Title:

Temporal and Spatial Variation in Temperature and Oxygen at the Microscale: Key Niche Axes for Aquatic Life

Authors:

W.C.E.P. Verberk[1], D.T. Bilton[2,3]

1) Department of Ecology, Radboud Institute for Biological and Environmental Sciences, Radboud University, Nijmegen, P.O. Box 9010, 6500 GL, Nijmegen, The Netherlands.

0000-0002-0691-583X; wilco.verberk@ru.nl

2) Marine Biology and Ecology Research Centre, School of Biological and Marine Sciences, University of Plymouth, Drake Circus Plymouth PL4 8AA, UK.

3) Department of Zoology, University of Johannesburg, PO Box 524, Auckland Park, Johannesburg 2006, South Africa.

0000-0003-1136-0848; D.Bilton@plymouth.ac.uk

Abstract

To understand animal adaptations we need accurate estimates of the ecological factors impacting on organisms in nature. Whilst temperature is a well-established driver of physiological performance, its effects in aquatic systems are closely linked to water oxygenation. Oxygen levels are expected to differ spatially and fluctuate temporally much more strongly in water than on land, but our understanding of variation in temperature and oxygen levels in freshwaters remains limited. It is essential that environmental variation is recorded at spatial and temporal resolutions relevant to the organism. Here, we analyze spatial and temporal variation in water temperature and oxygenation across running and standing waters, using both microscale spot measurements and continuous loggers collecting data from the water column. Our results reaffirm that small-scale thermal gradients are much less pronounced in water than on land due to the high thermal conductivity and heat capacity of water. Regional weather conditions can therefore reliably predict water temperature across scales. By contrast, oxygen levels are much harder to predict from large-scale data as they can fluctuate sharply over very small spatial scales and within a single day, particularly in standing waters, exposing aquatic organisms to steep oxygen gradients. Our findings underscore the importance of incorporating fine-scale oxygen dynamics when studying aquatic species distributions and ecological strategies.

Keywords:

Aquatic ecology, biogeography, microclimate, modelling, climate change, downscaling, refugia, resolution, species distribution models, ponds, rivers, dissolved oxygen, hypoxia

Introduction

Organismal fitness varies across environmental gradients and temperature is a key variable directly impacting physiological rates, with a substantial body of research exploring thermal responses in performance, mostly through laboratory studies [1–3]. In water, thermal responses are modulated by water oxygenation, affecting organismal survival [4], body size [5], and distributional ranges [6]. To understand species-environment relationships and predict species responses to environmental change, it is essential to quantify the environmental conditions experienced by organisms in nature [7]. In his 1977 presidential address to the BES, Southwood argued that the habitat could be considered as the templet on which ecological strategies were forged and emphasized the importance of measuring at relevant spatial and temporal scales, by relating the scale of the measurements to the generation time and movements of an organism [8]. Herein lies a challenge, as the spatial and temporal resolution of environmental data is frequently much more coarse grained compared to scales that are relevant for individuals in nature [9]. Although there is broad recognition of the need to incorporate habitat characteristics at finer scales to answer ecological and biogeographical questions at local, regional and even larger scales [7,10,11], such data are often lacking or difficult to obtain, particularly in aquatic systems.

Most work on habitat conditions at the microscale has been performed on land. Here small-scale variations in temperature, humidity and solar radiation can be substantial, mediated by differences in topography, vegetation and soil type. These factors are often considered together as the microclimate given the strong interactive effects of air humidity, temperature, and insolation. In arthropods, for example, air temperature modulates water balance [12], whilst moisture modulates thermal preference [13]. In water, the high conductivity and heat capacitance of water reduces the opportunities for fine scale spatial variation in temperature compared to on land. Most work on thermal variation in freshwater ecosystems relates either to vertical clines due to lake stratification or temporal variation in water temperature, and very few studies have focused on thermal variation in the shallow littoral zones of freshwater ecosystems [14–17]. Oxygenation, already mentioned as an important modulator for thermal responses of aquatic organisms, can exhibit substantial spatial variation in aquatic ecosystems, contrasting with the situation on land, where oxygen levels are much more invariant. For example, strong diurnal fluctuations in oxygen levels have been documented in shallow freshwater ecosystems [18–20].

Given the importance of the coupling between water temperature and water oxygenation for aquatic organisms, we investigated spatial and temporal variation in both water oxygenation and temperature across running (2 sites) and standing waters (2 sites) in southern Britain. We compare and measure temperature and oxygen at the microscale using spot measurements and at the scale of the waterbody using data loggers. We explore how time of day and season drive variation in both temperature and oxygen and whether their impacts differ for running and standing waters. We also ask to what extent small scale variation can be predicted from coarse resolution data, by relating microhabitat variation in temperature and oxygen to measurements from the water column and to regional weather data. Our study characterizes oxygen conditions at the microhabitat scale across running and standing water bodies and how the dynamics and its predictability differs from those of water temperature.

Methods

Data collection

Data were collected in four different water bodies (i.e. sites), two running and two standing (Fig. S1). These were all located on private lands in Devon (UK, 50°29'N 3°48'W). Running waters were the river Mardle, which originates on Dartmoor and discharges into the river Dart and a small first order stream, which discharges into the river Mardle. Standing waters comprised a duckpond in a forest and a sun-exposed reservoir, both close to Buckfastleigh. Handy Polaris Loggers (OxyGuard) were deployed in each site. Periodically these were retrieved, read out, calibrated, serviced and redeployed during the period from December 23rd 2011 to July 17th 2012. Loggers were placed such that they measured the oxygen conditions in the water column, 5-10 cm above the sediment, at a depth of 20-40 cm (note that this is equivalent to the open water microhabitat sampled below).

We also performed spot measurements to characterise microhabitat conditions during 5 field visits (Table S1). On each visit, water temperature and water oxygenation were measured across representative microhabitats in each site. Typically, 3-5 microhabitats would be measured, and each type of microhabitat would be measured at 5 different spots in the waterbody (i.e. replicates) in the morning and in the afternoon (two sampling times). Spot measurements were made in the littoral zone at a depth up to ~40 cm, and replicate measurements were made in close proximity of one another (within a few meters along the shoreline). Since all four water bodies were quite shallow (< 2 m), no attempt was made to characterise the vertical gradient. Instead, measurements were focussed on the shallow, littoral zone, where insolation is highest and where the vast majority of macroinvertebrates reside. Over these 5 field visits, we collected 775 spot measurements (3-5 microhabitats x morning and afternoon x 5 replicates x 4 sites x 5 visits). We used a battery powered, portable Fibox 3 LCD Trace oxygen meter with a temperature sensor and a DP-PST3 optical oxygen sensor, the end of which is covered in a steel tube to protect both the sensor material and the optical fiber (PreSens GmBH, Germany).

We retrieved weather data on daily temperature and cloud cover from a nearby weather station (Teignmouth) via the Met Office MIDAS Open website [21]. Rainfall data were sourced from the HadUK-Grid Gridded Climate Observations [22], extracting the rainfall data from the 1km^2 that encompassed our study area, and also the 4 adjacent 1km^2, and these data then averaged.

Data analyses

To evaluate variation in spot measurements of water temperature and oxygenation at the microscale, we ran models that included as fixed factors Julian day (as a proxy for seasonal change), time of day (morning or afternoon), site and microhabitat. In addition, we allowed for time of day to vary across site and microhabitat by including the appropriate interactions. We ran the same model for water temperature and oxygen so we could evaluate the relative contribution of the different fixed factors.

To evaluate temporal variation in logger data for water temperature and oxygenation across sites, we ran models that included as fixed factors weather conditions, site and time of day (as a continuous variable). Weather conditions included air temperature, cloud cover and rainfall, averaged over the last 5 days. Preliminary analysis also tested whether 5-day averages for air temperature and cloud cover improved model performance. We included the appropriate interactions to allow the effects of weather conditions and site to vary with time of day. In addition, weather conditions were allowed to affect water temperature and oxygenation differently across sites. We constructed temporal variograms by calculating correlations between water temperature and dissolved oxygen measurements taken at the same location but separated by varying time lags. Ten time lags were used, increasing in length by approximately a factor of two: 15 minutes, 30 minutes, 1 hour, 3 hours, 6 hours, 12 hours, 1 day, 3 days, 1 week, and 2 weeks.To test how well variation in temperature and oxygen at the microhabitat level can be predicted from coarser resolution data, we first tested the relationships between microhabitat spot measurements and logger data, selecting, for each timepoint the microhabitat that was measured, the corresponding reading from the logger for that day and site. Next, we fitted simple linear models relating spot measurements to logger data for both water temperature and oxygenation. We then ran the same models on either the two running water sites or the two standing water sites to evaluate the effect of water body type. To test for potential measurement differences across equipment, we also compared spot measurements obtained for the open water microhabitat (i.e. near the location at which the loggers were deployed), to the data as recorded by the loggers. Finally, variation in spot measurements at the microhabitat level were related to weather conditions. To do so, we included water temperature or water oxygenation (spot measurements) as dependent factors and weather conditions and time of day and their interaction as fixed factors. We also tested whether including site identity and all 2-way interactions further improved model fits.All analyses were performed using R Statistical Software [23]. For oxygen conditions, we focussed our analysis on percent saturation (i.e. 100% saturation = ~21 kpa), rather than dissolved oxygen (moles per litre), as the effects of temperature on oxygen solubility are already accounted for when expressing oxygen conditions in this manner [24].

We also translated the observed variation in water temperature and dissolved oxygen into estimated changes in organismal performance. For temperature, we applied a simple Q_{10} relationship (Q_{10} was set to 2, meaning that a 10 °C increase would result in a two-fold increase in performance), with performance set to 100% at the mean temperature. For oxygen, we related performance directly to oxygen saturation, assuming the focal species to be an oxyconformer [25]. We acknowledge that these are simplified approximations, and that the precise responses to temperature and oxygen will vary across species. Nevertheless, as an initial approach, this provides a useful first-order insight.

Results & Discussion

Microhabitat conditions (small scale spatial variation)

Across the research period, large differences were recorded for both temperature (min: 4.0 °C; max: 14.1 °C) and oxygen saturation (min: 0.52%; max: 183.7%). However, microhabitat variation was partitioned very differently for either temperature or oxygen (Fig. 1; Fig. 2). Variation in temperature was driven predominantly by seasonal differences (Julian day) and much less by diurnal differences and differences across sites (Table 1). In contrast, variation in oxygen saturation was predominantly driven by diurnal differences (i.e. whether measurements were taken in the morning or in the afternoon), especially in standing waters. Here, decomposition processes consuming oxygen and photosynthesis generating oxygen resulted in larger diurnal fluctuations, with oxygen saturation sometimes exceeding 100% (i.e. becoming supersaturated). We also found a strongly significant interaction between time of day and microhabitat (Table 2), indicating that such daily fluctuations in oxygen were more pronounced in some microhabitats in standing waters (e.g. submerged vegetation; Fig. 2). In running waters, both rates of both decomposition and photosynthesis were likely reduced (algae and leaf litter are continuously transported downstream, rather than accumulating) and fluctuations in oxygen saturation are further reduced due the continuous mixing and (re-)aeration in flowing conditions. In addition, there were consistent differences across the different microhabitats sampled (site; Table 2). This means that whilst benthic aquatic invertebrates do not encounter strong thermal gradients on a given day, oxygen gradients may be strong across relatively small distances, especially in standing waters (e.g. moving from a leaf pack to an algal mat). These distances can be as small as a few centimeters when comparing the inside of a leaf pack with the overlying algal mat and may mean the difference between severe hypoxia and physiologically challenging hyperoxia. In running waters, differences in oxygen and temperature are smaller, but occasionally we measured lower oxygen saturation under stones, presumably when leaf litter accumulated and obstructed flow and/or reduced oxygen locally due to decompositional processes. Again, the distances involved are small (<10 cm) and stream invertebrates are sufficiently mobile to escape from putative hypoxic stress in these situations by selecting more exposed microhabitats with higher flow, which they readily do [26,27]. Taken together, this strongly contrasts with the situation on land, where oxygen clines are virtually absent, but short distances may feature strong thermal gradients [10,11].

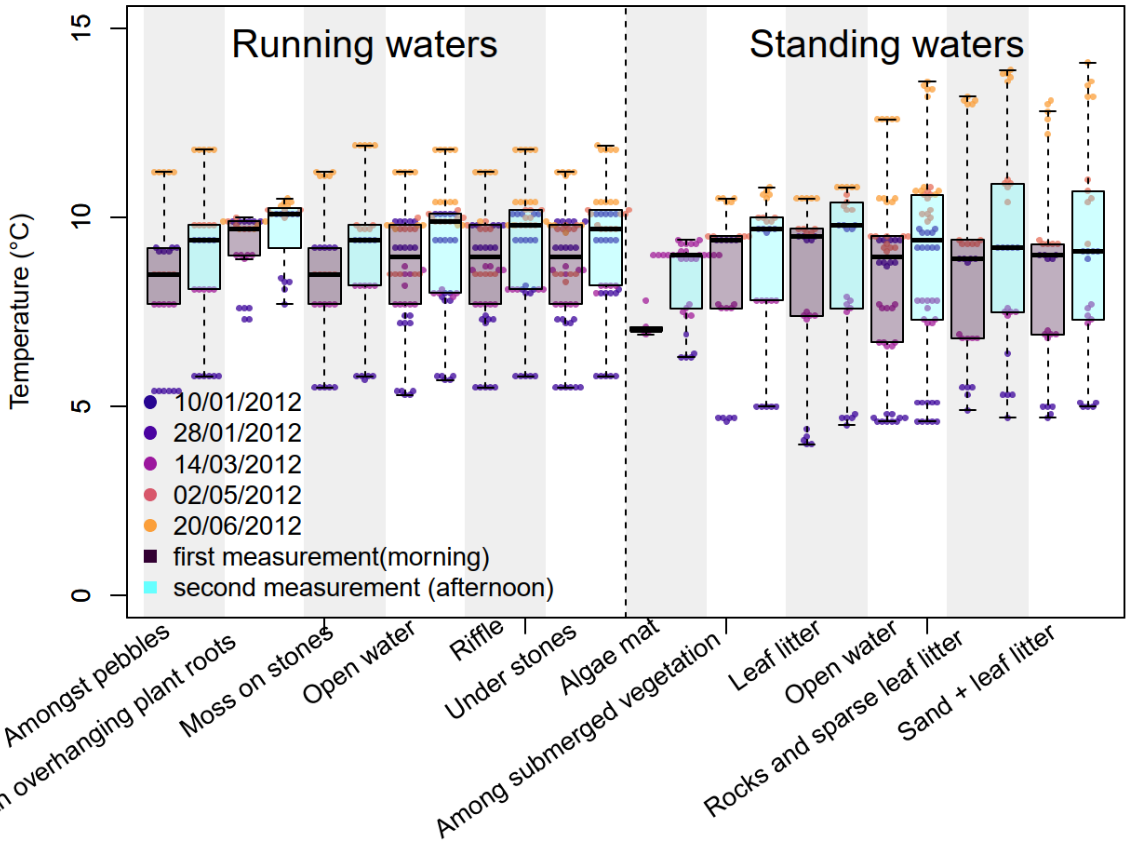

Fig. 1: Microhabitat temperature measured in the morning or afternoon at different microhabitats and at different sites (2 running water sites and 2 standing water sites)

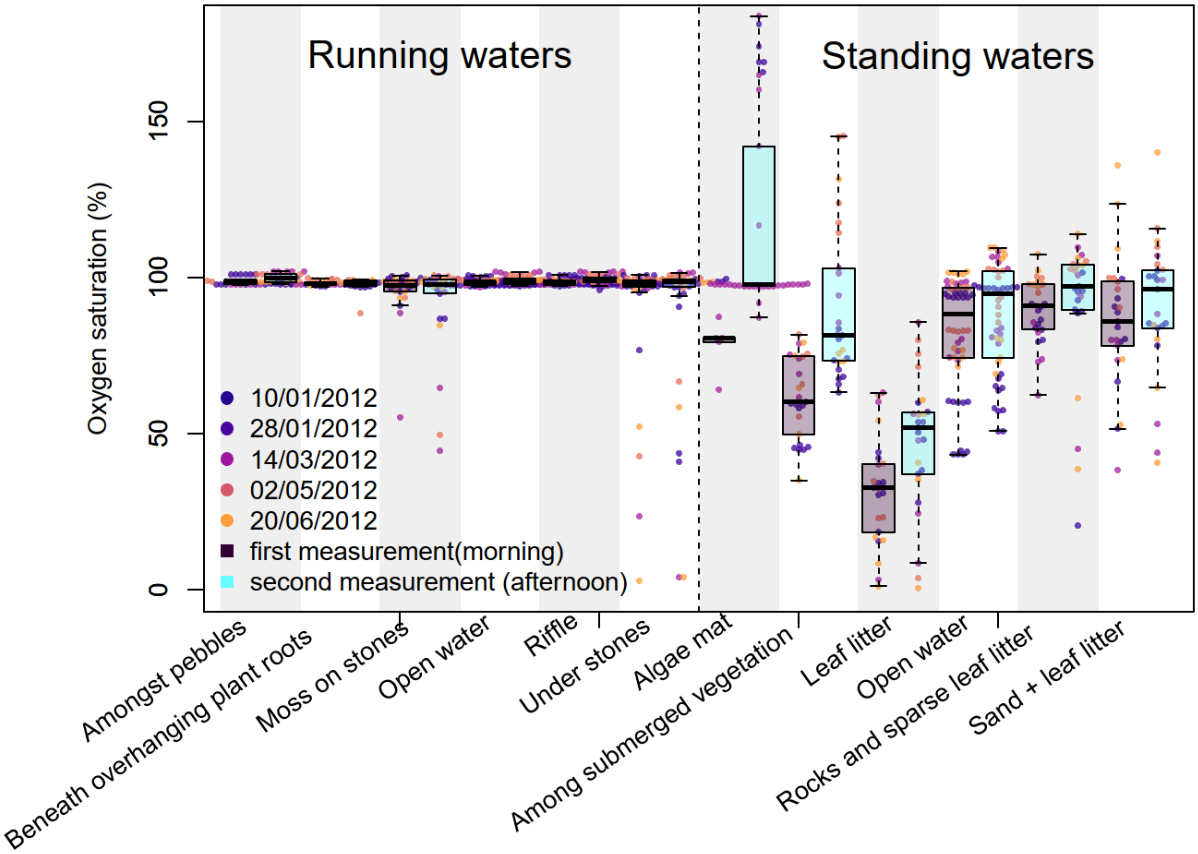

Fig. 2: Microhabitat oxygen saturation measured in the morning or afternoon at different microhabitats and at different sites (2 running water sites and 2 standing water sites)

Table 1: Type III ANOVA results for the model relating variation in microhabitat temperature to season (Julian day), time of day, site, and microhabitat, including their interactions.

Predictor	**Sum Sq**	**Df**	**F value**	***P - value***
(Intercept)	506.34	1	286.02	< 0.001
Julian day	1206.51	1	681.53	< 0.001
Time of day	17.88	1	10.10	0.0015
Site	38.21	3	7.20	< 0.001
Microhabitat	55.15	10	3.12	< 0.001
Time of day × Site	62.83	3	11.83	< 0.001
Time of day × Microhabitat	41.19	10	2.33	0.0106
Residuals	1320.65	746		

Table 2: Type III ANOVA results for the model relating variation in microhabitat oxygen saturation to season, time of day, site, and microhabitat, including their interactions.

Predictor	**Sum Sq**	**Df**	**F value**	***P - value***
(Intercept)	*75055*	*1*	*332.90*	< 0.001
Julian day	*1513*	*1*	*6.71*	*0.0098*
Time of day	*14156*	*1*	*62.79*	< 0.001
Site	*15700*	*3*	*23.21*	< 0.001
Microhabitat	*38205*	*10*	*16.95*	< 0.001
Time of day × Site	*233*	*3*	*0.34*	*0.7932*
Time of day × Microhabitat	*18841*	*10*	*8.36*	< 0.001
Residuals	*168191*	*746*		

Logger data (large scale temporal variation)

The logger data (Fig. S2) show that water temperature varies predictably, largely as a function of air temperature (Fig. 3). Strong relationships between air temperature and water temperature are frequently reported [28], but the exact relationship differs from water body to water body depending on volume, flow, insolation and seepage. For example, our first order stream is notable for being least responsive to air temperature, likely because water temperatures are buffered by seepage of groundwater. Differences in rainfall and cloud cover only lead to an appreciable increase in water temperatures in the sun exposed pond. In contrast, levels of oxygen saturation were affected by air temperature to a much lesser degree (Fig. S3).

We measured pronounced diurnal variation in oxygen saturation in standing waters, especially in the sun exposed pond (Fig. 4). Diurnal variation in temperature was much smaller (Fig. S4). Variation in water temperature could be reasonably accurately modelled from information on weather, site and time of day (R^2 = 72.1%; Table 3), whereas for oxygen saturation the explained variation was lower (R^2 = 63.6%; Table 4). Moreover, air temperature was the strongest predictor for variation in water temperature (already explaining 60.9% of the variation in water temperature by itself), whereas for water oxygenation, differences between water bodies and their diurnal rythm were more important. Since water temperatures were strongly related to air temperature, it is possible to downscale and model water temperature accurately from larger scale predictors. Global maps of freshwater temperature have been constructed and used to predict range limits in fish and geographical variation in amphipod performance [29,30]. Generating such models for water oxygenation will be more difficult as variation in water oxygenation was largely dependent on site specific characteristics (Table 4). Thus, oxygen levels are affected by differences between sites such as sun exposure, seepage, thickness of leaf litter, nutrient input, and primary productivity, as well as the differences between running and standing waters mentioned above. A fruitful direction for future research would therefore be to expand this type of work to include more water bodies and relate site-specific characteristics to their oxygen regimes in more detail.

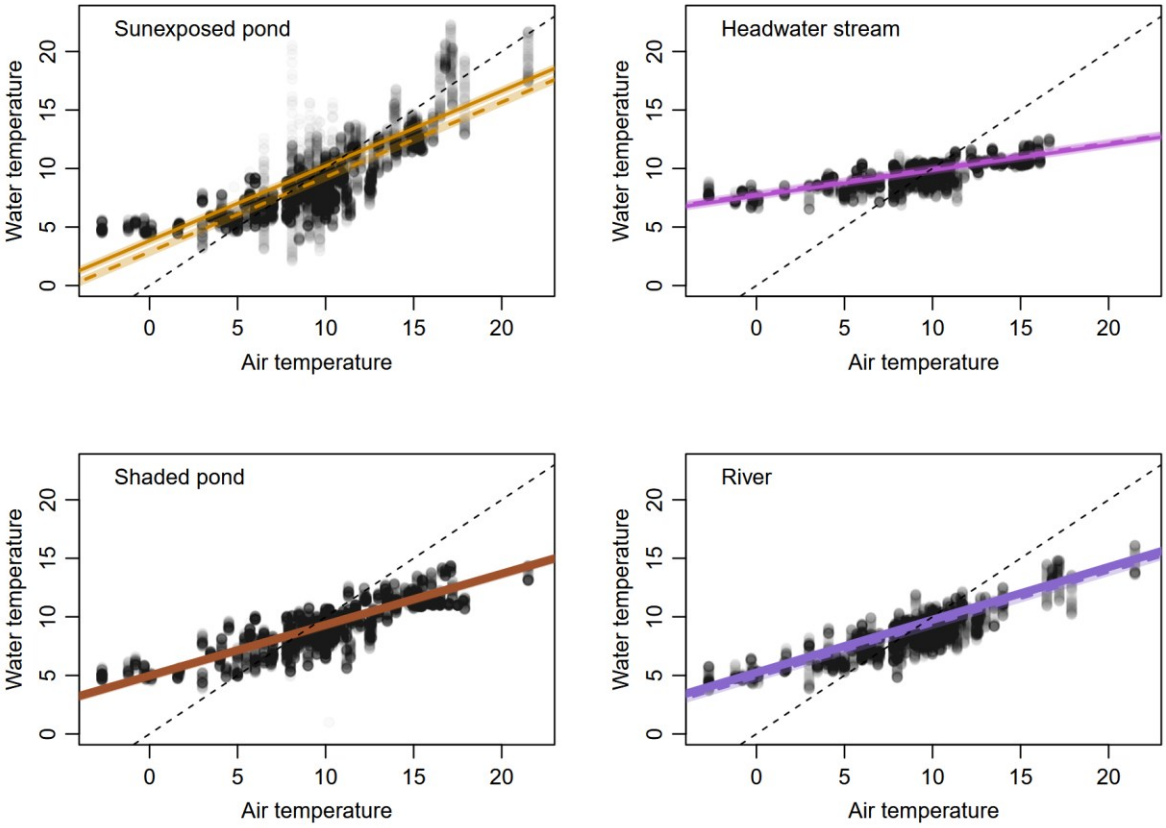

Fig. 3: Logger temperature data, plotted against air temperature for each of the four sites separately, Note the two standing waters are plotted on the left, while the two running waters are plotted on the right. Solid lines indicate days with low cloud cover and no rainfall, while dashed lines indicate day with high cloud cover and rainfall.

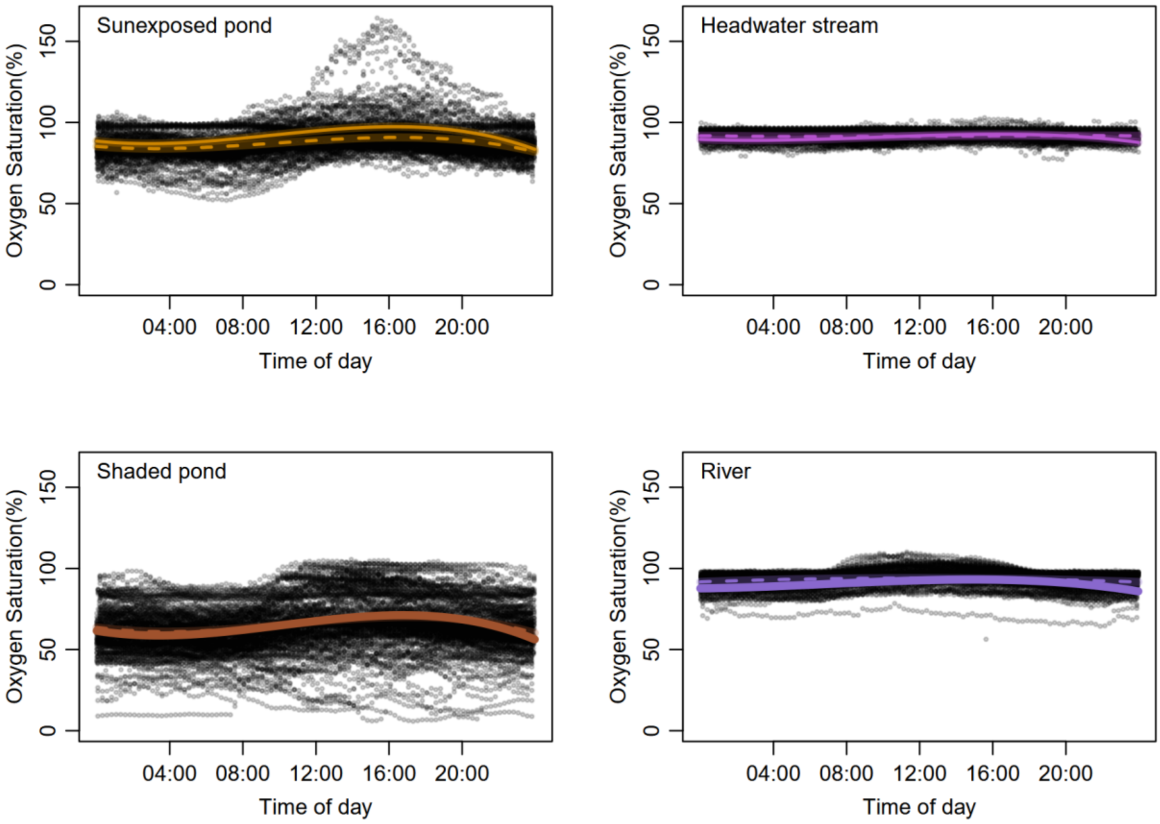

Fig. 4: Logger oxygen saturation data, plotted against time of day for each of the four sites separately, Note the two standing waters are plotted on the left, while the two running waters are plotted on the right. Solid lines indicate days with low cloud cover and no rainfall, while dashed lines indicate day with high cloud cover and rainfall.

Table 3: Type III ANOVA results for the model relating variation in logged water temperature to differences across sites and time of day (Time, modelled as a 3rd degree polynomial), and differences in weather conditions (Air temperature, Cloud cover, Rainfall), including their interactions.

Predictor	**Sum Sq**	**Df**	**F value**	***P - value***
(Intercept)	20498	1	14089.23	< 0.001
Site	7135	3	1634.75	< 0.001
Time (polynomial, df = 3)	1057	3	242.14	< 0.001
Air temperature	87726	1	60299.34	< 0.001
Cloud cover	2144	1	1473.52	< 0.001
Rainfall (lag 5 days)	7	1	5.12	0.0237
Site × Air temperature	17245	3	3951.25	< 0.001
Site × Cloud cover	1666	3	381.71	< 0.001
Site × Rainfall	599	3	137.14	< 0.001
Time × Air temperature	481	3	110.24	< 0.001
Time × Cloud cover	577	3	132.15	< 0.001
Time × Rainfall	207	3	47.32	< 0.001
Site × Time	744	9	56.80	< 0.001
Residuals	77417	53213		

Table 4. Type III ANOVA results for the model relating variation in logged water oxygen saturation to differences across sites and time of day (Time, modelled as a 3rd degree polynomial), and differences in weather conditions (Air temperature, Cloud cover, Rainfall), including their interactions.

Predictor	**Sum Sq**	**Df**	**F value**	***P - value***
(Intercept)	9,597,610	1	97,914.62	< 0.001
Site	1,048,381	3	3,565.19	< 0.001
Time (polynomial, df = 3)	40,885	3	139.04	< 0.001
Air temperature	118,079	1	1,204.64	< 0.001
Cloud cover	13,125	1	133.90	< 0.001
Rainfall (lag 5 days)	47,841	1	488.07	< 0.001
Site × Air temperature	206,027	3	700.63	< 0.001
Site × Cloud cover	68,784	3	233.91	< 0.001
Site × Rainfall	95,405	3	324.44	< 0.001
Time × Air temperature	8,773	3	29.83	< 0.001
Time × Cloud cover	1,925	3	6.55	< 0.001
Time × Rainfall	21,040	3	71.55	< 0.001
Site × Time	106,050	9	120.21	< 0.001
Residuals	5,215,949	53213		

Temporal variograms assess the autocorrelation in the data by calculating correlations between water temperature and dissolved oxygen measurements taken at the same location but separated by varying time lags (Fig. 5). These show that the ability to predict oxygen saturation from prior measurements decays faster than for temperature. Within 12 hours, predictability for oxygen saturation drops below 50% in all four sites, whilst predictability for temperature is above 50% for up to a week. At exactly 24 hours, explained variation increases, as it is then in sync with the diurnal fluctuations, and as we have seen above, this effect is stronger for oxygen saturation than for water temperature. This means that not only are there more factors involved in driving oxygen dynamics compared to temperature dynamics (which is largely governed by air temperature), but these also likely act over shorter time scales.

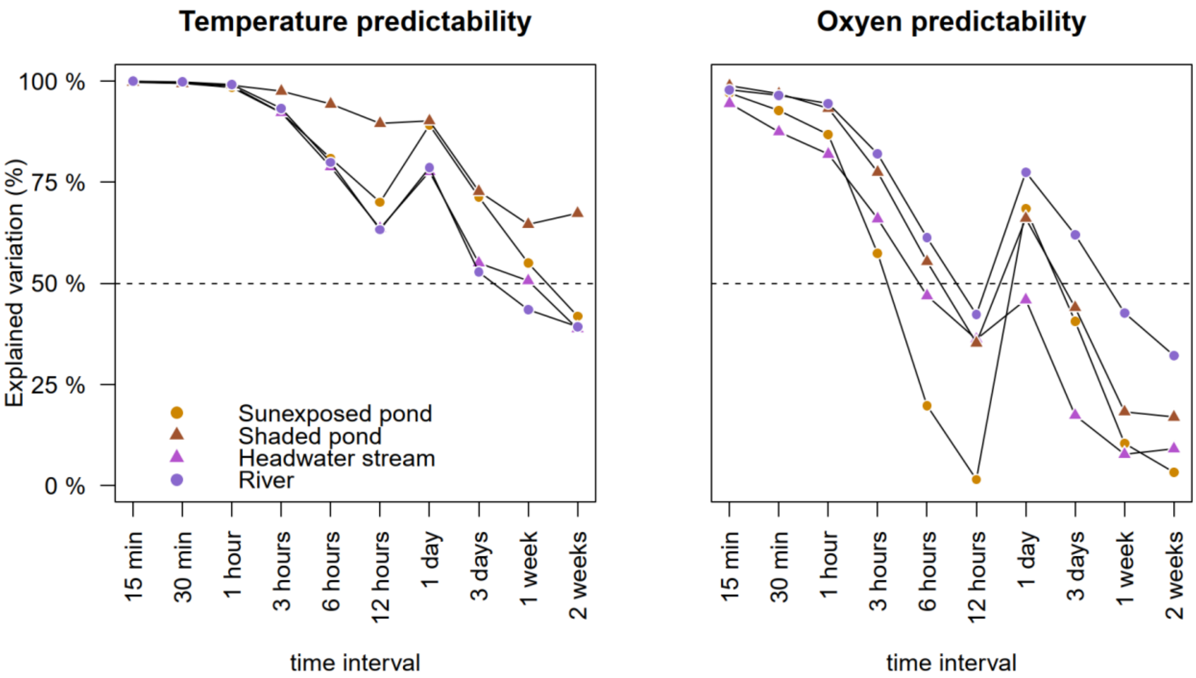

Figure 5. Temporal variograms showing the explained variation when correlating measurements of water temperature (left panel) and oxygen saturation (right panel) taken at the same location but separated by varying time lags. Each site is indicated by a separate line and symbol. The time lags chosen such that they increase in length by approximately a factor of two (see methods).

Relating logger data and microhabitat data

We tested how well variation in temperature and oxygen at the microhabitat level (i.e. spot measurements) can be predicted from measurements in the water column obtained by the logger. For temperature, this yielded strong correlations, which were close to the y=x line (Fig. 6). This follows from the fact that on any given day there are no strong temperature gradients so the logger data with a coarser spatial resolution can accurately reflect the temperatures in the microhabitats. For oxygen saturation, we also found a line close to the y=x line for standing waters, but with much more scatter. In running waters, variation in microhabitat oxygen saturation could not be explained because loggers showed approximately constantly high oxygenation (Fig. 7). Note that the scatter in oxygen saturation levels in standing waters arises due to differences across microhabitats; when relating oxygen measurements for the microhabitat open water, i.e. near the location at which the loggers were deployed, we observed a strong correlation, so differences in measurement errors across equipment are small (Fig. S5).

The next step is to further scale up and see how well variation in microhabitat conditions can be related to coarse resolution weather data. For temperature, variation at the microhabitat scale could be related to coarse scale weather conditions and time of day (R^2 = 87.1). For oxygen, variation at the microhabitat scale was weakly associated with coarse scale weather conditions and time of day (R^2 = 3.7%). Including site as a factor in these models increased the explained variation (Temperature: R^2=97.9%; Oxygen: R^2=47.1%). However, site effects here primarily account for unmeasured, site-specific characteristics and therefore lack general predictive power.

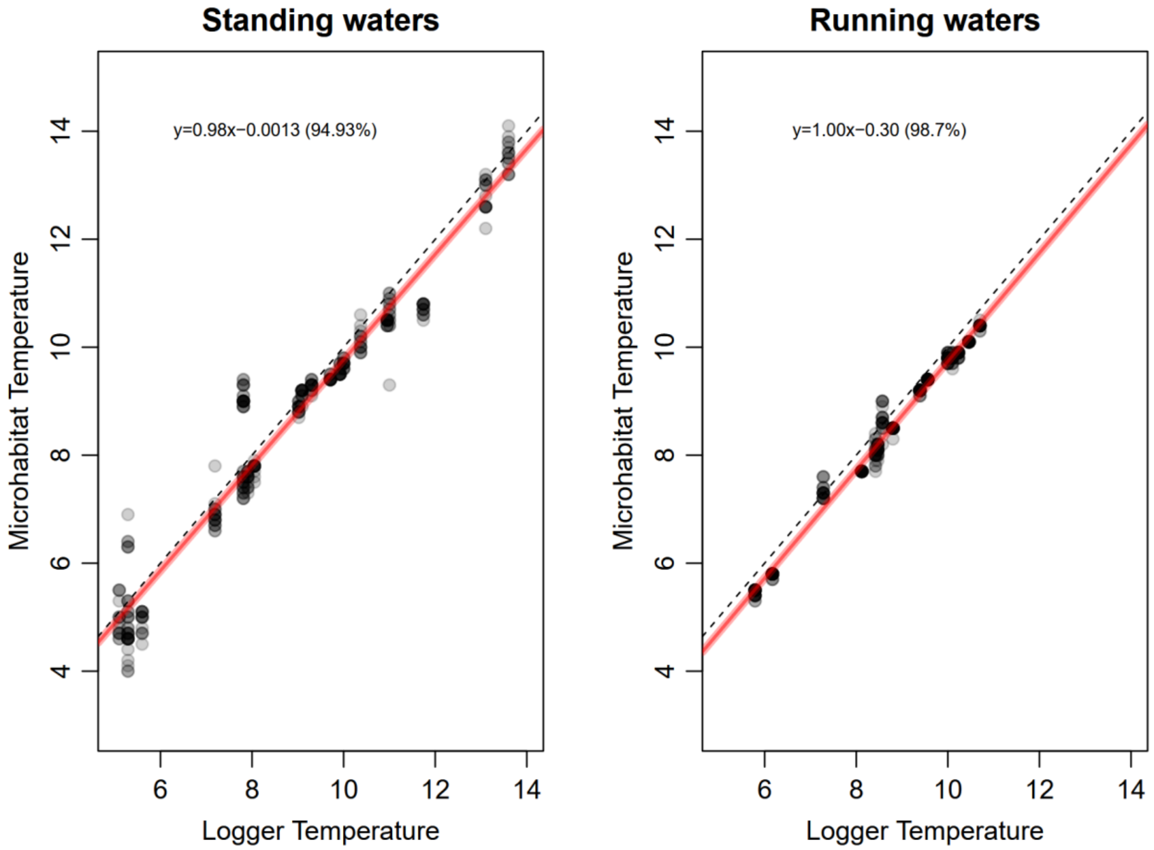

Fig. 6. Relationship between temperature measured by the logger and the temperature measured in microhabitats.

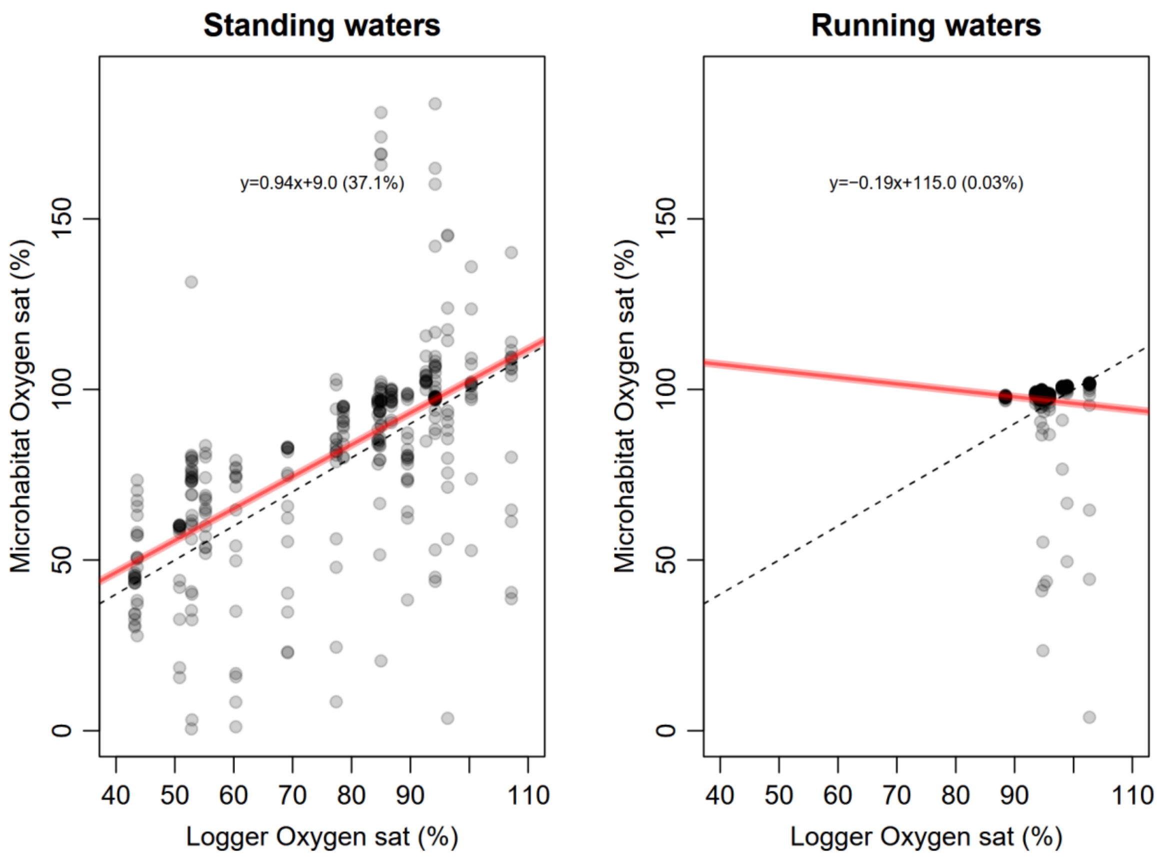

Fig. 7. Relationship between oxygen saturation measured by the logger and the temperature measured in microhabitats.

Effects of water temperature and oxygenation on performance

Quantifying the conditions that freshwater life is exposed to is of course only the first step. By combining exposure with species' sensitivities, we can potentially gauge how it will affect their performance. Although freshwater species differ in their sensitivity to both temperature, oxygen and their interaction [4,31,32], we provide a first-order insight by translating the observed variation in water temperature and oxygenation into estimated changes in organismal performance (see methods). Differences in performance due to small scale spatial variation, as captured by the spot measurements in the microhabitat, are primarily due to variation in oxygen (Fig. 8): At a given measurement moment, differences in performance due to spatial variation in temperature are minor (<6%), wheras differences in oxygen saturation may strongly affect performance (up to 69%), even in running waters (34%).

Temporal differences in performance due to daily fluctuations show a larger effect of temperature (10-12%) (Fig. 9). As oxygen does not fluctuate strongly in the water column in running waters, performance is not much affected (6%), but in the water column of standing waters, oxygen fluctuations have greater effects on organismal performance (23%) than thermal fluctuations (12%).

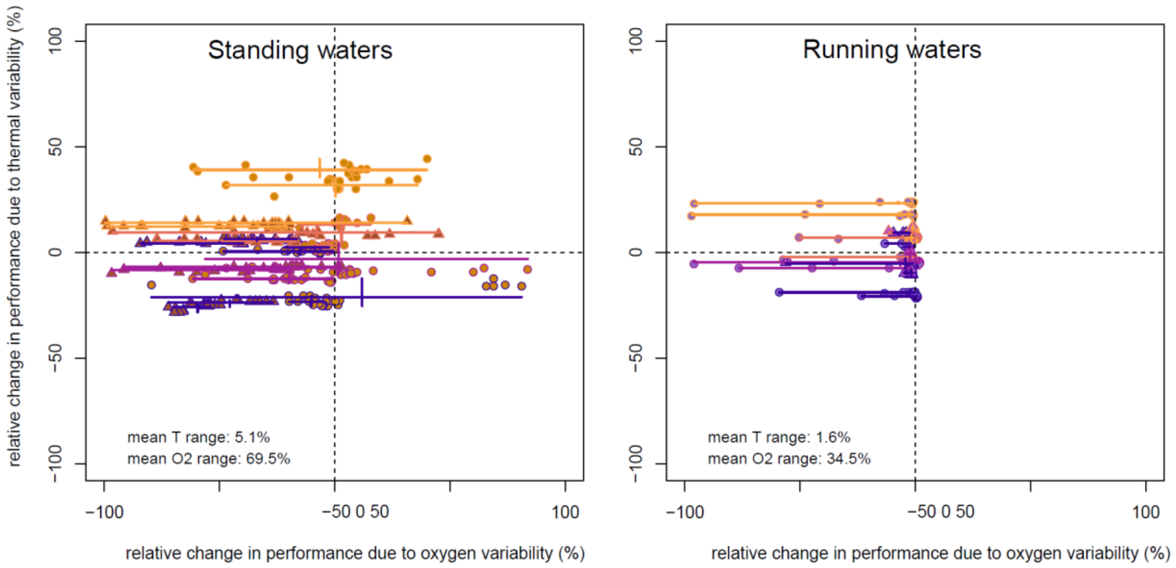

Figure 8. Relative changes in performance due to microhabitat scale variation in water temperature and oxygenation for standing waters (left panel) and running waters (right panel). See methods for how variation in temperature and oxygen was translated into performance differences. All spot measurements are shown, and for each sampling day and sampling moment (5 days x 2 sampling times), we calculated the range in performance, shown as vertical (oxygen) and horizontal (temperature) lines.

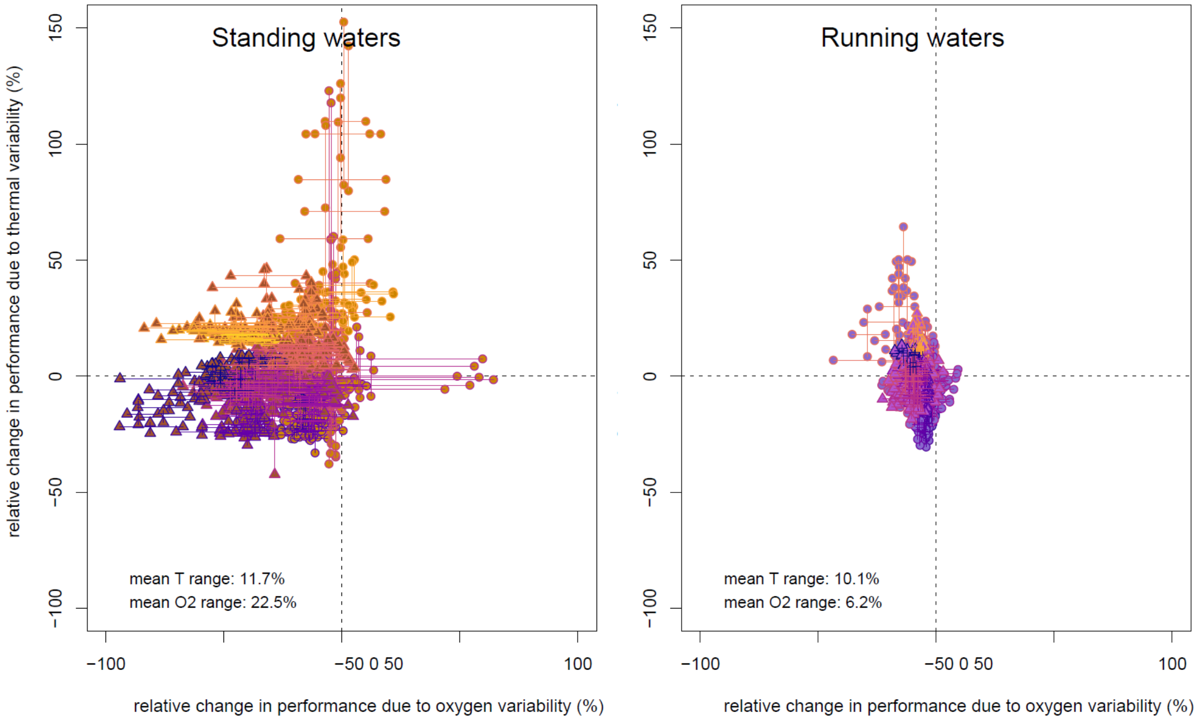

Figure 9. Relative changes in performance due to temporal variation in water temperature and oxygenation for standing waters (left panel) and running waters (right panel). See methods for how variation in temperature and oxygen was translated into performance differences. All logged data obtained from the water column are shown, and for each sampling day, we calculated the range in performance, shown as vertical (oxygen) and horizontal (temperature) lines.

Conclusion

According to Southwood, the habitat is the templet for ecological strategies [8]. Here we have quantified variation in temperature and oxygen, two key niche axes for aquatic life, something which is rarely done, particularly across biologically relevant spatial scales. Both spatial and diurnal variation in water temperature was minor (in most cases well below °2 C)), at least for the water bodies investigated here, and could be reasonably well predicted from coarser resolution data. In contrast, steep gradients in water oxygenation across small distances (0-15 cm) and over short time periods (daily fluctuations) are the norm in shallow freshwaters. Such gradients were especially pronounced in standing waters, but even in generally well-oxygenated running waters there are pockets of hypoxia.

Running water organisms can to some extent escape hypoxic conditions by selecting areas with higher flow [26,27], reducing the boundary layer around their bodies and enhancing oxygen diffusion [33]. However, this likely carries costs in terms of abrasion, predation and dislocation. The fact that oxygen conditions in the microhabitat may be different from water oxygenation measured in the water column, may explain why the latter has sometimes been found to be a poor predictor for the occurrence of taxa such as Ephemeroptera, which was better captured by variation in biochemical oxygen demand (BOD) [27], as BOD likely better reflects oxygen minima to which stream insects may be exposed in their microhabitats. In standing waters, benthic invertebrates will frequently experience hypoxia in their microhabitats, driving the evolution of strategies to tolerate this, explaining why they are usually fairly resistant to some degree of hypoxia [34]. In conclusion, we show clear contrasts, when comparing temperature-oxygen conditions on land and in water, suggesting that animals in water will have much more pronounced adaptations to cope with fluctuations in oxygen [35], whilst those on land will have evolved adaptations to cope with thermal heterogeneity.

Acknowledgements

We thank Donna and Kevin Cox for their generosity and providing access to their land for this study. We are also indebted to Lies Verberk-de Jonge, who assisted with typewriting the logger measurements, when the loggers failed to automatically transfer the data.

Data availability statement

The data and code used in this manuscript are openly available [36].

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Supplementary information.

Table S1. Characterisation of the different microhabitats sampled.

Microhabitat	Description	Site(s) where present
Amongst pebbles	spot measurements taken in between small pebbles (2-5 cm in length), laying on the river bed.	River
Beneath Overhanging plant roots	spot measurements taken in between plant roots hanging in the water at the edge of the stream.	Headwater stream
Moss on stones	spot measurements taken in between moss growing on shallow stones (5-10 cm deep) in the riffle.	River
Open water	spot measurements taken in the water column, i.e. away from the bottom substrate, stones and submerged vegetation, at a depth of 20-40 cm.	All four sites
Riffle	spot measurements taken directly in the flowing water at a riffle, at a depth of 5-10 cm.	River, Headwater stream
Under stones	spot measurements taken in under larger stones (20-50 cm in length), laying on the river bed.	River, Headwater stream
Algae mat	spot measurements taken in between submerged patches of algae growing near the shoreline at a depth of 10-30 cm.	Sunexposed pond
Among submerged vegetation	spot measurements taken in between submerged vegetation at a depth of 30-50 cm.	Shaded pond
Leaf litter	spot measurements taken in between submerged leaves that accumulated near the shoreline, at a depth of 10-30 cm.	Shaded pond
Rocks and sparse leaf litter	spot measurements taken in between submerged leaves that accumulated near the shoreline on a rocky substrate, at a depth of 10-30 cm.	Sunexposed pond
Sand + leaf litter	spot measurements taken in between submerged leaves that accumulated near the shoreline on a sandy substrate, at a depth of 10-30 cm.	Sunexposed pond

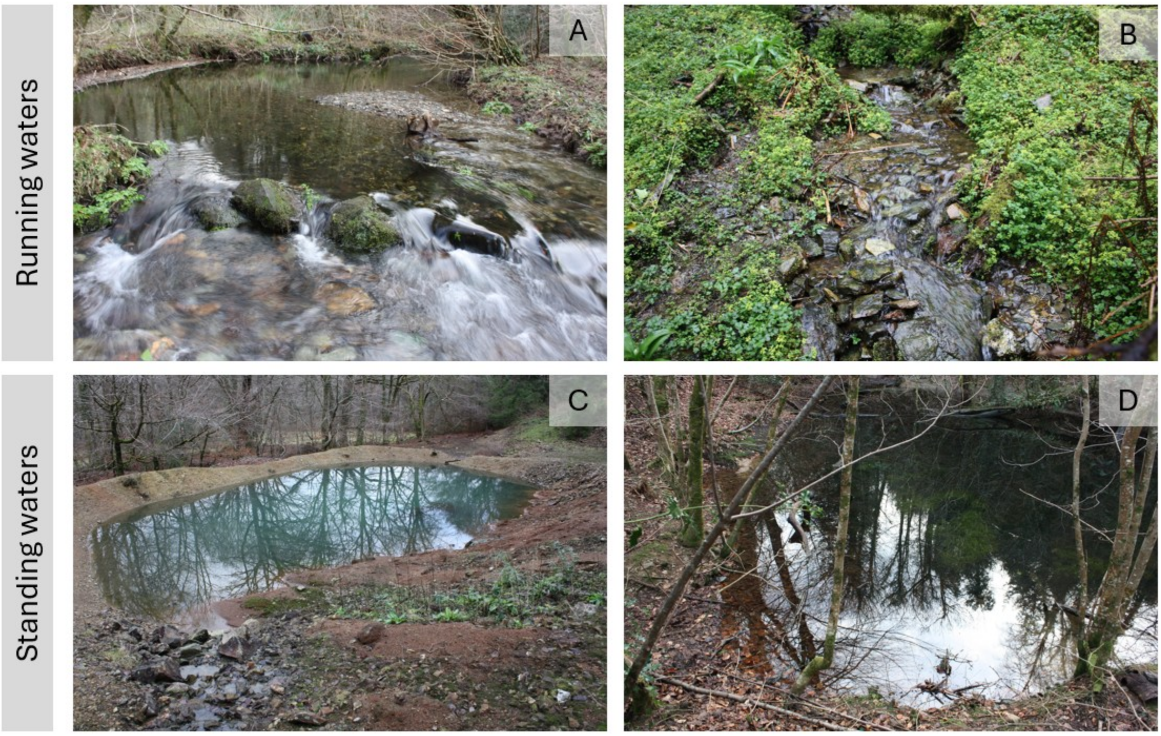

Fig. S1: Pictures of each of the sampled sites, comprising running waters (A,B) and standing waters (C,D). A: Small river, B: Headwater stream, C: Sun-exposed pond, D: Shaded pond. Photo credit: Wilco Verberk.

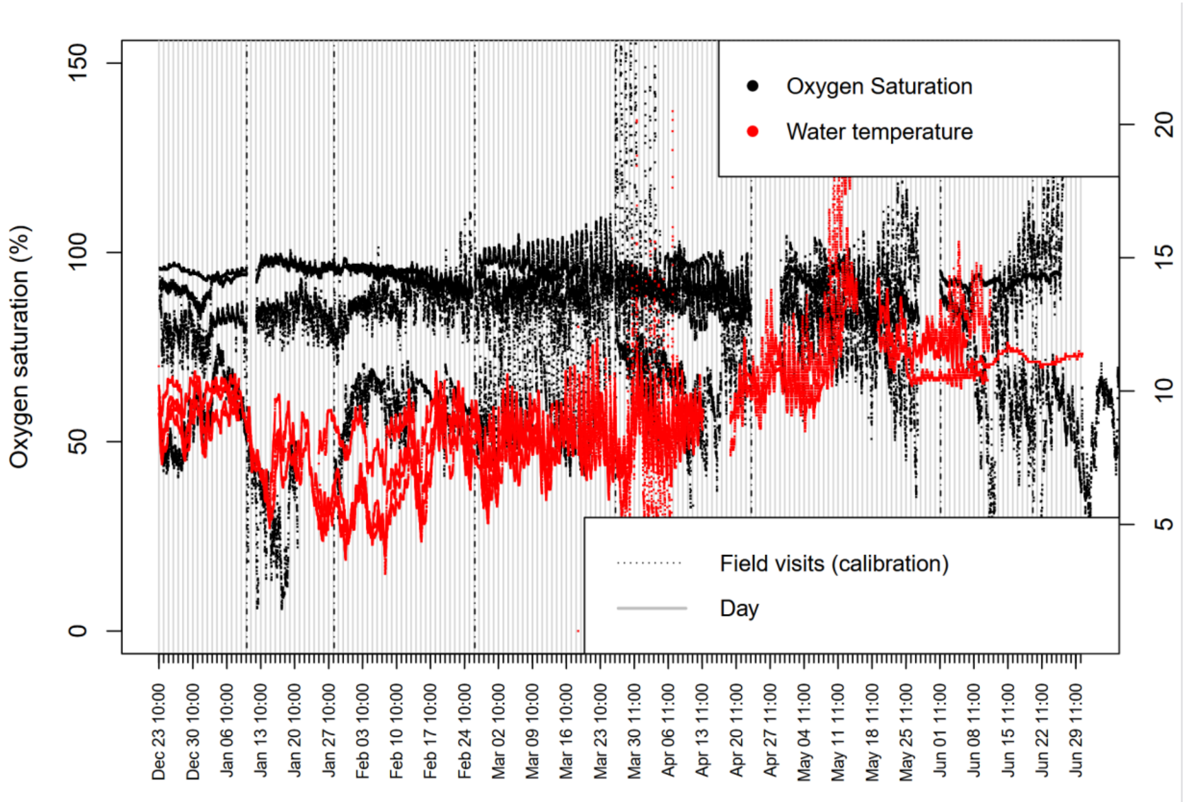

Fig. S2: Raw data of the loggers in all four sites, showing temperal variation in oxygen saturation (black, left axis) and water temperature (red, right axis).

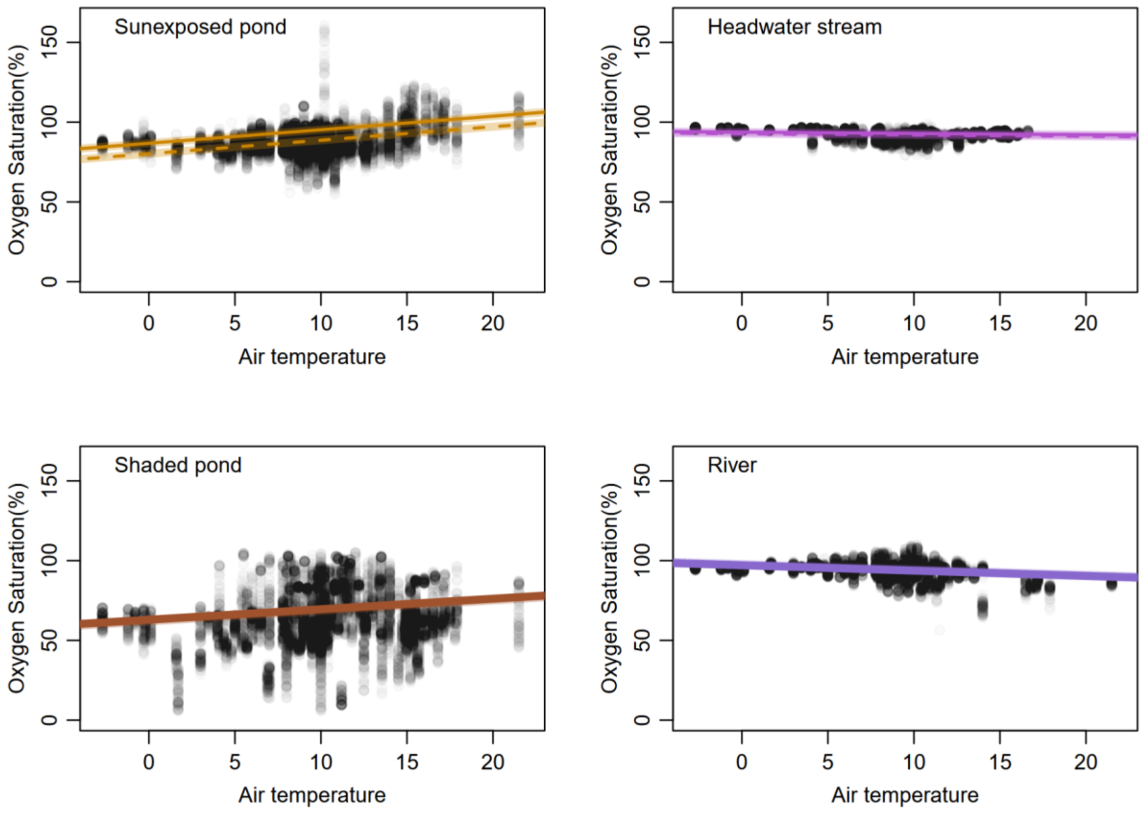

Fig. S3: Logger oxygen saturation data, plotted against air temperature for each of the four sites separately, Note the two standing waters are plotted on the left, while the two running waters are plotted on the right.

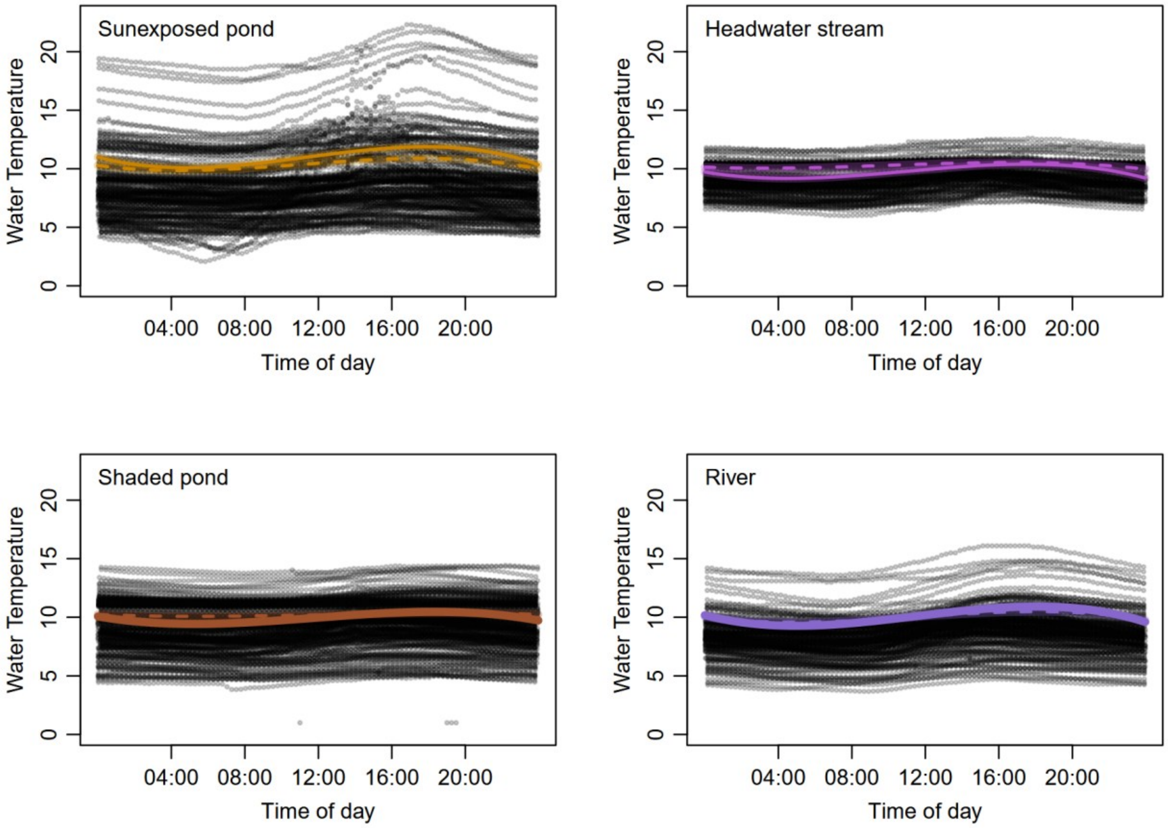

Fig. S4: Logger water temperature data, plotted against time of day for each of the four sites separately, Note the two standing waters are plotted on the left, while the two running waters are plotted on the right.

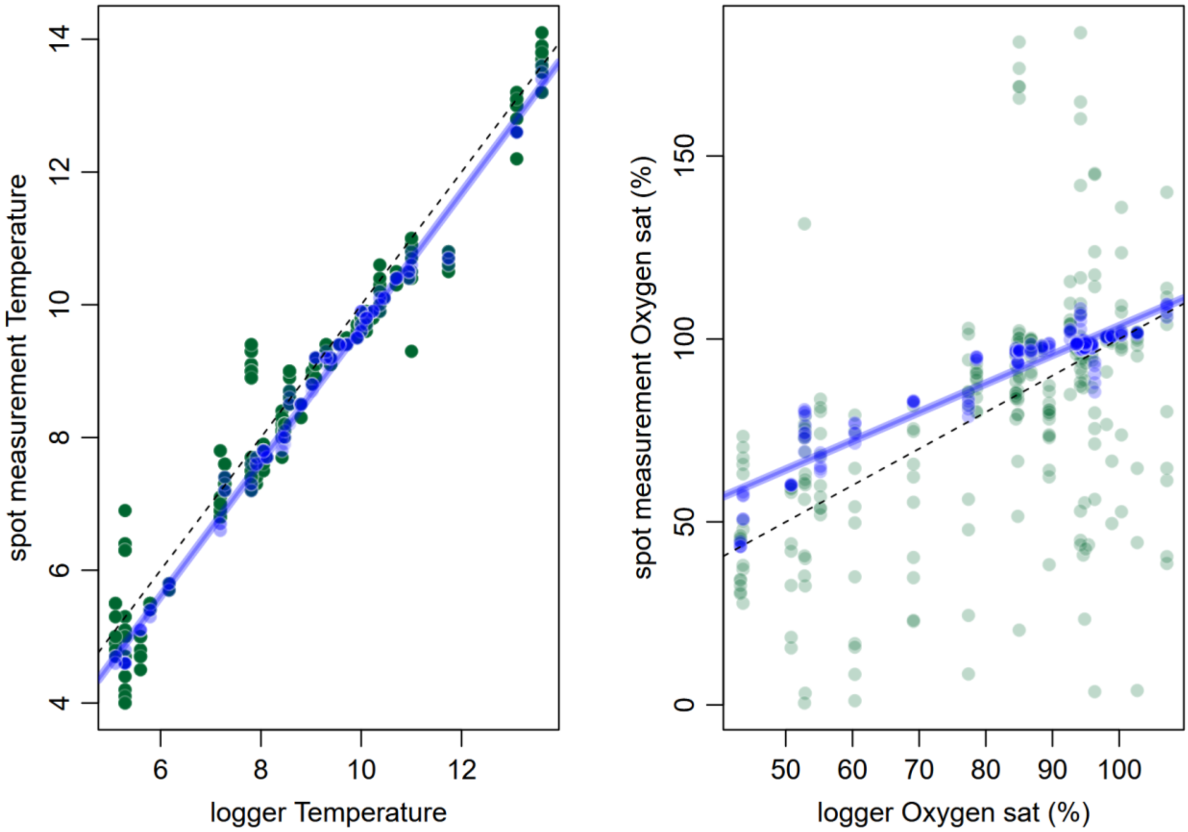

Fig. S5: Relationship between data obtained by the logger and data from spot measurements in the microhabitat for temperature (left) and oxygen (right). In each panel, blue points represent measurements in the open water (i.e. near where the logger was deployed), while green points represent spot measurements in other microhabitats. The black dashed line represents y=x. For the open water microhabitat the relationship is also shown as a (blue) line.