the last ten years due to mainly anthropogenic impacts and poor management (Delaney *et al.,* 2013).

The hydrological regime (water permanence timing, depth, frequency and seasonality) of temporary freshwater systems plays a crucial role in shaping the dynamics of the different biological communities that inhabit them (Brooks, 2004, 2005; Bauder, 2005; Sim *et al.,* 2013; Camacho *et al.,* 2016). In dune slacks, this leads to phases of drying in the summer and flooding in the winter, regulated by water-table fluctuations within surrounding sand dunes (Davy *et al.,* 2006), and this has a major influence on biological assembly in dune slacks species, by influencing life cycles (Bauder, 2005; NPWS, 2008; Ruiz, 2008). HDS are an extremely rich and specialised environment, but are greatly threatened by the lowering of water tables (EU, 2007; Houston, 2008). Understanding the factors that control the hydrological regime is essential for assessing likely future impacts on the ecosystem functioning and species composition and diversity in dunes slack systems (Robins and Wilson, 2017). Climate change is expected to cause major alterations in dune habitats by modifying the biogeographical range of species, but, more specifically, through changes in temperature and precipitation, impacting the hydrological regime of these seasonal wetlands (Céréghino *et al.,* 2008; Brooks, 2009;

Curreli *et al.,* 2013; Trigo *et al.*, 2013). Consequently, the potential impacts of climate change, which will drive shifts in the duration and intensity of rainy and dry seasons, might be considerable (Sarma *et al.,* 2005; Brooks, 2009; Dimitriou *et al.,* 2009) with major impacts on the ecological characteristics and conservation value of dune slack habitat.

The community of aquatic organisms inhabiting the dune wetland environment contain many features that make them useful as biological indicators in seasonal water bodies such as also described by Boix *et al.* (2005). Zooplankton, for example, are very rich and dynamic in freshwater systems (Fahd *et al.,* 2000) and easy to collect (Lamotte and Bourlière, 1971). The zooplankton community structure reacts to trophic status and environmental changes, and its high taxonomic resolution allows thorough ecological assessments (Eggermont and Martens, 2011; van den Broeck *et al.,* 2015). Cladocera, commonly known as water fleas, are mostly freshwater crustaceans that inhabit a wide range of aquatic habitats. Cladocera play a central role in the trophic energy of pelagic food webs, forming the plankton community as algae, bacteria and detritus grazers, but also as predators, living on the bottom sediments (benthic species), as free swimmers (pelagic) or amongst submerged vegetation (Lynch, 1980; Davidson *et al.,* 2010; Błędzki and Rybak, 2016). Cladoceran species are very sensitive to aquatic environmental changes (Crosetti and Margaritora, 1987; Caramujo *et al.,* 2013) and are especially adapted to the temporary water ecosystem. They have developed a rapid life-cycle (Fahd *et al.,* 2000) and have evolved mechanisms that allow their survival in extreme environmental conditions, such as reproduction by parthenogenesis and production of resting eggs. Environmental aspects, such as hydroperiod (length of the water phase), salinity, biotic and abiotic factors, pond morphology, water chemistry, temperature and overall climatic conditions, directly influence cladocera populations and the impact of this is seen in a wide range of biogeographical regions (Crosetti and Margaritora, 1987; Alonso, 1991; Sarma *et al.,* 2005).

The aim of this paper is to assess the hydrological seasonality on the ecological dynamics of a dune slack cladoceran community and the climatic role on the status of coastal dune wetlands water balance by describing seasonal and inter annual variability in hydrology, weather and species (cladocera and vegetation). Furthermore, it aims to increase awareness of these water dependent habitats as biodiversity pools, through an integrated analysis of ecology, hydrology and geomorphology, which will contribute to the state of knowledge of these coastal dune freshwater systems at a larger scale.

Methodology

Study area

In west Donegal, freshwater slacks occupy a number of coastal dune systems, where the extremely rare 'Decalcified Empetrum Dunes' (2140) and 'Decalcified Dune Heath' (2150) habitats are also found (Delaney *et al*., 2013). The Tramore-Magheramore at Sheskinmore dune system is located on the north margin of the Loughros More

estuary. The dune system is set between two rocky headlands, and borders both open coast and estuarine beaches (Burningham, 2008). It also forms a large barrier that has obstructed a small valley, leading to the development of the large, shallow freshwater lake, Sheskinmore Lough (Gardner, 2016). The Tramore-Magheramore dune system is protected within the local Special Areas of Conservation (West of Ardara/Maas Road SAC and Slieve Tooey/Tormore Island/Loughros Beg Bay SAC) and Special Protection Area (Sheskinmore SPA) (NPWS, 2015). The site is topographically varied, and slacks are formed within both constructional and erosional depressions in the dunes, in troughs between successive dune ridges, but also within blowouts. The underlying bedrock here comprises the metamorphic granodiorite and pelite fringe associated with the Ardara pluton (Burningham, 1999). Variations in geomorphological context, depression size, shape and vertical position, and subsurface structural geology have led to the development of a variation of hydrological regimes and wetland types. Permanent ponds, temporary waterbodies, and wetlands comprising no open-water, are all present within the dune system (Figure 1).
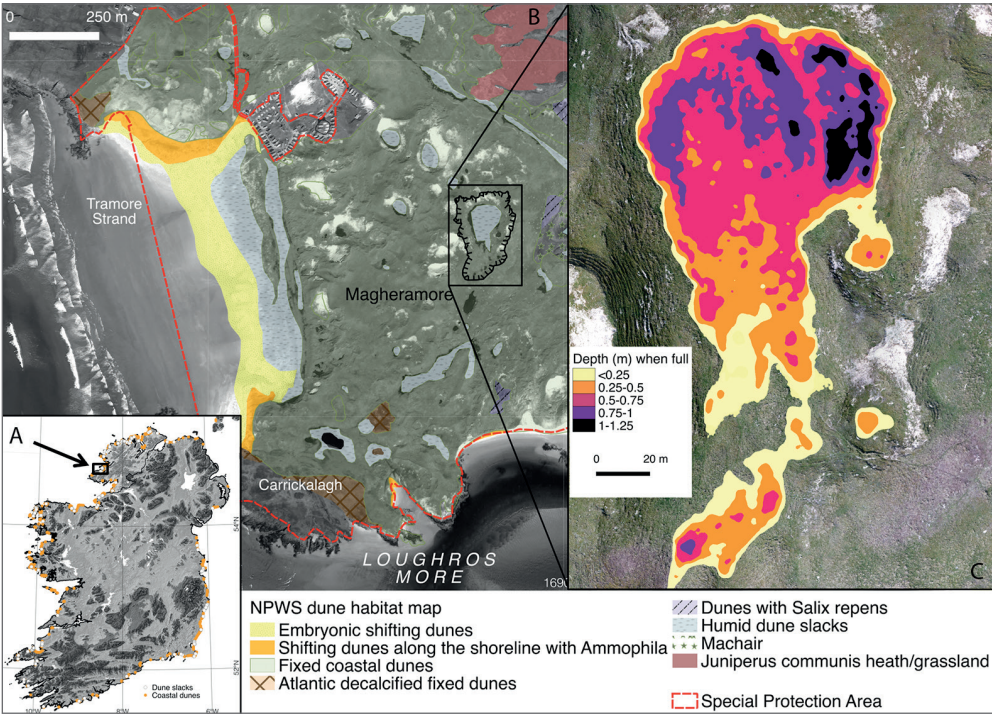
Figure 1: Distribution of dunes and humid dune slacks in Ireland (A), the dune habitats of the Tramore-Magheramore dune system within Sheskinmore Nature Reserve (B), and the blowout-located slack that is the focus of this paper (C)

In the dunes to the rear of the westerly Tramore strand exists one of the largest blowouts and dune slack systems. This blowout has a wide, flat bed (c. 120m x 85m) where topography varies by less than 1m (Figure 1C). The rim of the blowout rises between 7 and 17 metres above this, and the lowest point of the slack is at 6.75m OD (Ordnance Datum Malin, c. mean sea level); the level of mean high water springs is locally c. 2m OD, and the slack is, therefore, well above the tidal frame. The shallow bed topography means that the shift between dry, wet and waterbody phases can occur with just a small change in the water table. When the water depth exceeds 1.4m (at the deepest point), the slack overtops the low topography in a narrow neck along the south rim and connects to series of slacks to the south. This connection does not arise every flood season but does present a physical threshold on the maximum water depth that can be achieved. Several other slacks in the dune system have comparable geomorphological properties, but this particular slack is the largest, and has the longest hydrological monitoring record (Gardner, 2016).

Hydrology and weather monitoring

The research presented here draws from a wider study of ecohydrology within Sheskinmore Nature Reserve incorporating a range of surveying and monitoring undertaken since 2012. To examine the hydrological regime of the slack, an In-Situ Rugged TROLL Data Logger was installed in the deeper part of the slack depression, during dry conditions in summer 2012 (Gardner, 2016). A hand auger was used to drill a well into the sediment bed to below the water table. The structure comprised a vertically installed PVC tube (Ø 5cm) within which the TROLL autonomous pressure sensor (piezometer) was deployed (suspended) at depth (i.e., below the water table). The PVC tube was pre-drilled with holes to allow free water movement and wrapped in weed control membrane to prevent siltation inside the tube. The pressure sensor was programmed to monitor total pressure and temperature, initially at 15-minute intervals, but latterly at hourly intervals. All data were down-sampled to generate an hourly record from June 2012 to May 2018. Dune topography, slack bed and piezometer elevations were surveyed using a dGPS (Leica GS15). Positions were referenced to Irish Grid and elevations to mean sea level (Ordnance Datum Malin). A Davis Vantage Pro2 weather station was also installed in summer 2012, about 2km to the east of the blowout, measuring a full suite of climate variables at an hourly interval.

Biological data

Two seasonal surveys of data collection (cladocera and vegetation) were undertaken from the summer of 2015 to the winter of 2017, covering two hydrological years. Survey timing approximated the maximum flood extent (late Winter) and mid-way through the drying phase (early Summer), enabling sampling of species with different life cycles and hatching or flowering timings (Amami *et al.,* 2010). Cladocera samples were collected using a tube-sampler (Ø 7.5cm; 60-100cm) that collected water along the water column

(Waterkeyn *et al.,* 2008). In shallow areas of the slack (margins and dense vegetation), samples were also collected using a 5L container. Both the tube length and volume of water collected were recorded, and water was subsequently filtered through a 53µm mesh trawling plankton net. The total volume of water sampled was proportional to the size (area) of the slack and captured all microhabitats and depths present (margin and open water), with an average of 24 Litres per sampling. The sample was combined into one single composite in a bottle and immediately preserved with 95% ethyl alcohol. The sample was later examined in the laboratory, where 5ml at a time from the main sample were placed in a Bogorov counting chamber and analysed using a stereomicroscope (10x) until 400 individuals in total or 200 individuals from one species were counted. All cladocerans were picked and counted under a compound microscope (100x) and identified to species following Scourfield and Harding (1941), Amoros (1984), Flobner (2000) and Błędzki and Rybak (2016). Plants specifically rooted in water (i.e., the cladoceran habitat) were surveyed to provide a direct comparison with cladoceran community composition. Plant data was obtained by walking around the margin of the slack and wading in to the centre, covering the variety of microhabitats and different vegetation patches present. For every different taxon, abundance was noted using the DAFOR scale: Dominant (5), Abundant (4), Frequent (3), Occasional (2), and Rare (1).

Environmental variables

Concurrent seasonal surveys of environmental data were also collected. *In-situ* measurements of dissolved oxygen concentration, conductivity, temperature and pH were made using Hach 1001 Intellical probe and a HQ30d Hach meter, at three randomly distributed locations across the slack. Water samples were also collected to undertake a number of measurements of water chemistry. Alkalinity was measured on site using the Hach test kit model AL-DT and Hach method 8203. Titration of 1.6N H_2SO_4 was performed to a single endpoint of pH 4.5 using Bromocresol-green Methyl-red indicator as described in Hach, 2015. Chlorophyll *a* was collected using a 1.2µm pore size GF/C filter paper in a 500ml Nalgene filter holder with receiver using a hand operated vacuum pump (DWQ 2011). Both filtered and unfiltered samples were obtained to determine total phosphorus (TP), soluble reactive phosphorus (SRP) and nitrate/nitrogen (NO_3^-) later in the laboratory. SRP was determined by the standardised method described in American Public Health Association (1999). To determine TP, water samples were digested after the persulfate method described in D'Elia *et al.* (1977). For the nitrogen analysis, spongy cadmium was used as a catalyst for the reduction to nitrite (Elliott and Porter, 1971). A Hach CAMLABDR/4000U spectrophotometer with a 1cm light path was used to analyse the SRP, TP and N samples against replicate blanks, at a wavelength of 885nm for TP and SRP and 543nm for nitrates. Chlorophyll *a* samples were analysed using standard procedures.

Data analysis

Normality distribution of the data was tested using Shapiro-Wilk test and logarithmic transformation of the data was performed where required. Environmental variables, including water chemistry and hydrological data were standardised through linear transformation of the data due to the notable differences in scale range of the parameters analysed. Following this, analysis of variance was applied to test whether cladoceran abundance means differed between each season using Kruskal-Wallis tests and the significance level of $p<0.05$ was applied. All exploratory analyses were done using PAST software (Hammer *et al.,* 2001). Shannon diversity (H) index and equitability (as a measure of evenness within the present taxa) based on the same index were also calculated. A non-metric multidimensional scaling (nMDS) ordination plot was used to explore associations between samples (Kruskal, 1964).

Results

Climatic controls on hydrological variability

During the survey period of this study, the hydrological seasons did not follow the usual early spring-flooded, early summer-drying trend. The flood extent and mean depth for each survey is shown on Figure 2, which displays some evidence of expected lowering of the water table during the summer survey (Jun-16), compared to the maximum extent of flooding. However, the winter conditions show major differences; sampling corresponded to 'fully flooded', high water table conditions in Mar-16, the equivalent period in 2017 exhibited very reduced water levels which were evident across the whole site (Magee, 2017; Burningham, 2018).

Hydrological monitoring of the slack showed a strongly seasonal regime that shifts between flooded and dry conditions over the course of the year (Figure 3). But the results also show that this water level regime is very variable (mean water depth at the deepest part of the pond is 0.36cm with a standard deviation 0.4cm), and the presence of a small, localised depression to the east means that it does not dry completely every year. The maximum flooding occurs between February and April each year, whilst lowest water levels are experienced between September and December. The hydrological regime each year is slightly skewed in that the time taken to reach maximum flooding is on average 2 months shorter than the time taken to reach minimum water levels from the winter maximum flooding. The winter of 2016-17 shows a distinctly dry period in the pond relative to other winters, with conditions more comparable to those during an average summer. The slack stayed largely dry throughout the period from late summer 2016 through to the winter of 2017-18; the small depression at the deepest point within the slack did flood, but only to a maximum depth of 16cm. This 'flood' period lasted just 12 weeks in comparison to the average flooded phase of 28 weeks at the centre of the pond and 44 weeks at the deepest point.

Annual precipitation values change year-to-year, and there is notable variability in seasonal totals throughout. Precipitation is greatest in the winter, with a distinct rise
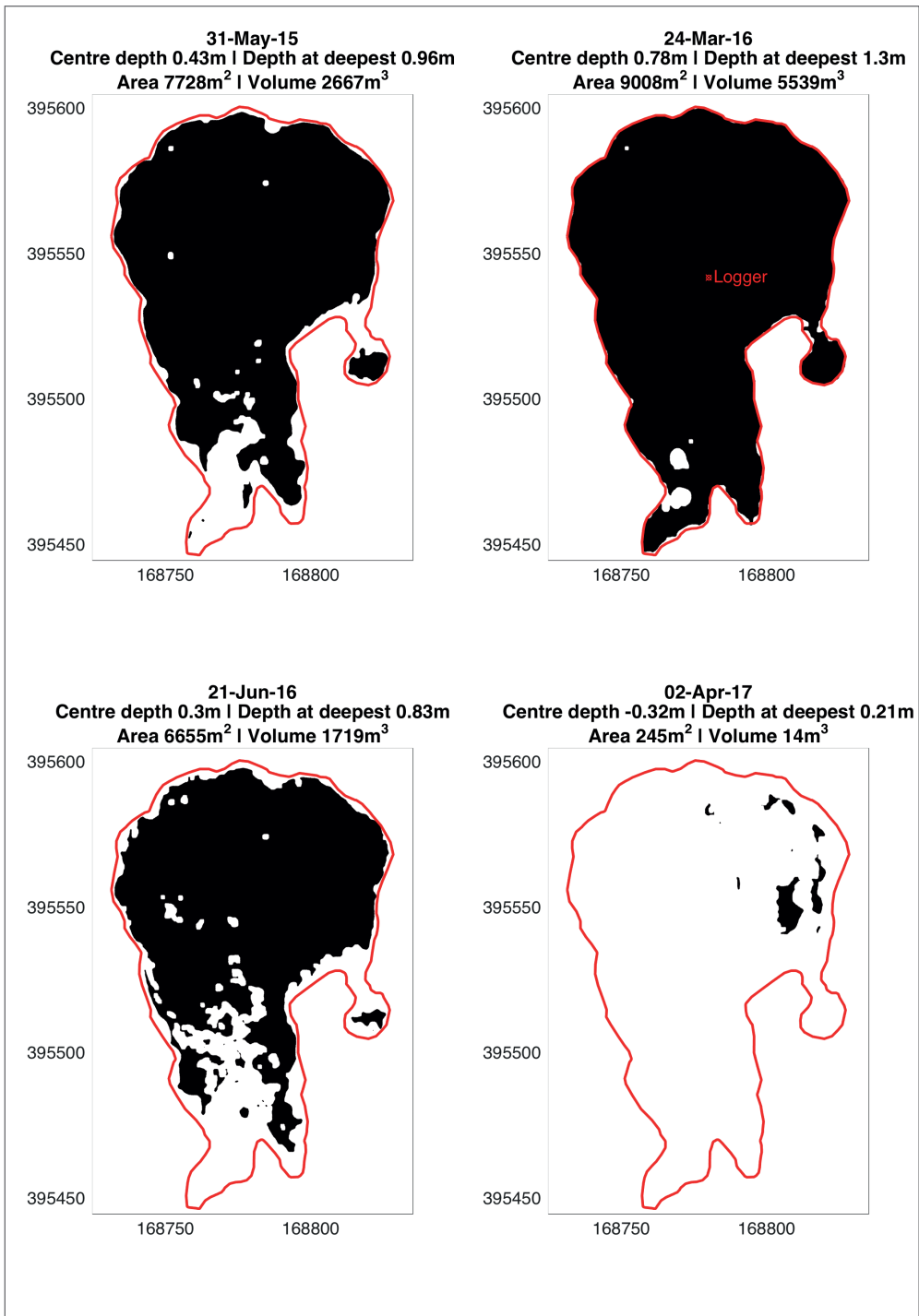
Figure 2: The average conditions of mean depth, area and volume of the slack for the 28 days up to the survey date. The outer line shows the maximum recorded extent of the flooded area during the monitoring period

from a minimum around September (30-35mm month), peaking between December and February. Differences in maximum values were considerable in two consecutive years (178mm in December 15 compared to 80mm for the same month in 2016). Evapotranspiration has a stronger seasonal signature, with a relatively symmetrical rise to a summer high and fall to a winter low. Peak flooding of the slack occurs in the period between peak precipitation and peak evapotranspiration, whilst the drier phases occur on the final decline in evapotranspiration and at the start of the rise in precipitation. The slack receives water directly through precipitation, but also via the groundwater body held in the dunes surrounding the slack. There is no evidence to suggest that this groundwater
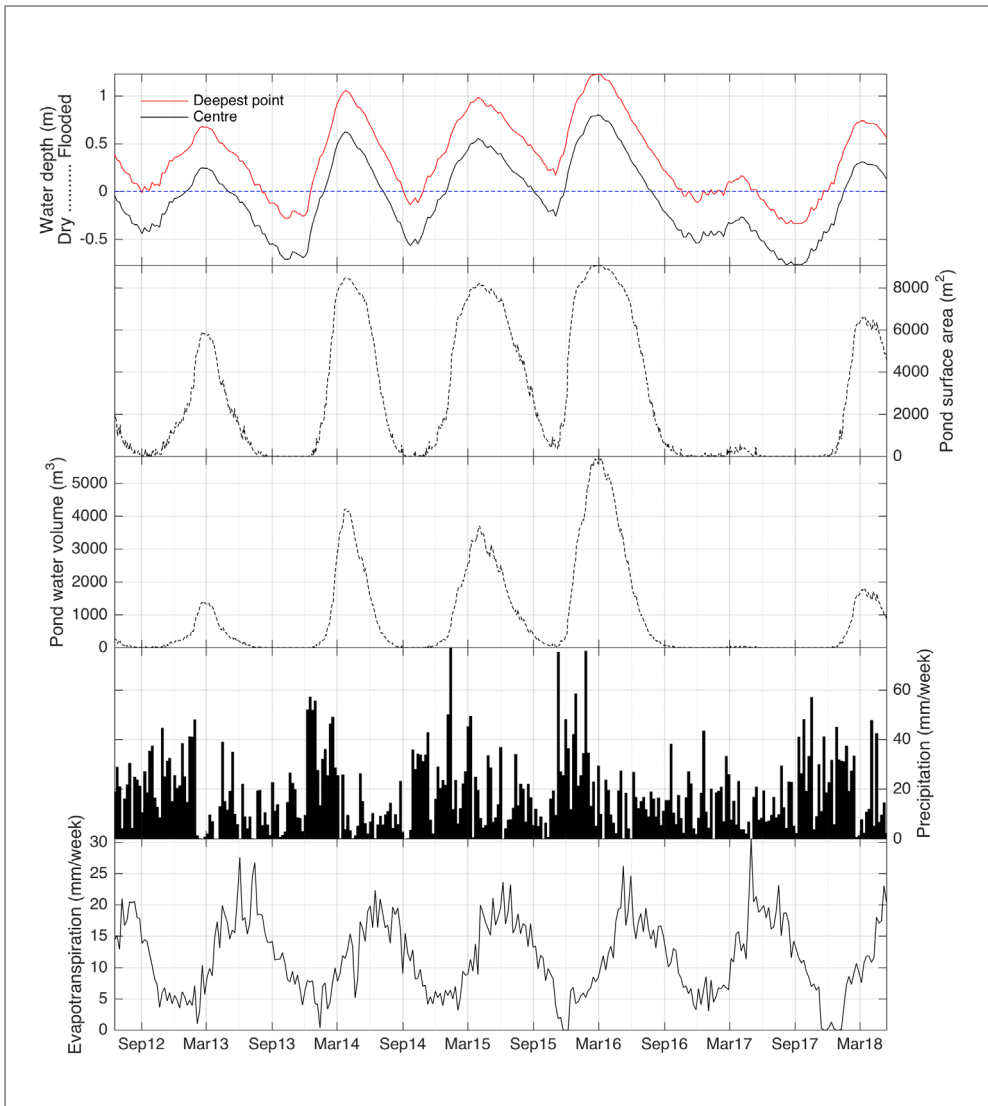
Figure 3: Time series of weekly water level (relative to the pond bed), pond surface area and water volume, precipitation and evapotranspiration recorded from mid-2012 to mid-2018

is fed beyond precipitation across the dune surface, and the timing of flooding and drying reflect the interaction between direct rainfall and lateral groundwater. Given the vertical extent of the adjacent dunes though, it is likely that the slack receives a considerable supply of water through lateral groundwater flow. Connections between input and output of water in the slack combine to drive a hydrology that responds to changeable weather, for example, when the water table is kept high through seasons and evapotranspiration is minimised and vice versa, which leads to either sustained flooding throughout all months in some years (e.g., autumn 2015), or a shorter hydroperiod in others.

Seasonal variability in water chemistry

Water chemistry varies seasonally (Table 1): some measures are more variable within the same season, as is the case of nitrogen, total phosphorus, alkalinity, conductivity and water depth levels, as seen on standard deviation values. Some show slight differences in mean value between season: for example, water temperature in the summer is 16°C, compared to 13°C in the winter; SRP measures are also higher in the summer (4.37 µg/L) compared to winter (2.68 µg/L; pH and oxygen are very much constant through the sampling period.

Table 1: Mean ± standard deviation for summer and winter water chemistry

	Winter	Summer
N	27.76 (19.1)	17.23 (5.2)
SRP	2.68 (0.2)	4.37 (0.9)
TP	59.39 (43.3)	32.70 (16.0)
Wd	51.5 (40.3)	73.5 (6.4)
Alk	120 (31.1)	106.0 (7.1)
pH	8.11 (0.2)	8.07 (0.4)
T	12.95 (5.0)	16.08 (1.5)
Ox	10.91 (0.7)	9.79 (3.5)
Con	460.5 (40.3)	423.0 (67.9)

Cladocera community

A total of fifteen species of cladocera were found, belonging to four families: Chydoridae, Bosminidae, Daphnidae and Macrothricidae. These were: *Alona costata, Alonella exigua, Alonella nana, Acroperus harpae, Alona affinis, Bosmina longirostris, Ceriodaphnia quadrangula, Ceriodaphnia setosa, Chydorus sphaericus, Coronatella rectangula, Eurycercus lamellatus, Graptoleberis testudinaria, Macrothricidae spp, Simocephalus exospinosus* and *Simocephalus vetulus*. All species are widely distributed in Europe, mostly with a preference for littoral oligotrophic habitats, rich in vegetation and with occurrence in

temporary waters (Błędzki and Rybak, 2016). Some species are more frequent in shallow/small waterbodies (*A. costata*, *A. exigua*, *E. lamellatus*), others prefer sandy bottoms (*A. harpae*, *A. nana*), but the vast majority thrives among vegetation (genus *Alona*, *Alonella*, *Ceriodaphnia*, *Coronatella* and *Graptoleberis*). *Chydorus sphaericus* and *Simocephalus spp* are very common species with a great plasticity, able to adapt to a wide range of habitats, temperature and environmental conditions (Błędzki and Rybak, 2016).

Cladoceran abundance was significantly different between winter and summer samples ($p<0.05$) (Table 2), and inter-annual variability is visible from summer 2015 to 2016. In this study, the lowest abundance of species was recorded on the W17 samples with seven species present – *A. costata*, *S. vetulus* and *G. testudinaria* with the lowest abundance (0.05 sp per L), followed by *Ceriodaphnia spp* and *C. rectangula* with 0.09 sp per L. *B. longirostris* had 1.55 sp per L and *C. sphaericus* dominated the sample with 2.73 sp per L.

Table 2: Cladoceran abundance *p*values for seasonal and inter annual variability (SS – summer 15 vs summer 16, WW – winter 2016 vs winter 2017, SW16 – winter and summer 2016)

|	*p* value
SS	0.023
WW	0.488
WS16	0.000

Biodiversity variability was calculated to evaluate the structure of the cladoceran communities' seasonal diversity, based on the Shannon index, throughout the samplings (Table 3). The increased diversity was reached in S16, when species such as *A. harpae* and all *Ceriodaphnia spp* appeared for the only time throughout the study. These species are well represented and widely distributed in Ireland having been found amongst dense vegetation such as *Chara sp*. and at sandy sediment freshwater habitats (Duigan, 1992; Błędzki and Rybak, 2016).

Table 3: Seasonal changes in cladoceran biodiversity indices based on Shannon abundance records

	S15	W16	S16	W17
diversity	0.926	0.418	1.935	0.968
equitability	0.421	0.201	0.715	0.498

Hydrological measurements and water chemistry factors combined were used to evaluate the influence of the overall environmental controls on cladoceran community composition patterns (Figure 4) on an nMDS ordination. With a stress value of zero generated by the algorithm, the multivariate distance between the samples is considered a good fit, indicating that the nMDS ordination is not arbitrary (Clarke, 1993; Letten,

2017). Cladoceran abundance is significantly different between winter and summer samples ($p<0.05$), where summer (S) samples have greater abundance and diversity of species, compared to winter (W). Some species were recurrently seasonal, for example, *A. affinis* was only found in summer samples directly related to higher water temperature values. By contrast, the smaller sized *B. longirostris* was only found on winter samples, linked to increased water volume, nitrogen and chlorophyll *a* values. However, a more significant difference in communities recorded is evident between S 2015 (left hand side of Figure 4) and W 2017 (right hand side of same Figure). S 2016 and W 2016 are more similar (aligned on the first axis). When considered with reference to environmental controls, oxygen, chlorophyll *a*, nitrogen and water volume of the slack seem to have a stronger influence on the winter communities. Conversely, water and air temperature, evapotranspiration, soluble reactive phosphorus and vegetation richness (varying from
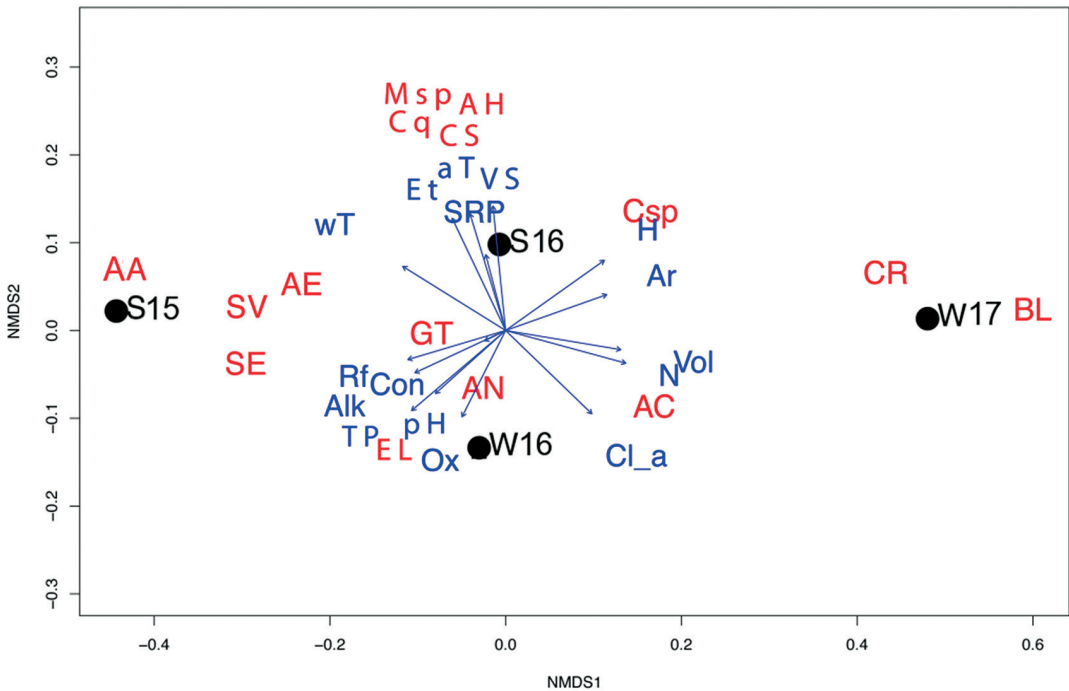

Figure 4: NMDS ordination, where arrows correspond to the strength of the environmental variables in relation to the spatial distribution of the cladoceran species, relative to different sampling seasons (dots): S (summer) and W (winter). Environmental variables: aT – air temperature; Et – evapotranspiration; VS – vegetation richness; SRP – soluble reactive phosphorus; wT – water temperature; H – hydroperiod (sampling days since last dry); Ar – surface area; Vol – water volume; N – nitrogen; Cl_a – chlorophyll a; Rf – rainfall; Con – conductivity; Alk – alkalinity; TP – total phosphorus; pH – pH; Ox – oxygen. Cladoceran species: AA – *Alona affinis*; AE – *Alonella exigua*; SV – *Simocephalus vetulus*; SE – *Simocephalus exospinosus*; Msp – Macrothricidae sp; Cq – *Ceriodaphnia quadrangula*; AH – *Acroperus harpae*; CS – *Ceriodaphnia setosa*; GT – *Graptoleberis testudinaria*; AN – *Alonella nana*; EL – *Eurycerus lamellatus*; Csp – *Chydorus sphaericus*; AC – *Alona costata*; CR – *Ceriodaphnia reticulata*; BL – *Bosmina longirostris*

an average of 22 species found in summer as opposed to 14 species in winter) influence the cladoceran communities of the summer samples. Variables that can explicitly link S-W differences are water temperature (high in S, low in W), water volume, nitrate and chlorophyll *a* (all three high in W, low in S).

Plant patterns

Vegetation records, observations and aerial photography help to demonstrate the role of hydrology on the spatial patterns in plant species and communities across the slack. Figure 5 shows the slack in the later stages of the flood season where shallow water extends across much of the slack, and deeper water (to around 50cm) is present in the depression in the northeast part of the slack. Vegetation zonation is evident, with distinct rings of different vegetation communities around the margins of the slack, but it is also clear that much of the central part of the slack comprises patches of different species assemblages.
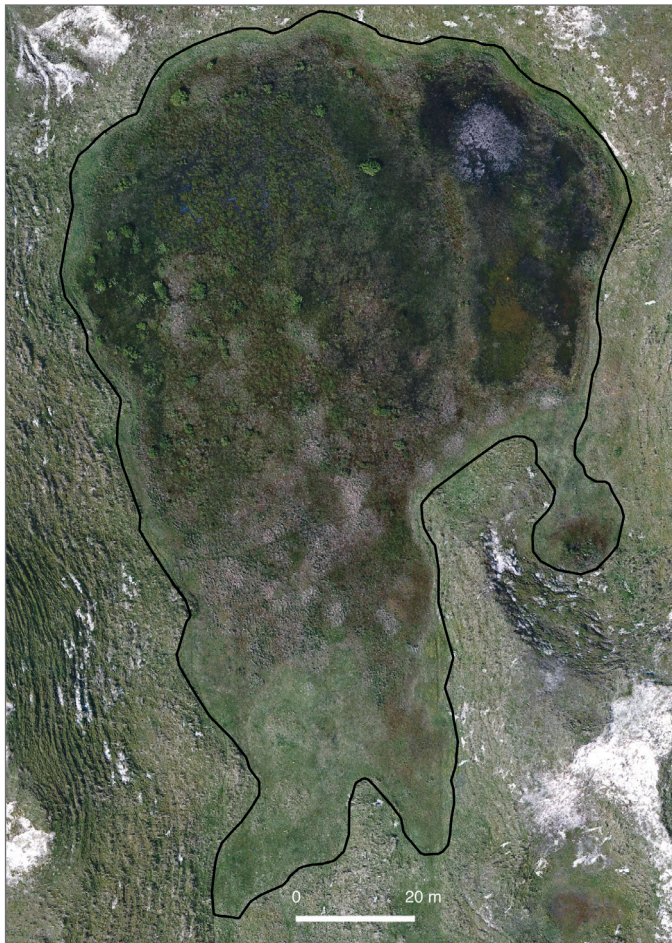
Figure 5: Aerial image acquired in May 2018, showing both zonation and patchiness in vegetation patterns

The margins of the slack comprise moss carpets (*Sphagnum spp*) combined with wet tolerant species (e.g., *Hydrocotyle vulgaris*) with occasional colonisation fragments of terrestrials, mainly *Salix repens*. There is a distinction between the southern dryer side of the slack, represented by wet tolerant species like *Carex spp* and the northern wetter side, with more emergent/submerged species (e.g., *Eliocharis palustris*). The inner region comprises elevated patches of *Juncus spp* surrounded by underwater and emergent growing species, like *Gallium palustris*, *Carex spp* and *Eleocharis spp*, on slightly deeper localised depressions. Groups of submerged species, or species with shorter growth (e.g., *Galium palustre*), are found adjacent to other submerged species from deeper patches (e.g., *Chara spp, Potamogeton sp*) (to the northeast). Emergent and wet tolerant groups of species (e.g., *Eleocharis spp* and *Carex spp*) occur very much all over the slack, but with more incidences on the northern side.

Discussion

The results show notable variability in climate and hydrology over the monitoring period, but the controls that climate and hydrology exert on species composition and water chemistry are more complex. Seasonal differences on crustaceans abundance have been reported largely in the literature from tropical and Mediterranean regions (Mengestou and Fernando, 1991; Mwaluma *et al.*, 2003; Miracle *et al.*, 2010) with higher values in spring/summer compared to autumn/winter. And the same results occurred in this study. Temperate climate seasonal cladoceran variability in slacks is not so well documented and this study improves knowledge of Irish dune slack habitat dynamics.

The effects of climate on hydrological variability

The period of sampling and monitoring covered two consecutive hydrological cycles (summer 2015 through to winter 2017), during which the slack followed two different annual hydrological cycles. The first period, S15 to W16, was as expected where water table rise followed a gradual increase from the autumn to spring. But the second year, S16 to W17, was unexpected, where the low rainfall during the autumn/winter was not sufficient to supply water to the extent needed to flood the slack. Maximum temperatures during the summer of 2016 were higher than average (26°C) and the minimum temperatures were also high, but similar to the previous year (over 6°C), with rainfall through the following winter registering values lower than average. During the winter of 2017, the area suffered a significant water table lowering affecting all dune wetlands at Sheskinmore Nature Reserve (Magee, 2017; Burningham, 2018). There is no doubt that inter-annual variability in weather conditions imparts a significant control on the hydrology and ecology of dune wetlands. The strong seasonal hydrological regime in dune slack systems dictated primarily by water inputs (precipitation) and outputs (evapotranspiration) are directly related to climate. Change in these at the multi-annual to multi-decadal scale will determine the overall availability of water, the evolutionary path of the ponds and wetlands, and the ecological functions that the dune slacks fulfil and hence eventually alter the ecological development within.

The hydrological regime of the slack at Sheskinmore follows a similar trend to other local dune slack systems, for example, at Magilligan in Northern Ireland (Robins and Wilson, 2017) where water table levels reach their maximum toward the end of winter, leading to a period of flooding across the slack floor. The hydroperiod variation within the slack is a consequence of the topographic layout of the slack bed. In larger slacks such as the one reported here, this can lead to distinct patchiness of water availability throughout the year, following small-scale variations in bed level; the deepest part of the slack is more permanent versus a marked seasonal temporary water availability from the deepest part to the side. The present study reveals a distinct shift in water balance from one year to the other, especially from winter 2016 to winter 2017 in comparison to the more balanced seasonal input (precipitation) and output (evapotranspiration) in other monitoring years. Results from the year 2012-2013 also show low precipitation, with a particular gap from February 2013 onwards (just 7.4mm that month) paired with high peaks of evapotranspiration recorded in June and August of the same year, limiting the water availability in 2013. Although not frequent, results show that occasional inter-annual alterations on the climatic conditions seem to impact the overall ecological dynamics of the slacks at Sheskinmore dune system, caused through a reduction in precipitation and elevated evapotranspiration. The hydrology of this slack clearly relies on groundwater, and whilst short periods of reduced rainfall (e.g., winter 2012-13) can reduce the flood season, more persistent phases of low rainfall that extend beyond a year (e.g., spring 2016 through to summer 2017) evidently draw down important groundwater supply from the adjacent dunes.

Vegetation patterns

The topographic layout of the slack dictates the patchiness of vegetation; the slack comprises depressions where water accumulates and persists for longer, and slightly elevated areas where water disappears more frequently. This leads to a mix of vegetation communities along both north-south and east-west gradients. In systems comprising topographic heterogeneity, this is a common observation. Fernnández-Aláez *et al.* (1999) found that the elevated number of helophytes (broadly designated by wet tolerant species) as well as the great variation in water levels reflected the variability and shallowness of the system and also influenced vegetation growth and spatial distribution in Mediterranean waterbodies. Plant species in temporary waterbodies depend on soil type and humidity conditions, as well as water depth and topography (Ruiz, 2008). Some plants are amphibious species being able to live in both wet and dry soil conditions, for example, *M. aquatica* and *Ranunculus repens* (Ruiz, 2008; Camacho *et al.,* 2009; Bagella and Caria, 2012). Aquatic vegetation creates the habitat for a wide diversity of invertebrate species (Carpenter and Lodge, 1986; Katende, 2004; Ali *et al.,* 2007; Peretyatko *et al.,* 2009; Davidson *et al.,* 2010). Blackstock *et al.* (1993) compared a seasonal inundated Welsh lake vegetation zonation to the Irish *turloughs*, due to its similarity in species composition. The study shows resemblance in the type of species that dominated different water depths with dominance of wet tolerant and emergent species

along the gradient of the wetland. Blackstock *et al.* (1993) also stress that the appearance of terrestrial marginal vegetation is a consequence of lack of grazing, thus suggesting that the small existence of some terrestrial woody vegetation may be a consequence of the existing grazing that restrains the overgrowth of this type of species. In the Sheskinmore slack, patterns of vegetation communities seem to follow the topography of the system, but as the bed of the slack comprises small local variability, the pattern of vegetation is more complex, and this is likely implicating different niches and habitats for cladocerans.

Seasonality differences in cladoceran abundance

In this study, the cladoceran community was inter-annually changeable in the summer months, but also seasonally varied. Cladoceran annual seasonal abundance ranged from 5 to 12 sp/L in consecutive summer samplings. In consecutive winter samplings it changed from 0.9 to 0.7 sp/L. That abundance was higher in summer samples is in agreement with other similar studies, where winter/pioneer communities have lower diversity at the beginning of the wet season, compared to more established summer communities (Mengestou and Fernando, 1991; Antón-Pardo *et al.,* 2015). Results show that cladocerans responds as much to inter-annual variability in hydro-climate as it does to seasons – this is primarily a product of the size of the pond system (area, depth, water permanence) and the consequences of a lowering of the water table in W17 on water chemistry. But this does not explain why there is such a large difference between the two summers in terms of species richness and abundance, as hydrologically – at the time of sampling – they are very similar. What appears to be the case is that the slack condition preceding the sampling in S16 influenced the appearance of new taxa. Perhaps important here is the fact that the pond dried in the autumn of 2014 (before the subsequent summer sampling), but did not dry during the autumn of 2015, meaning that there had been a persistent water body prior to the S16 sampling, but not before the S15 sampling.

It may also be the case that this is caused by vegetation diversity differences. The ecological preferences of the 'new' species that occurred in S16 are very similar, with particular emphasis to the fact that they all prefer habitats rich in vegetation (Fryer, 1968; Błędzki and Rybak, 2016). A closer analysis on vegetation and cladoceran seasonal richness (Figure 6) shows that the number of species correlates throughout the samplings, and inter-annual differences are more evident in the summer, with higher values of vegetation in S16. The different patterns of vegetation seem to be promoting a wider variety of microhabitats and shelter for cladocerans, as also found by Choi *et al.* (2014), and this could be the justification for the high number of different cladoceran species found, increasing the diversity of this taxa, following the same pattern of plant richness. These plant microhabitats can be created by finer taller species (e.g., *Juncus spp*, *Eleocharis spp*) that promote light penetration, clearer water and space for planktonic cladocerans to swim (e.g., *Bosmina sp* and *Ceriodaphnia spp*), contrasting with other patches of broad leaf submerged vegetation (e.g., *Potamogeton spp*, *Galium sp*), with larger plant structure and increased shading, promoting the habitat for the more epiphytic cladoceran species (e.g., *Alona spp* and *Alonella spp*).
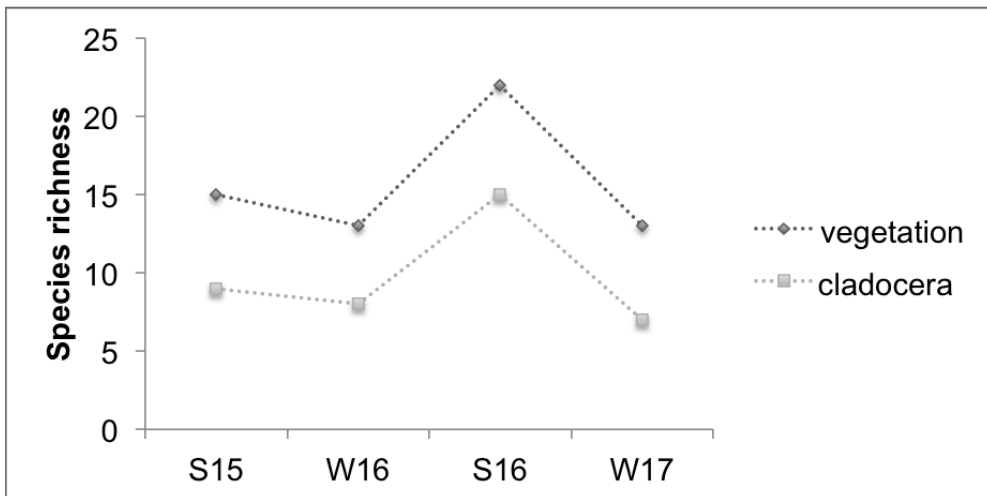
Figure 6: Cladoceran and vegetation richness in relation to each sampling season

Climate change and future impacts on slack ecohydrology

The Sheskinmore Nature Reserve dune system is not immune to a wide range of pressures ranging from land use and management (overgrazing by cattle and rabbits; low to moderate disturbance of the dunes by their closeness to walking paths and the caravan site), to climatic variability (inter annual changes in precipitation and evapotranspiration, and widespread lowering of the water table). Similarly to what occurs in the studied slack, Gardner (2016) reported that water levels at the Sheskinmore Lough (a close large wetland located at the back of the dunes) were determined by precipitation and evapotranspiration, and based on climate change modelling, that the future of the ecohydrological dynamics in the wetland of the Sheskinmore was determined by changes in climate in combination with management practices. Human development has imposed its rules on the natural evolution and dynamic of coastal environments for the past millennia. However, climate change is likely to become a stronger influential force of alteration on the coast for the forthcoming decades, with expected modifications on the natural patterns of precipitation and temperature (Jones *et al.,* 2011).

Cladocerans combine benthic or pelagic species that play an essential ecological role in energy flow on food webs. At 20°C, cladocerans are able to reach sexual maturity in 5-10 days (Crosetti and Margaritora, 1987). At lower temperatures, the rate at which cladocerans hatch is slightly increased. Vandekerkhove *et al.* (2005) compared hatching timings at 15°C for a set of temperate and Mediterranean cladocerans and from 50% to over 70% of species hatched at different temperatures within 12 days. This means that cladocera rapidly reaches high densities even when the wet phase is short. On the other hand, the slow rate at which cladoceran eggs evolve into juveniles in sexual reproduction make cladocerans highly impacted by changes in environmental conditions such as temperature rising and water levels dropping (Jones and Gilbert, 2016). These

combined factors make them vulnerable and sensitive to the surrounding environment and, therefore, suitable for tracking short- and long-term environmental changes (Davisdon *et al.,* 2011; Błędzki and Rybak, 2016). At the Irish scale, the greatest threats that dune slacks face are related to changes in natural dynamics of the hydrology, as well as increased agriculture and recreation activities (NPWS, 2013).

As this study shows, cladoceran richness was linked to vegetation richness and both are related to presence of water and the hydrological regime of the slack. With the predictions of increased temperatures, the likelihood of decreased wetter areas is expected. And this is not only visible at a large scale, but as shown here, at the individual slack patch scale as well, where the impacts of this may be seen in the reduction of species richness of these systems. Climate change in the 21st century is likely to cause impacts on hydrology with implications for biodiversity (Bates *et al.,* 2008), by reducing habitat suitability and threatening species with limited dispersal mobility (Hulme, 2005). Global precipitation and temperature trends show considerable variation from the past 100 years, with temperature increments of 0.5°C to 2°C expected by 2030 and between 2°C and 3.5°C by 2080 (Hulme *et al.,* 2002). In Europe, changes in precipitation intensity and frequency are expected for the future, with increased frequency in the north and decreased frequency in the south, but subject to substantial seasonal, yearly and regional variations (Hulme *et al.,* 2002; Bates *et al.,* 2008). The UK Climate Impacts Programme (UKCIP) projects that future climate in the UK and Ireland will be hotter and drier in the summer and warmer and wetter in winter (Hulme *et al.,* 2002). Based on the Irish Environmental Protection Agency report (McGrath *et al.,* 2005), climatic conditions in Ireland are due to be impacted as well, with mean monthly temperature increasing 1.25°C and 1.5°C over the next 40 years. Precipitation is likely decreasing about 10% in July in the south and in the north-west, precipitation will rise 25% in winter and increase in the frequency of extreme climatic events (strong winds and storms) with predictions of over 20mm rainfall per day. Under these scenarios, Clarke & Na Ayutthaya (2010) suggests that changes in the balance caused by expected lower summer rainfall, higher evapotranspiration, together with higher winter rainfall amounts, will cumulatively reduce the annual recharge of coastal dune systems in NW England, with clear impacts on water dependent species.

Conclusions

Even though part of a Nature Reserve, the dune systems at Sheskinmore are showing vulnerability from impacts caused by land use, management and climate variability. The effects of decreased precipitation during the autumn and winter was more severe than a summer drought, and its consequences extended across several months. In the case of the water table dependent habitats and species that exist in dune slacks, the effects of climatic changes over the short- and long-term can be extreme. The level of the water table is in fact the most important driver of impact on the overall ecology of the studied slack, with incidence on biological communities expressed by the increased variability

inter annually, as opposed to annual seasonal variation. Hydrological seasonal variability as well as topographic patchiness creates habitats for different plant species, which supports high richness and diversity of cladoceran species.

Climate is undoubtedly an important influence on the optimal ecological functioning of dune slacks, and this work shows that inter annual climate variability is capable of forcing more significant shifts in hydrology and ecology than seasons. As such, it is likely that climate variability is the most important aspect of future climate change. The increase in temperature and reduction of rainfall causing dune slacks to dry out or reduce significantly their hydroperiod, will result in a loss of many rare species (Jones *et al.,* 2011). This study adds to the examples of the climate impacts on sensitive water dependant habitats and their communities, and complements to this knowledge the Irish dune slack ecohydrological habitat dynamics.

Acknowledgments

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