Diel variations in the assemblage structure and foraging ecology of larval and 0+ year juvenile fishes in a man-made floodplain waterbody

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Running headline: DIEL ECOLOGY OF 0+ YEAR FISHES

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ABSTRACT

This study investigated diel variations in zooplankton composition and abundance, and the species composition, density, size structure, feeding activity, diet composition and prey selection of larval and 0+ year juvenile fishes in the littoral of a man-made floodplain waterbody over five 24-h periods within a 57-day period. There was a significant difference in the species composition of diurnal and nocturnal catches, with most species consistently peaking in abundance either during daylight or at night, reflecting their main activity period. However, there were no *consistent* diel patterns in assemblage structure or the abundance of some species, most likely, respectively, due to the phenology of fish hatching and ontogenetic shifts in diel behaviour or habitat use. There were few clear diel patterns in the diet composition or prey selection of larval and 0+ year juvenile roach *Rutilus rutilus* and perch *Perca fluviatilis*, with most taxa consistently selected or avoided irrespective of the time of day/night, and no obvious shift between planktonic and benthic food sources, but dietary overlap suggested that interspecific interactions were likely strongest at night. It is essential that sampling programmes account for the diel ecology of the target species, as diurnal surveys alone could produce inaccurate assessments of resource use. The relative lack of consistent diel patterns in this study suggests that multiple 24-h surveys are required in late spring and early summer to provide accurate assessments of 0+ year fish assemblage structure and foraging ecology.

Key words: behaviour; diet composition; feeding activity; prey availability; prey selection; zooplankton.

INTRODUCTION

Temporal variations in organism abundance and population structure are fundamental to the processes driving biological diversity, community ecology and ecosystem functioning. They can also have implications for the surveillance, conservation and management of species of particular interest (Cowx *et al*., 2009; Reynolds *et al*., 2011; Nunn & Cowx, 2012; Nunn *et al*., 2014). In addition to species-specific generational fluctuations and seasonal cycles in abundance, fish assemblage structure can vary on a diel basis, with some species or life stages undertaking substantial migrations to forage or avoid predators (Copp & Jurajda, 1993; Copp, 2010; Mehner, 2012; Janáč & Jurajda, 2013; Muška *et al.*, 2013). In deep lakes, for example, larval and juvenile smelt *Osmerus eperlanus* (L.), perch *Perca fluviatilis* L. and roach *Rutilus rutilus* (L.) often migrate into the epilimnion at dusk and the hypolimnion (smelt) or littoral (perch and roach) at dawn (Gliwicz & Jachner, 1992). Diel variations in fish feeding activity and diet composition can also occur, as a consequence of shifts in behaviour, habitat use or prey abundance (Horppila, 1999; Copp *et al.*, 2005; Gliwicz *et al.*, 2006); some species forage only during daylight, for example, whereas others may switch from particulate feeding during daylight to benthic feeding at night (Garner, 1996*a*). Diel variations in invertebrate distributions (*e.g.* Gliwicz, 1986; Lauridsen *et al.*, 1996) can have significant implications for the foraging ecology, and potentially the growth, survival and recruitment success, of fishes (see Nunn *et al.*, 2012). This is of particular importance during early development, when fishes are invariably most vulnerable to competition, as well as predation, disease and environmental perturbations (Cryer *et al.*, 1986; Nunn *et al.*, 2007*a*; Longshaw *et al.*, 2010).

Knowledge of the temporal ecology of fishes is fundamental both to understanding the processes that function at the individual, population and community levels, and for the management and conservation of their populations and habitats (Nunn *et al.*, 2012, 2014). Although a number of studies have investigated diel variations in the assemblage structure of fishes, few appear to have examined the impacts of diel variations in prey availability on the foraging ecology of larvae and 0+ year juveniles. The aim of this study was thus to investigate diel variations in (1) zooplankton composition and abundance, and (2) the species composition, density, size structure, feeding activity, diet composition and prey selection of larval and 0+ year juvenile fishes in the littoral of a man-made floodplain waterbody. The rationale was that resource use may be substantially greater over the diel cycle than during daylight or darkness alone, and that estimates of niche breadth, competition or resource partitioning based solely upon diurnal (or nocturnal) studies are potentially inaccurate (Copp, 2008). The hypotheses were that there would be diel variations in fish species composition, density, size structure and feeding activity, and that diel variations in zooplankton composition and abundance would have an impact on their foraging ecology.

MATERIALS AND METHODS

Diel variations in the assemblage structure and foraging ecology of larval and 0+ year juvenile fishes were examined in the littoral of a man-made floodplain waterbody (52.9476 °N, 1.09361 °W, surface area ~1 ha, max. water depth ~2 m, max. water depth in sampling area 1.5 m) connected to the River Trent in Nottingham, central England, by a 30-m long × 20-m wide channel. A floodplain waterbody was chosen because they provide important nursery habitats and invariably superior feeding opportunities than the mainstem for planktivorous fishes (Bass *et al.*, 1997; Nunn *et al.*, 2007*b*). The Trent is the third longest river in the UK (274 km), with a long-term mean discharge of ~85 m^3s^{-1} and a catchment area of 10 500 km^2. The river is impounded by a number of large weirs and sluices, resulting in a relatively stable discharge regime (Nunn *et al.,* 2007*a*), and channelised in many areas, but attempts are being made to re-establish the link between the mainstem and floodplain (Nunn *et al.,* 2007*b*; Bolland *et al*., 2012). The substratum in the study site consists largely of gravel and silt, and vegetation (mainly *Acorus calamus* L., *Glyceria maxima* (Hartm.) and *Sparganium erectum* L.) is present in the shallow water along the shoreline. Rotifers, copepod nauplii and small cladocerans (*Bosmina longirostris* (Müller) and Chydoridae) are the most abundant zooplankton groups (Nunn *et al*., 2007*b*, *c*), and *Hemimysis anomala* G. O. Sars, a non-native mysid, is also present and exhibits diel variations in distribution and behaviour (Nunn & Cowx, 2012). The 0+ year fish assemblage is characterised by eurytopic and rheophilic species, with the presence of the latter indicating that fishes are able to move from the mainstem into the study site (Nunn *et al*., 2007*b*; Bolland *et al*., 2012).

DATA COLLECTION

Fishes were captured every 3 h over a 24-h cycle on 19/20 May, 2/3 and 16/17 June, 30 June/1 July and 14/15 July 2010 using a micromesh beach seine (25 m long by 3 m deep, 3 mm hexagonal mesh; Cowx *et al.,* 2001); a 3-h interval between samples was considered sufficient for gut passage given the water temperature (15-20 ˚C) and sizes of the fish (Persson, 1986; Garner, 1996*a*; Horppila, 1999). Sampling was conducted in the same location (96 m^2) on each occasion, and was restricted to the margins in water ≤1.5-m deep, where 0+ year fishes tend to aggregate (Copp & Garner, 1995). Fish were identified to species, categorised as larvae or 0+ year juveniles (the juvenile period begins with disappearance of any remnants of the preanal finfold, complete differentiation of the fins and the onset of squamation; Peňáz, 2001) and measured for standard length (L_S, nearest 1 mm), then returned to the water; randomly selected sub-samples were retained for diet analysis.

Zooplankton populations were surveyed via five randomly selected samples collected concurrently with and in the same area as the fish samples, using a 10-L container (Viroux, 1997). Each sample was sieved through a 100-μm-meshed net and preserved using 4% formalin solution, and later stained with Rose Bengal to facilitate observation of small transparent organisms. Whilst the mesh size of the net likely underestimates the densities of the smallest rotifers (Bottrell *et al.*, 1976), it was considered satisfactory for the sizes eaten by larval and 0+ year juvenile fishes (Bass *et al.*, 1997; Nunn *et al.*, 2007*b*, *d*). In the laboratory, each zooplankton sample was made up to 100 mL with 4% formalin solution and thoroughly mixed before withdrawing a 500 μL sub-sample with a wide-bore, automatic pipette. Sub-samples were emptied into a Sedgewick Rafter counting chamber, and all organisms were identified to the lowest practicable taxonomic level and enumerated using a binocular microscope. Three sub-samples were analysed for each sample.

For each sampling occasion, the contents of the entire gastrointestinal tract were removed from a minimum of ten larval and ten 0+ year juvenile roach (n = 279) and perch (n = 228), when present; these species were chosen as they were the most abundant in all surveys and have been the focus of competition/resource partitioning studies during daylight (*e.g.* Persson, 1983, 1987; Persson & Greenberg, 1990), but not darkness. Food items were identified to the lowest practicable taxonomic level and recorded as percent volume. The points method (0 points = empty gut, 2 = ¼ full, 4 = ½ full, 6 = ¾ full, 8 = completely full, 10 = distended; Hynes, 1950) was used to assess feeding activity.

DATA ANALYSIS

A Bray-Curtis similarity matrix (Bray & Curtis, 1957) was calculated using the abundance (no. m^{-2}, fourth-root transformed) of each fish species in each sample and ordinated (all replicates and group centroids with trajectories) using non-metric multidimensional scaling (MDS) to investigate similarities in the species composition of diurnal and nocturnal micromesh seine catches (Clarke & Warwick, 2001). The matrix was then submitted to permutational multivariate analysis of variance (PERMANOVA) (9999 random permutations) to assess the statistical significance of any differences in the species composition of diurnal and nocturnal catches, and also between surveys (Anderson, 2001; Anderson *et al.*, 2008). In addition, similarity percentages (SIMPER) analysis was used to calculate the percentage contributions of each fish species to dissimilarities in diurnal and nocturnal catches (Clarke & Warwick, 2001). For each survey, the length distributions of all (including >0+ year) roach and perch, the most abundant species in all surveys, were compared between day and night using two-sample Kolmogorov-Smirnov tests to investigate diel variations in size structure (Dytham, 2003). In addition, pike *Esox lucius* L. densities were compared between day and night using an independent samples *t*-test to investigate diel variations in predation risk to 0+ year fishes (Dytham, 2003).

The feeding activity of larval and 0+ year juvenile roach and perch was compared between day and night using Mann-Whitney *U*-tests, and diel variations in diet composition were examined using PERMANOVA and SIMPER analysis, as described for fish species composition. In addition, dietary overlap between sympatric roach and perch during daylight and darkness was calculated using the Bray-Curtis similarity index. The abundance (no. L^{-1} ± S.D.) of each zooplankton taxon was calculated for each sampling occasion, and diel variations in composition were examined using PERMANOVA and SIMPER analysis. Prey selection by larval and 0+ year juvenile roach and perch was investigated using the relativized electivity index (E^*) of Vanderploeg & Scavia (1979); E^* ranges from –1 to +1, with negative values indicating avoidance, positive values indicating selection, and 0 representing no preference. Electivity values were set at +1 for prey comprising ≥5% of the diet but not detected in the environment, and 0 for prey comprising <5% of the diet and not detected in the environment (Nunn *et al.,* 2007*d*). Electivity values for the most abundant zooplankton taxa were compared between day and night using independent samples *t*-tests (Ghan & Sprules, 1993).

RESULTS

SPECIES COMPOSITION AND ABUNDANCE

There was a statistically significant difference in the species composition of diurnal and nocturnal catches (PERMANOVA, d.f. = 1, $F = 3.805$, $P = 0.015$), and also between surveys (PERMANOVA, d.f. = 4, $F = 6.709$, $P < 0.001$), but there was no significant interaction between these factors (PERMANOVA, d.f. = 4, $F = 1.034$, $P = 0.4332$) (Table I; Fig. 1). The abundance of roach larvae peaked at night in late May, but during daylight in early to mid-June, whereas the abundance of 0+ year juveniles (in late June and mid-July) peaked at night (Fig. 2). There were no clear diel patterns in the abundance of perch, bleak *Alburnus alburnus* (L.) and gudgeon *Gobio gobio* (L.) but, in all surveys, the abundance of dace *Leuciscus leuciscus* (L.) peaked during daylight, with very few captured at night (Fig. 2). By contrast, the abundance of spined loach *Cobitis* *taenia* L., bullhead *Cottus gobio* L., ruffe *Gymnocephalus cernua* (L.) and pike peaked at night (Fig. 2). Indeed, there was a significant increase in the abundance of pike (mostly 0+ year juveniles) at night (independent samples t-test, d.f. = 16, $t = 2.698$, $P = 0.016$).

SIZE STRUCTURE

There was a significant difference in the sample length distributions of perch during daylight and at night in late May (two-sample Kolmogorov-Smirnov test, $Z = 1.591$, $P = 0.013$), caused by an absence of the smallest larvae and an appearance of >0+ year individuals at night. There was also an increase in the number of >0+ year perch at night in June and July, but there were no statistically significant differences in diurnal and nocturnal length distributions (two-sample Kolmogorov-Smirnov tests, $Z = 1.264$ and $P = 0.082$, $Z = 0.854$ and $P = 0.460$). By contrast, there was a significant difference in the sample length distributions of roach during daylight and at night from mid-June to mid-July (two-sample Kolmogorov-Smirnov tests, $Z = 1.436$ and $P = 0.032$, $Z = 1.362$ and $P = 0.049$, $Z = 2.465$ and $P < 0.001$), but not in early June (two-sample Kolmogorov-Smirnov test, $Z = 0.167$ and $P = 1.000$); the differences were caused by an increase in the number of the smallest larvae at night in mid-June, an absence of the smallest larvae at night in late June, and an increase in the number of the smallest larvae and a reduction in the number of the largest 0+ year juveniles at night in mid-July.

PREY AVAILABILITY

Densities of *Daphnia* spp., cyclopoid copepods and *Chydorus* spp. mostly increased at night, whereas rotifers and copepod nauplii generally declined at night; no consistent diel patterns were recorded for other taxa (Fig. 3). Overall, however, there was no statistically significant difference in zooplankton composition during daylight and at night (PERMANOVA, d.f. = 1, $F = 1.452$, $P = 0.304$), but there was between surveys (PERMANOVA, d.f. = 4, $F = 13.098$, $P < 0.001$).

FEEDING ACTIVITY

There were no significant differences in the feeding activity of larval (diurnal median = 4 points, nocturnal median = 4 points) and 0+ year juvenile (diurnal median = 5 points, nocturnal median = 4 points) roach during daylight and at night (Mann-Whitney *U*-tests, d.f. = 199, $U = 4949$ and $P = 0.745$, d.f. = 76, $U = 619$ and $P = 0.389$). By contrast, the feeding activity of perch larvae (diurnal median = 8 points, nocturnal median = 6 points) declined significantly at night (Mann-Whitney *U*-test, d.f. = 69, $U = 303$ and $P < 0.001$), whereas that of 0+ year juveniles (diurnal median = 8 points, nocturnal median = 8 points) did not (Mann-Whitney *U*-test, d.f. = 155, $U = 1994$ and $P = 0.063$).

DIET COMPOSITION

Bosmina sp. was the main prey of roach larvae throughout the diel cycle, but relative abundance generally increased at night (Fig. 4). By contrast, consumption of cyclopoid copepods and aufwuchs (the periphyton and associated microfauna that grow on underwater surfaces) was generally higher during daylight than at night, but there were no apparent diel variations in the consumption of rotifers, *Eurycercus lamellatus* (Müller), *Chydorus* spp. and chironomid larvae (Fig. 4). Consumption of *E. lamellatus* by 0+ year juvenile roach generally increased at night, but there were no apparent diel variations in the consumption of chironomid larvae, aufwuchs and *Chydorus* spp. (Fig. 4). Overall, there was no statistically significant difference in the diet composition of larval (PERMANOVA, d.f. = 1, $F = 0.996$, $P = 0.384$) and 0+ year juvenile (PERMANOVA, d.f. = 1, $F = 1.434$, $P = 0.331$) roach during daylight and at night.

Consumption of cyclopoid copepods by perch larvae was generally higher during daylight than at night, but there were no diel variations in the consumption of *Bosmina* sp. and *Daphnia* spp. (Fig. 4). Consumption of *E. lamellatus* by 0+ year juvenile perch was high during all of the 24-h periods, but no consistent diel variation was observed (Fig. 4). By contrast, consumption of cyclopoid copepods was low, but generally highest at night, whereas the relative abundance of *Simocephalus* spp. declined at night (Fig. 4). There were no consistent diel variations in the consumption of *Daphnia* spp., *Chydorus* spp. and chironomid larvae (Fig. 4). Overall, there were no statistically significant differences in the diet composition of larval (PERMANOVA, d.f. = 1, F = 1.899, P = 0.176) and 0+ year juvenile (PERMANOVA, d.f. = 1, F = 1.056, P = 0.400) perch during daylight and at night. Dietary overlap was 25% in daylight vs. 32% in darkness between larval roach and 0+ year juvenile perch, and 15% in daylight vs. 29% in darkness between 0+ year juvenile roach and perch (larval perch were not captured with larval or 0+ year juvenile roach).

PREY SELECTION

Bosmina sp. and *E. lamellatus* were generally selected by roach larvae, irrespective of the time of day/night, whereas *Chydorus* spp. and cyclopoid copepods were generally avoided (Table II). Electivity values for *Alona* spp., *Daphnia* spp. and *Simocephalus* spp. were variable, although all three were generally avoided, especially at night, but rotifers and copepod nauplii were consistently avoided throughout the diel cycle (Table II). *Eurycercus lamellatus* was generally selected by 0+ year juvenile roach throughout the diel cycle, whereas rotifers, cyclopoid copepods, copepod nauplii, *Alona* spp. and *Daphnia* spp. were consistently avoided (Table II). Electivity values for *Chydorus* spp.

were variable and no consistent diel pattern was observed, although mean electivity was significantly higher during daylight than at night (Table II).

Perch larvae consistently avoided rotifers, *Chydorus* spp., *Daphnia* spp., *Alona* spp., copepod nauplii and *Simocephalus* spp., irrespective of the time of day/night, whereas cyclopoid copepods were consistently selected, although electivity declined significantly at night (Table II). No consistent diel pattern was observed for *Bosmina* sp., although mean electivity was significantly lower during daylight than at night (Table II). Juvenile perch consistently selected *E. lamellatus* and *Simocephalus* spp., with no diel patterns in the electivity values, although mean electivities were significantly higher at night and during daylight, respectively (Table II). In general, rotifers, *Alona* spp., *Chydorus* spp., copepod nauplii, *Bosmina* sp. and cyclopoid copepods were avoided, with the electivity values of the latter two taxa declining further at night (Table II). Electivity values for *Daphnia* spp. were variable and no consistent diel pattern was observed, although mean electivity was significantly lower at night than during daylight (Table II).

DISCUSSION

ASSEMBLAGE STRUCTURE

Diel variations in assemblage structure and foraging ecology are fundamental components of the temporal dynamics of fish communities. In this study, there was a statistically significant difference in the species composition of diurnal and nocturnal catches, with dace most abundant during daylight and bullhead, spined loach and ruffe most abundant at night, reflecting the main activity period of these species (Okun *et al.*, 2005; Nunn *et al.*, 2010, 2014). Densities of pike (especially 0+ year juveniles) and >0+ year perch, both potential predators of larval and 0+ year juvenile fishes, increased at night, which could also have had an influence on assemblage structure (Copp & Jurajda, 1993; Jacobsen & Berg, 1998).

In contrast to other studies, there were no *consistent* diel patterns in species composition or the abundance of roach, perch, bleak and gudgeon. The latter could suggest that these species did not exhibit diel shifts in activity or habitat use, but would be unusual as roach, perch and bleak are generally diurnal and gudgeon is often nocturnal (Winfield & Townsend, 1988; Garner, 1996*a*; Okun *et al.*, 2005; Nunn *et al.*, 2010). More likely is that any diel patterns in species composition and the abundance of these species were masked, respectively, by the phenology of fish hatching and ontogenetic shifts in diel behaviour or habitat use. Roach and perch hatch as a single cohort over a short time period, whereas bleak and gudgeon are capable of producing multiple cohorts over a longer period, which will inevitably have an influence on 0+ year fish assemblage structure (Nunn *et al.*, 2007*e*). In addition, many species exhibit ontogenetic shifts in habitat use (Garner, 1996*b*; King, 2004), and may switch between diurnal and nocturnal activity during development (Winfield & Townsend, 1988; Specziár & Erős, 2014). In this study, the abundance of roach larvae peaked at night in late May, but during daylight in early to mid-June, whereas the abundance of 0+ year juveniles (in late June and mid-July) peaked at night, which, in addition to significant diel differences in length distributions, is likely to have contributed to the lack of consistent diel patterns in both species composition and abundance. It is also possible that any diel variations in habitat use by roach, perch, bleak and gudgeon were at a smaller resolution (*e.g.* microhabitat level) than examined in this study.

FORAGING ECOLOGY

Differences in foraging behaviour (*e.g.* diurnal vs. nocturnal, filter vs. particulate, vision vs. olfaction) between species, individuals or during ontogeny can have an important influence on fish feeding activity, diet composition and prey selection (see Nunn *et al.*, 2012). Perch, for example, is a visual feeder and, as for the larvae in this study, feeding activity is therefore generally highest during daylight (Diehl, 1988; Okun *et al.*, 2005). By contrast, the capture efficiency of roach is less affected by light intensity (Diehl, 1988; Okun *et al.*, 2005), and there were no significant diel differences in the feeding activity of larvae and 0+ year juveniles in this study. Persson & Greenberg (1990) demonstrated that roach had a negative impact on the growth of juvenile perch, which was related to competition for food resources. In this study, dietary overlap was 25% in daylight vs. 32% in darkness between larval roach and 0+ year juvenile perch, and 15% in daylight vs. 29% in darkness between 0+ year juvenile roach and perch, suggesting that interspecific interactions are likely to be strongest at night.

A number of studies have revealed diel variations in the diet composition of fishes, often linked to changes in habitat use, foraging behaviour and/or prey availability (see Nunn *et al.*, 2012). In deep waterbodies, for example, larval and 0+ year juvenile roach and perch often migrate into the epilimnion at dusk and the littoral at dawn, which is reflected by changes in prey consumption (Gliwicz & Jachner, 1992; Gliwicz *et al.*, 2006). There were few clear diel patterns in fish diet composition or prey selection in this study, with most taxa consistently selected or avoided, irrespective of the time of day/night, and no obvious shift between planktonic and benthic food sources (*cf.* Garner, 1996*a*; Horppila, 1999). Notwithstanding, some diel changes were observed, possibly caused by shifts in foraging behaviour. For example, the weaker selection of cyclopoid copepods by perch larvae, and the stronger avoidance of *Alona* spp., *Daphnia* spp. and *Simocephalus* spp. by roach larvae, at night was possibly a consequence of reductions in foraging efficiency during darkness. By contrast, the stronger selection of *Simocephalus* spp. by 0+ year juvenile perch during daylight was probably the result of an increase in foraging efficiency.

In shallow still waters, some zooplankton species exhibit diel horizontal migrations between the littoral and open water, which can influence the quantity and species of prey available to fishes (Lauridsen *et al.*, 1996). In this study, densities of rotifers and copepod nauplii generally declined at night, whereas *Daphnia* spp., cyclopoid copepods and *Chydorus* spp. usually increased. This suggests that *Daphnia* spp., cyclopoid copepods and *Chydorus* spp. moved into the sampling area at night, either from open water or, more likely, elsewhere in the littoral (*e.g.* diurnal refuges, such as aquatic macrophytes; Stansfield *et al.*, 1997; Balayla & Moss, 2003). Similarly, the increased consumption and selection of *E. lamellatus* by 0+ year juvenile roach and perch at night may have been caused by localised increases in abundance, as they emerged from diurnal refuges, that were not reflected in the zooplankton samples. Rotifers and copepod nauplii are unlikely to move large distances on a diel basis, so the cause of the reductions in their densities at night is unclear, but may have been linked to changes in microhabitat use.

Copp *et al.* (2005) stated that relatively consistent diel patterns in the fish and invertebrate assemblages in the River Lee, England, over three 24-h periods within a 10-day period (28 July-8 August), suggest that data from single 24-h surveys in late summer can be representative of daily patterns. By contrast, the relative lack of *consistent* diel patterns in this study, over five 24-h periods within a 57-day period (19 May-15 July), suggests that a number of complex and interacting factors have an influence on the assemblage structure and foraging ecology of larval and 0+ year juvenile fishes, and that multiple 24-h surveys are required in late spring and early summer to account for the phenology of fish hatching and ontogenetic shifts in diel behaviour and habitat use.

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REFERENCES

Anderson, M. J. (2001). Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 626–639.

Anderson, M. J., Gorley, R. N. & Clarke, K. R. (2008). *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods.* Plymouth: PRIMER-E.

Balayla, D. J. & Moss, B. (2003). Spatial patterns and population dynamics of plant-associated microcrustacea (Cladocera) in an English shallow lake (Little Mere, Cheshire). *Aquatic Ecology* **37**, 417–435.

Bass, J. A. B., Pinder, L. C. V. & Leach, D. V. (1997). Temporal and spatial variation in zooplankton populations in the River Great Ouse: an ephemeral food resource for larval and juvenile fish. *Regulated Rivers: Research and Management* **13**, 245–258.

Bolland, J. D., Nunn, A. D., Lucas, M. C. & Cowx, I. G. (2012). The importance of variable lateral connectivity between artificial floodplain waterbodies and river channels. *River Research and Applications* **28**, 1189–1199.

Bottrell, H. H., Duncan, A., Gliwicz, Z. M., Grygierek, E., Herzig, A., Hillbright-Ilkowska, A., Kurasawa, H., Larsson, P. & Wegleńska, T. (1976). A review of some problems in zooplankton production studies. *Norwegian Journal of Zoology* **24**, 420–456.

Bray, J. R. & Curtis, J. T. (1957). An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs* **27**, 325–349.

Clarke, K. R. & Warwick, R. M. (2001). *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation.* Plymouth: PRIMER-E.

Copp, G. H. (2008). Putting multi-dimensionality back into niche: diel vs. day-only niche breadth separation in stream fishes. *Fundamental and Applied Limnology* **170**, 273–280.

Copp, G. H. (2010). Patterns of diel activity and species richness in young and small fishes of European streams: a review of 20 years of point abundance sampling by electrofishing. *Fish and Fisheries* **11**, 439–460.

Copp, G. H. & Garner, P. (1995). Evaluating the microhabitat use of freshwater fish larvae and juveniles with point abundance sampling by electrofishing. *Folia Zoologica* **44**, 145–158.

Copp, G. H. & Jurajda, P. (1993). Do small riverine fish move inshore at night? *Journal of Fish Biology* **43** (Supplement A), 229-241.

Copp, G. H., Spathari, S. & Turmel, M. (2005). Consistency of diel behaviour and interactions of stream fishes and invertebrates during summer. *River Research and Applications* **21**, 75–90.

Cowx, I. G., Nunn, A. D. & Harvey, J. P. (2001). Quantitative sampling of 0-group fish populations in large lowland rivers: point abundance sampling by electric fishing versus micromesh seine netting. *Archiv für Hydrobiologie* **151**, 369–382.

Cowx, I. G., Harvey, J. P., Noble, R. A. A. & Nunn, A. D. (2009). Establishing survey and monitoring protocols for the assessment of conservation status of fish populations in river Special Areas of Conservation in the UK. *Aquatic Conservation: Marine and Freshwater Ecosystems* **19**, 96–103.

Cryer, M., Peirson, G. & Townsend, C. R. (1986). Reciprocal interactions between roach *Rutilus rutilus* (L.) and zooplankton in a small lake: prey dynamics and fish growth and recruitment. *Limnology and Oceanography* **31**, 1022–1038.

Diehl, S. (1988). Foraging efficiency of three freshwater fishes: effects of structural complexity and light. *Oikos* **53**, 207–214.

Dytham, C. (2003). *Choosing and Using Statistics: a Biologist's Guide*. Oxford: Blackwell Science.

Garner, P. (1996*a*). Diel patterns in the feeding and habitat use behaviour of 0-group fishes in a regulated river: the River Great Ouse, England. *Ecology of Freshwater Fish* **5**, 175–182.

Garner, P. (1996*b*). Microhabitat use and diet of 0+ cyprinid fishes in a lentic, regulated reach of the River Great Ouse, England. *Journal of Fish Biology* **48**, 367–382.

Ghan, D. & Sprules, W. G. (1993). Diet, prey selection, and growth of larval and juvenile burbot *Lota lota* (L.). *Journal of Fish Biology* **42**, 47–64.

Gliwicz, Z. M. (1986). Predation and the evolution of vertical migration in zooplankton. *Nature* **320**, 746–748.

Gliwicz, Z. M. & Jachner, A. (1992). Diel migrations of juvenile fish: a ghost of predation past or present? *Archiv für Hydrobiologie* **124**, 385–430.

Gliwicz, Z. M., Slon, J. & Szynkarczyk, I. (2006). Trading safety for food: evidence from gut contents in roach and bleak captured at different distances offshore from their daytime littoral refuge. *Freshwater Biology* **51**, 823–839.

Horppila, J. (1999). Diel changes in diet composition of an omnivorous cyprinid – a possible source of error in estimating food consumption. *Hydrobiologia* **400**, 33–39.

Hynes, H. B. N. (1950). The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. *Journal of Animal Ecology* **19**, 36–58.

Jacobsen, L. & Berg, S. (1998). Diel variation in habitat use by planktivores in field enclosure experiments: the effect of submerged macrophytes and predation. *Journal of Fish Biology* **53**, 1207–1219.

Janáč, M. & Jurajda, P. (2013). Diel differences in 0+ fish samples: effect of river size and habitat. *River Research and Applications* **29**, 90–98.

King, A. J. (2004). Ontogenetic patterns of habitat use by fishes within the main channel of an Australian floodplain river. *Journal of Fish Biology* **65**, 1582–1603.

Lauridsen, T. L., Pedersen, L., Jeppesen, E. & Søndergaard, M. (1996). The importance of macrophyte bed size for cladoceran composition and horizontal migration in a shallow lake. *Journal of Plankton Research* **18**, 2283–2294.

Longshaw, M., Frear, P. A., Nunn, A. D., Cowx, I. G. & Feist, S. W. (2010). The influence of parasitism on fish population success. *Fisheries Management and Ecology* **17**, 426–434.

Mehner, T. (2012). Diel vertical migration of freshwater fishes – proximate triggers, ultimate causes and research perspectives. *Freshwater Biology* **57**, 1342–1359.

Muška, M., Tušer, M., Frouzová, J., Draštík, V., Čech, M., Jůza, T., Kratochvíl, M., Mrkvička, T., Peterka, J., Prchalová, M., Říha, M., Vašek, M. & Kubečka, J. (2013). To migrate, or not to migrate: partial diel horizontal migration of fish in a temperate freshwater reservoir. *Hydrobiologia* **707**, 17–28.

Nunn, A. D. & Cowx, I. G. (2012). Diel and seasonal variations in the population dynamics of *Hemimysis anomala*, a non-indigenous mysid: implications for surveillance and management. *Aquatic Invasions* **7**, 357–365.

Nunn, A. D., Harvey, J. P., Britton, J. R., Frear, P. A. & Cowx, I. G. (2007*a*). Fish, climate and the Gulf Stream: the influence of abiotic factors on the recruitment success of cyprinid fishes in lowland rivers. *Freshwater Biology* **52**, 1576–1586.

Nunn, A. D., Harvey, J. P. & Cowx, I. G. (2007*b*). Benefits to 0+ fishes of connecting man-made waterbodies to the lower River Trent, England. *River Research and Applications* **23**, 361–376.

Nunn, A. D., Harvey, J. P. & Cowx, I. G. (2007*c*). The food and feeding relationships of larval and 0+ year juvenile fishes in lowland rivers and connected waterbodies. I. Ontogenetic shifts and interspecific diet similarity. *Journal of Fish Biology* **70**, 726–742.

Nunn, A. D., Harvey, J. P. & Cowx, I. G. (2007*d*). The food and feeding relationships of larval and 0+ year juvenile fishes in lowland rivers and connected waterbodies. II. Prey selection and the influence of gape. *Journal of Fish Biology* **70**, 743–757.

Nunn, A. D., Harvey, J. P. & Cowx, I. G. (2007*e*). Variations in the spawning periodicity of eight fish species in three English lowland rivers over a 6 year period, inferred from 0+ year fish length distributions. *Journal of Fish Biology* **70**, 1254–1267.

Nunn, A. D., Copp, G. H., Vilizzi, L. & Carter, M. G. (2010). Seasonal and diel patterns in the migrations of fishes between a river and a floodplain tributary. *Ecology of Freshwater Fish* **19**, 153–162.

Nunn, A. D., Tewson, L. H. & Cowx, I. G. (2012). The foraging ecology of larval and juvenile fishes. *Reviews in Fish Biology and Fisheries* **22**, 377–408.

Nunn, A. D., Tewson, L. H., Bolland, J. D., Harvey, J. P. & Cowx, I. G. (2014). Temporal and spatial variations in the abundance and population structure of the spined loach (*Cobitis taenia*), a scarce fish species: implications for condition assessment and conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* **24**, 818–830.

Okun, N., Mendonca, R. & Mehner, T. (2005). Diel shifts in community composition and feeding of juvenile fish in the pelagic area of a large shallow lake. *Limnologica* **35**, 70–77.

Peňáz, M. (2001). A general framework of fish ontogeny: a review of the ongoing debate. *Folia Zoologica* **50**, 241–256.

Persson, L. (1983). Effects of intra- and interspecific competition on dynamics and size structure of a perch, *Perca fluviatilis* and a roach, *Rutilus rutilus* population. *Oikos* **41**, 126–132.

Persson, L. (1986). Patterns of food evacuation in fish: a critical review. *Environmental Biology of Fishes* **16**, 51–58.

Persson, L. (1987). Competition-induced switch in young of the year perch, *Perca fluviatilis*: an experimental test of resource limitation. *Environmental Biology of Fishes* **19**, 235–239.

Persson, L. & Greenberg, L. A. (1990). Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*)-roach (*Rutilus rutilus*) interaction. *Ecology* **71**, 44–56.

Reynolds, J. H., Thompson, W. L. & Russell, B. (2011). Planning for success: identifying effective and efficient survey designs for monitoring. *Biological Conservation* **144**, 1278–1284.

Specziár, A. & Erős, T. (2014). Dietary variability in fishes: the roles of taxonomic, spatial, temporal and ontogenetic factors. *Hydrobiologia* **724**, 109–125.

Stansfield, J. H., Perrow, M. R., Tench, L. D., Jowitt, A. J. D. & Taylor, A. A. L. (1997). Submerged macrophytes as refuges for grazing Cladocera against fish predation: observations on seasonal changes in relation to macrophyte cover and predation pressure. *Hydrobiologia* **342/343**, 229–240.

Vanderploeg, H. A. & Scavia, D. (1979). Calculation and use of selectivity coefficients of feeding: zooplankton grazing. *Ecological Modelling* **7**, 135–149.

Viroux, L. (1997). Zooplankton development in two large lowland rivers, the Moselle (France) and the Meuse (Belgium), in 1993. *Journal of Plankton Research* **19**, 1743–1762.

Winfield, I. J. & Townsend, C. R. (1988). Factors affecting prey selection by young bream *Abramis brama* and roach *Rutilus rutilus*: insights provided by parallel studies in laboratory and field. *Environmental Biology of Fishes* **21**, 279–292.

Table I. Similarity percentages (SIMPER) analysis of the mean abundance (no. m^{-2}) of key fish species and their contributions (%) to dissimilarities in diurnal and nocturnal micromesh seine catches in a man-made floodplain waterbody on the River Trent, England.

Species	**Day**	**Night**	**%**
Roach	2.80	5.72	50.35
Perch	0.97	2.11	22.70
Dace	1.15	0.01	9.41
Spined loach	0.07	0.37	5.28
Mean dissimilarity			**81.08**

Table II. Diurnal (D) and nocturnal (N) prey selection by larval and 0+ year juvenile roach and perch in a man-made floodplain waterbody on the River Trent, England.

	Roach								**Perch**							
	Larvae				**Juveniles**				**Larvae**				**Juveniles**			
Taxa	D	N	*P*	*n*	D	N	*P*	*n*	D	N	*P*	*n*	D	N	*P*	*n*
Alona spp.	–0.18	–0.51	0.023*	117	–1.00	–0.86	0.093	67	–1.00	–1.00	1.000	41	–0.97	–0.98	0.765	103
Bosmina sp.	+0.46	+0.65	0.194	79	–	–	–	–	–0.54	–0.10	0.056	71	–0.18	–	–	34
Chydorus spp.	–0.48	–0.44	0.841	187	+0.69	+0.04	0.002*	76	–1.00	–1.00	1.000	51	–0.77	–0.77	0.388	141
Copepod nauplii	–1.00	–1.00	1.000	186	–1.00	–1.00	1.000	78	–1.00	–0.97	0.248	70	–1.00	–1.00	1.000	147
Cyclopoida	–0.69	–0.79	0.332	176	–0.94	–0.79	0.200	78	+0.98	+0.37	0.000**	71	+0.04	–0.72	0.000**	149
Daphnia spp.	–0.42	–0.81	0.000**	139	–0.82	–0.93	0.339	58	–0.61	–0.40	0.291	71	+0.01	–0.93	0.000**	131
Eurycercus sp.	+0.48	+0.10	0.187	55	+0.57	+0.63	0.204	50	–	–	–	–	+0.81	+0.97	0.015*	136
Rotifera	–0.95	–0.94	0.782	184	–1.00	–1.00	1.000	78	–1.00	–0.90	0.042*	70	–1.00	–1.00	1.000	146
Simocephalus spp.	–0.54	–0.90	0.014*	58	–	–	–	–	–	–1.00	0.065	31	+0.61	+0.20	0.030*	94

independent samples *t*-tests; **P* < 0.05, ***P* < 0.01, – no data.

Fig. 1. Non-metric multidimensional scaling (MDS) ordination plots comparing the 0+ year fish species composition of diurnal (white points) and nocturnal (black points) micromesh seine catches in a man-made floodplain waterbody on the River Trent, England, using (a) replicates and (b) group centroids with trajectories over five 24-h periods.

Fig. 2. Diel variations in the abundance of nine 0+ year fish species in a man-made floodplain waterbody on the River Trent, England, over five 24-h periods. Nocturnal surveys are shaded.

Fig. 3. Diel variations in the abundance of eight zooplankton taxa in a man-made floodplain waterbody on the River Trent, England, over five 24-h periods. Nocturnal surveys are shaded.

Fig. 4. Diel variations in the diet composition of larval and 0+ year juvenile roach and perch in a man-made floodplain waterbody on the River Trent, England. Nocturnal surveys are shaded, no 0+ year juvenile roach were captured at 17:00. Prey category symbols are: *Alona* spp. (░); aufwuchs (■); *Bosmina* sp. (▨); Chironomidae larvae (▥); *Chydorus* spp. (▧); Cyclopoida (▤); *Daphnia* spp. (▩); Ephemeroptera larvae (⛝); *Eurycercus lamellatus* (▦); *Simocephalus* spp. (▣); and ‘other’ prey categories (□).

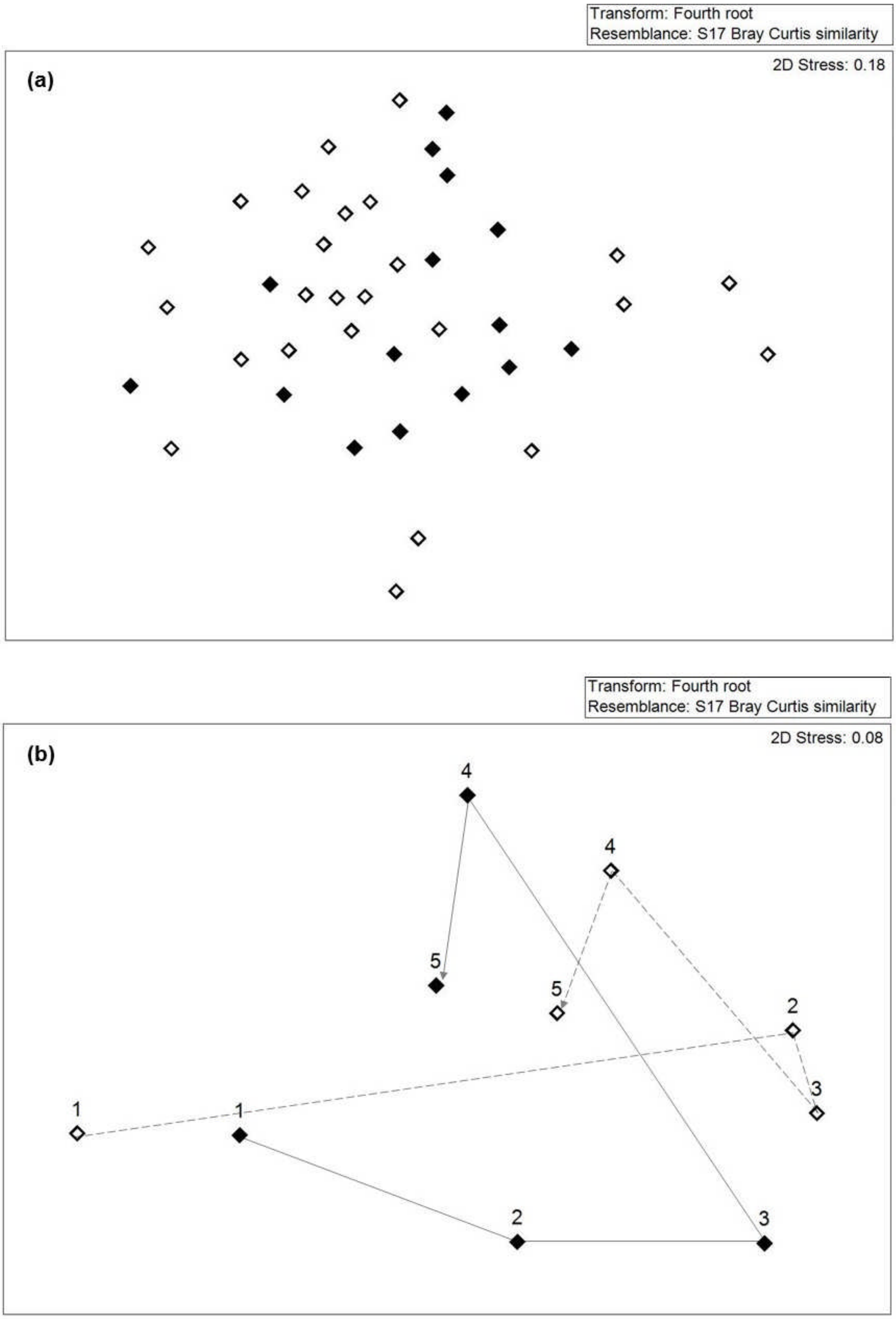
Transform: Fourth root
Resemblance: S17 Bray Curtis similarity
(a)
2D Stress: 0.18
Transform: Fourth root
Resemblance: S17 Bray Curtis similarity
(b)
2D Stress: 0.08
4
4
5
5
2
3
1
1
2
3

Fig. 1.

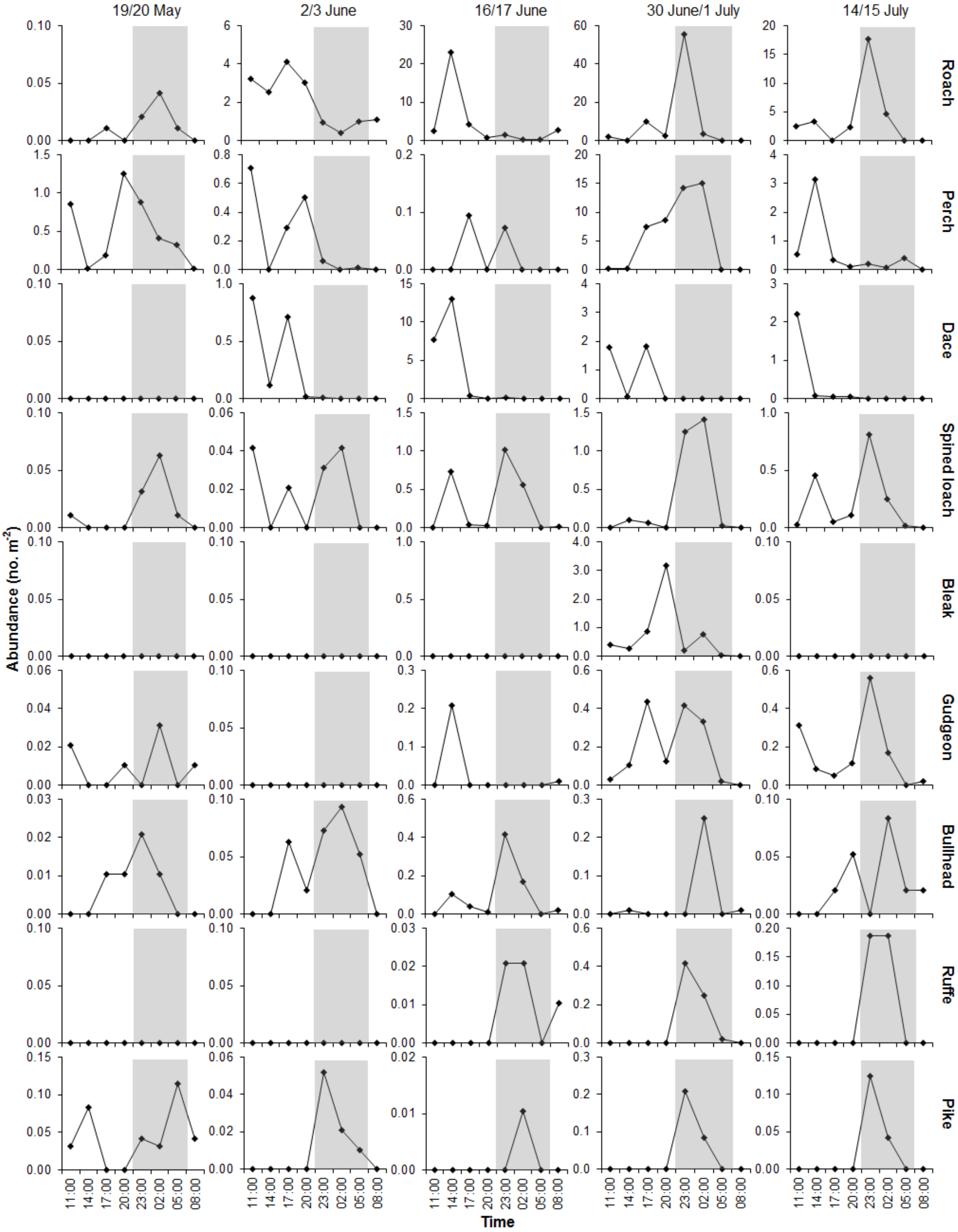
19/20 May
2/3 June
16/17 June
30 June/1 July
14/15 July
Roach
Perch
Dace
Spined loach
Bleak
Gudgeon
Bullhead
Ruffe
Pike
Abundance (no. m-2)
Time
11:00
14:00
17:00
20:00
23:00
02:00
05:00
08:00

Fig. 2.

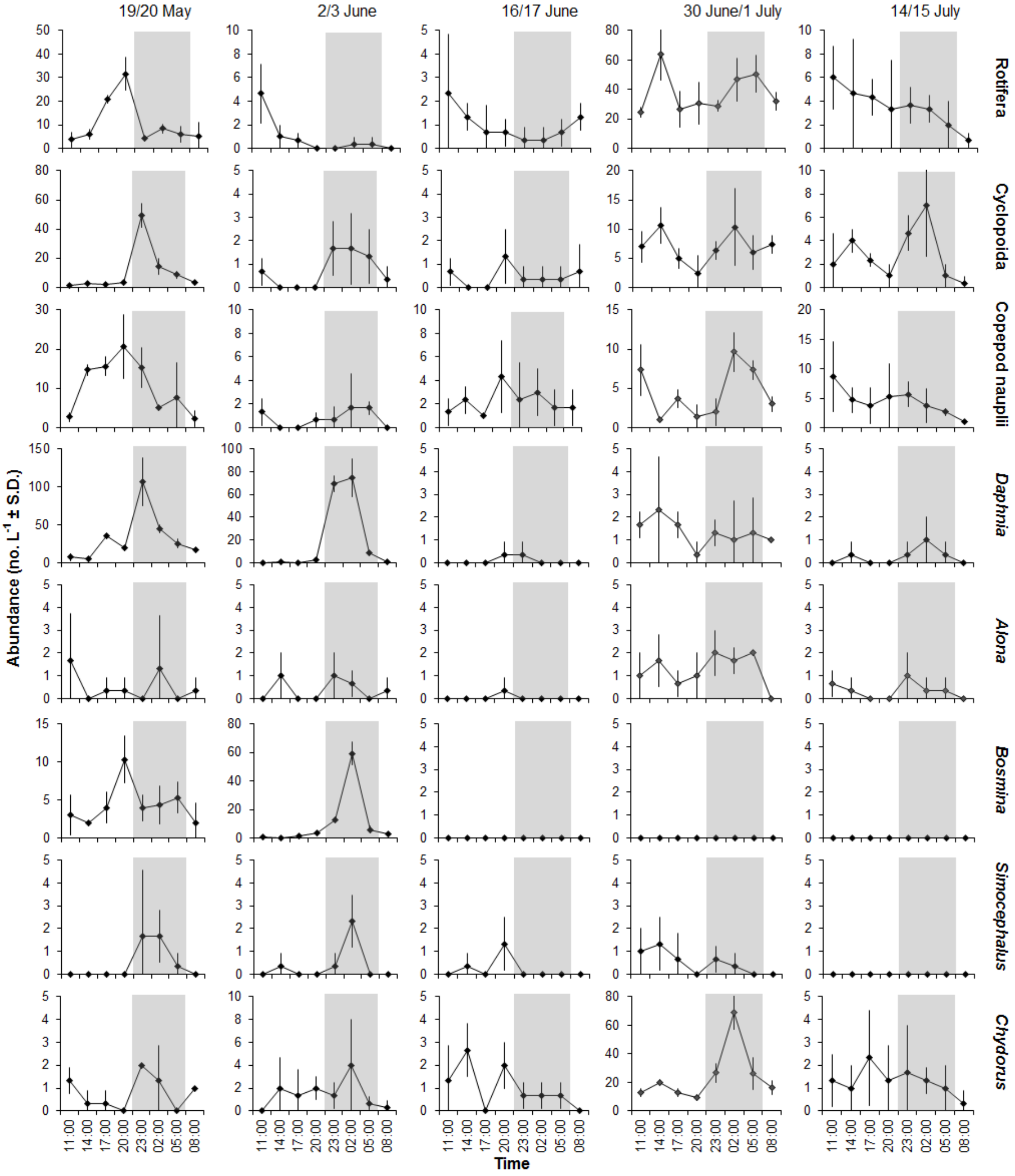
19/20 May
2/3 June
16/17 June
30 June/1 July
14/15 July
Rotifera
Cyclopoida
Copepod nauplii
Daphnia
Alona
Bosmina
Simocephalus
Chydorus
Abundance (no. L^{-1} ± S.D.)
Time
11:00
14:00
17:00
20:00
23:00
02:00
05:00
08:00

Fig. 3.

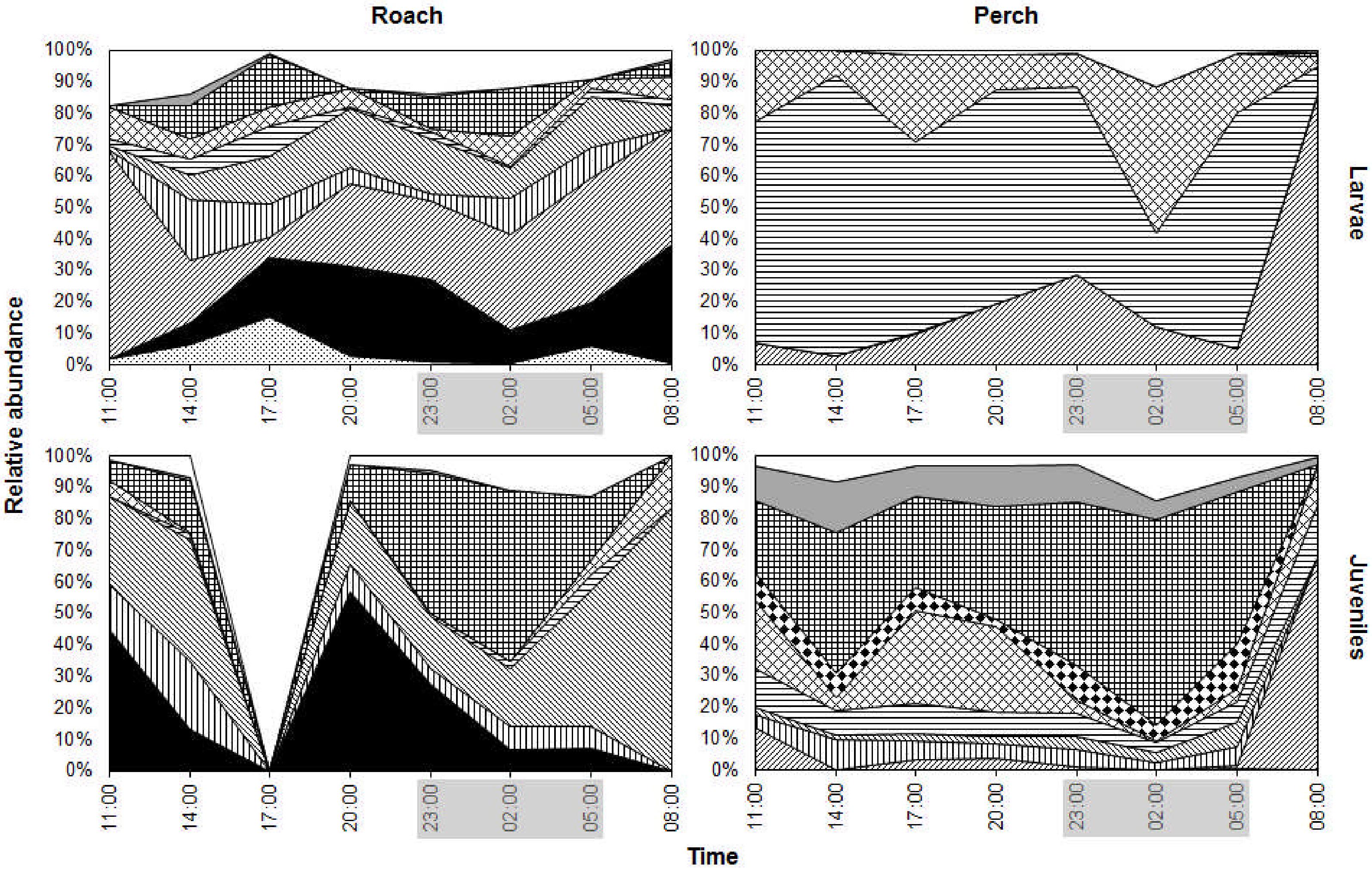
Roach
Perch
Larvae
Juveniles
Relative abundance
Time
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
11:00
14:00
17:00
20:00
23:00
02:00
05:00
08:00

Fig. 4.