

Diel habitat shifts of macrofauna in a fishless pond

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Abstract. Most studies of pond animals are undertaken during the daytime, despite evidence that many pond organisms demonstrate marked nocturnal changes in behaviour. Nocturnal studies of animals in fishless ponds are particularly rare, probably because diel changes in aquatic animal behaviour are often found to be a response to visual predation by fish. We used non-metric multidimensional scaling (MDS) and analysis of similarity (ANOSIM) to detect patterns of similarity in the community composition of macroinvertebrates and amphibians in samples taken from vegetated and unvegetated areas during the day and night in a fishless Vermont pond. We tested the hypotheses that (i) macrofaunal activity increased at night near the pond surface, and (ii) horizontal movement of the pond community was occurring on a diel cycle. At night, many taxa were more abundant in the surface waters and the community showed a general habitat expansion or shift from the littoral zone towards the edge and central waters. Our results challenge the assumptions that one would make about pond animal habitat use and interactions based solely on daytime studies. Even in fishless systems, where diel changes are unexpected, habitat use and behaviour might change at night and affect the strength and variety of species interactions.

Extra keywords: aquatic insect, horizontal migration, macroinvertebrate, macrophyte, tadpoles.

Introduction

Ecological studies undertaken during the day might be wholly appropriate for animals that show aperiodic distributions and behaviours or primarily daytime activity, but for many animals nocturnal habitat use and behaviours are simply unknown. Given that many animals do not depend entirely on sunlight to carry out important activities, it is not adequate to assume that animals cease to interact at night or that ecology is the same at night as it is during the day. Animals that navigate even partially by vision or depend on warming by the sun, or interact strongly with other animals that do, might exhibit a different suite of behaviours at night. Lack of knowledge about diel behavioural periodicity might, therefore, lead to erroneous conclusions about the variety and strength of biotic interactions for populations and communities.

In aquatic systems, diel changes in behaviour such as foraging activity, migration or habitat use are well documented among zooplankton (Haney 1988, Burks *et al.*

2002) and some stream macroinvertebrates (Johnson and Covich 2000). Although these diel patterns might be induced or modified by tactile predators (McIntosh and Townsend 1994; Peckarsky 1996) or resource distribution (Kohler 1985; Dini and Carpenter 1992), diel changes in habitat are overwhelmingly attributed to the presence of visually feeding fish (Dini and Carpenter 1992; Flecker 1992). Visual predation pressure presumably relaxes at night, allowing potential prey taxa to move or forage in areas that would be unsafe during the day. Some studies have assessed the dependence of various pond macroinvertebrates on vision for hunting (heteropterans: O'Brien and Vinyard 1978; Zalom 1978; Giller and McNeill 1981; Streams 1982; Cooper 1983; Blinn *et al.* 1993; Runck and Blinn 1994; Odonates reviewed in Corbett 1999), but nocturnal studies of lentic macroinvertebrate ecology are rare compared to zooplankton and stream invertebrates, particularly in fishless ponds where diel changes in behaviour might not be expected.

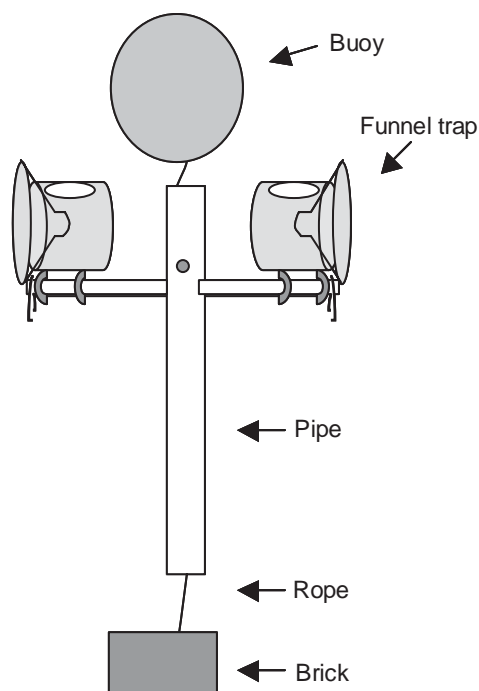


Fig. 1. Schematic of passive funnel traps used to sample pond animals. Front and rear traps have been omitted for clarity.

Incidental observations of macroinvertebrates in several fishless ponds in the north-eastern United States suggested that the behaviour of many animals changed from day to night in the absence of an obvious visual predator. We hypothesised that the macrofaunal community of a shallow fishless pond in Vermont would show: (i) a general increase in near-surface water activity at night; and (ii) a shift towards the open water of the pond at night. Such horizontal migrations are increasingly reported in shallow ponds for zooplankton (Burks *et al.* 2002), but are still generally attributed to the presence of visually feeding fish. Here we report dramatic changes in habitat use from day to night among a variety of invertebrate and vertebrate macrofauna in the absence of an obvious visual predator, a phenomenon that might be more common than is generally thought.

Materials and methods

Study site

Johnson Pond is located on privately owned land in Norwich, Vermont, USA (43°44'N, 72°18'W). It is small (0.1×0.05 km), shallow (maximum depth 1.5 m) and fishless. The littoral zone is dominated by *Typha* and there is a well developed *Potamogeton* stand in the centre of the pond. Low-lying *Chara* is abundant in between these areas.

Field collections

We collected animals daily and nightly twice a week with unbaited, passive live bottle traps from 10 May to 1 September 1999 (Fig. 1). The clear plastic traps were assembled as described by Streams (1992), with some modification. We riveted clear 15.0-cm funnels to the screw-top lids of clear plastic 1.8-L jars. The opening of the funnel into the jar was

2.3-cm wide. Four traps were suspended horizontally on a rack constructed of polyvinyl chloride (PVC) pipe. A rope was drawn through the vertical PVC pipe, with an anchor at the bottom and a float at the top. Four horizontal arms were fitted through holes in the pipe 0.3-m below the surface. Each trap floated horizontally from an arm by rings attached to the trap, held in place with hairpin cotter pins on the end of each arm. A pocket of air within the traps both reduced mortality of air breathing animals and provided buoyancy. Traps were thus oriented at right angles in four directions 0.3-m below the surface on each rack. After a 12-h period, we emptied all four traps from each rack into a bucket (comprising one sample for each rack), identified all animals in the field, and released them. For day samples, traps were set at 0700 hours and emptied at 1900 hours. We then re-set the traps, and night samples were collected at 0700 hours. Field identification and live release minimised impact on the community, but also limited taxonomic resolution. Identifications were based on keys in Peckarsky *et al.* (1990), Merritt and Cummins (1984), Hungerford (1933) and Truxal (1953).

We sampled littoral and open water (centre) habitats from 10 May through 1 September. The *Potamogeton* stand in the centre did not appear to create a distinct habitat early in the study, because it did not reach the upper stratum. We placed three racks in the littoral zone and three in the centre, for a total of six samples (four traps per sample) in each time period. From 16 June through 1 September, we placed three additional racks in the littoral-open edge, where the upper stratum of water was unvegetated and only *Chara* lay on the bottom. This use of a third habitat led to a total of nine samples per time period. During this period, *Potamogeton* reached the surface of the pond, which meant that the centre stations could no longer be considered open water.

Analysis

Non-metric multidimensional scaling (MDS) and analysis of similarities (ANOSIM) were used to detect patterns in community composition and to infer which important environmental variables were associated with the underlying trends.

MDS is a multivariate ordination technique that builds a 2-D 'map' of samples based on their similarity to each other as defined by a distance metric. A stress value measures the goodness of the map's fit, where zero indicates a perfect fit. The stress value is an assessment of how closely correlated the distances of points on the MDS map are to the distances in the original distance matrix. This technique is appropriate for data with non-normal distribution and provides results that are easily interpreted. In the present study, MDS was performed on the ranked similarity matrix based on the Bray-Curtis similarity coefficient (Clarke and Warwick 1994), which was calculated on fourth-root transformed abundance data of common taxa using the PRIMER 4.0 statistical package (Plymouth Marine Laboratory). We chose the fourth-root transformation to de-emphasise the most common taxa and increase the influence of important, but less abundant community members such as belostomatids and *Dytiscus*. Common taxa were defined as those comprising more than 3% of any sample; therefore, adult *Rana* (frogs) were excluded from analysis, resulting in 23 remaining taxonomic groupings. To assist in the determination of changes in taxonomic composition over time, sample periods were split a priori into three groups for convenience (10 May to 3 June, 16 June to 20 July, and 28 July to 1 September). Associations between sample distribution and environmental data (day or night, habitat type, sample period) were explored by superimposing environmental variables onto the ordinations.

ANOSIM was applied to the similarity matrix underlying the ordination to test whether the differences observed between the sample groups and environmental data were statistically significant. ANOSIM is a non-parametric permutation test used with multivariate data to test a priori hypotheses (Clarke and Warwick 1994). The analysis provides

Table 1. Total number of each taxon caught in funnel traps from 10 May 1999 to 1 September 1999
Traps collected animals over a 12-h period for both day and night samples, twice weekly (n = 348)

	Total
Notonectids	2519
Coleopterans	469
Newts	467
Tadpoles	228
Other Heteropterans	211
Odonates	115
Leeches	74
Mites	50
Mayflies	17

a measure of the dissimilarity of groups of samples in the form of an *R*-statistic that typically lies between 0 and 1; values close to one imply that the groups are very dissimilar and those approaching zero indicate that groups are very similar. As with univariate tests, it is possible for the *R*-value to be significantly different from zero yet trivially small, especially when sample size is relatively large (Clarke 1993). Thus, similarity of samples might be inferred from either a non-significant *P*-value, indicating that the *R*-value is not statistically different from zero, or a significant but extremely low *R*-value. ANOSIM was performed on the Bray–Curtis dissimilarity matrices (PRIMER 4.0, Plymouth Marine Laboratory) to test for significance of the effects of habitat and time of day on sample composition. For all tests, 999 permutations were executed. We adjusted the acceptable *P*-value ($\alpha = 0.05$) using a Dunn–Šidák correction to allow for non-independence of tests.

A shade diagram was constructed by re-sorting the original data matrix in order to indicate which taxa were principally responsible for the observed patterns. The samples were ordered on the *x*-axis by habitat and date. On the *y*-axis, taxa were ordered by cluster analysis (PRIMER 4.0, Plymouth Marine Laboratory) of samples based on taxonomic composition (Bray–Curtis similarity, fourth-root transformed abundance data) and from examination of the sample distribution in the MDS. In this way, taxa that have abundances that tend to fluctuate in parallel across samples are grouped together. On the re-ordered matrix, the increasing abundance (fourth-root transformed) of each taxon is plotted as a greyscale using Spyglass Transform V.3.3.0 (Fortner Research LLC), a computer program that produces greyscale plots from 3-D arrays of numbers. Shade diagrams are useful for visualizing the relationships of taxa to samples and environmental parameters because one can: (i) see large-scale patterns in the data quickly by assessing where the greatest abundance of animals lies in relation to important environmental factors and sample groupings; (ii) assess the similarity of taxa easily by comparing their positions on the *y*-axis; and (iii) obtain detailed information about relative abundance and distribution of particular taxa.

Results

Faunal composition

Notonectids numerically dominated the fauna caught in funnel traps (Table 1), with *Notonecta lunata* and *Buenoa macrotibialis* comprising 61% of the total catch and occurring in all areas of the pond during day and night. Various coleopteran species and red-spotted newts were also very common in the traps, each accounting for 11% of the

total. Taxa generally thought to be benthic or vegetation dwellers were also caught in the near-surface activity traps, such as odonates and the large heteropteran predators *Ranatra* and belostomatids. The low mayfly catch (Table 1) is characteristic for horizontally oriented funnel traps (Hampton and Friedenberg 2002).

Habitat associations and diel community changes

The stress value (0.22) of the MDS (Fig. 2) indicated that the model was a good representation of the sample relationships, especially given the large number of samples (see Clarke and Warwick 1994). Sampling period, habitat type and time of day were associated with sample distribution in the final MDS model (Fig. 2). Gradual seasonal succession was apparent in community composition (Fig. 2a), because early season samples distinctly clustered in the lower right area of the MDS plot and late season samples overlapped with mid-season samples across the middle and upper left. Habitat and time of day also were associated with characteristic taxonomic compositions. Littoral samples were grouped in the upper right of the MDS plot and centre samples were grouped in the lower left (Fig. 2b). However, edge and centre samples overlapped with the littoral samples, indicating that many edge and centre samples were compositionally similar to those from the littoral zone. Similarly, nighttime samples tended to cluster in the upper right of the MDS plot, but there was some overlap with daytime samples (Fig. 2c).

Diel community associations with habitat

Most of the overlap seen among habitats and between times of day in the MDS plot can be explained by an interaction between these factors. All habitats showed significant compositional differences from day to night (Table 2). To better understand these diel changes (Fig. 3), day and night samples were examined separately for each of the habitats. Whereas day and night samples from the littoral zone showed relatively little dissimilarity in taxonomic composition (Fig. 3a), day and night samples from the edge and centre habitats clustered separately (Fig. 3b and 3c). Daytime edge samples were similar in composition to daytime centre samples, but the edge samples at night were more similar to littoral zone samples. The association was seen by the clustering of night edge samples with littoral samples in Fig. 3b. This pattern was also apparent among centre samples: day centre samples were distinct from littoral samples, clustering in the lower left of the plot (Fig. 3c), but night samples from the centre were compositionally similar to littoral samples.

Results from the ANOSIM also indicated that edge and centre samples were more similar to littoral samples at night. For the centre samples, similarity to the day littoral samples increased from day to night, as indicated by a decreasing *R*-value (Table 2). The similarity of the open-water edge

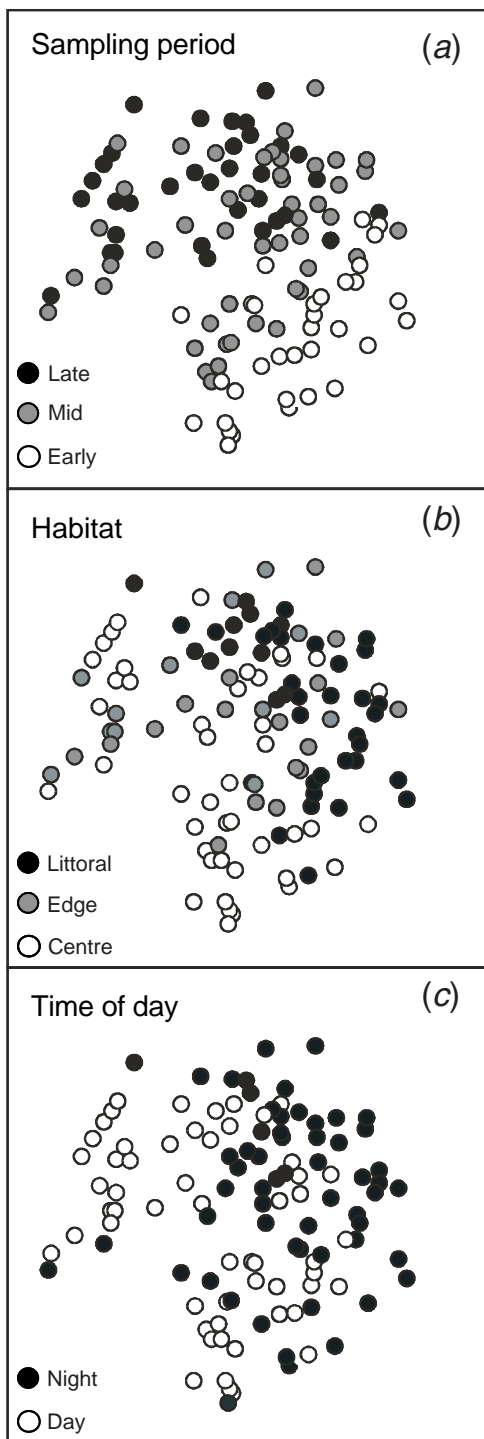


Fig. 2. Multidimensional scaling (MDS) plot of samples, based on abundant taxa caught. MDS is overlaid with (a) sampling period, (b) habitat and (c) time of day, to visualise how these parameters correspond with the sample distribution produced by MDS.

community to the littoral zone increased even more dramatically at night. The day edge and day littoral samples were significantly different (Table 2), but the differences

essentially disappeared at night (night edge samples were statistically indistinguishable from day littoral samples).

Species-specific diel patterns

All habitats showed the general trend of increasing species richness and abundance at night (Fig. 4). Taxa that were principally found at night were grouped at the lower end of the y -axis in the shade diagram (Fig. 4). Leeches, the large hemipterans *Ranatra* and *Lethocerus*, and dytiscid beetles were rarely found in the day, but were fairly abundant in the littoral zone at night. Additionally, leeches and the large hemipterans were absent from day edge samples, but were found in night edge samples. Other taxa grouped in the middle of the y -axis (Fig. 4) did not show striking diel changes within the littoral zone, but did become common in edge and centre samples only at night (*Hydaticus* and other beetles, tadpoles and damselflies). To a lesser degree, the same is true of corixids and libellulid and aeschnid dragonfly larvae (Fig. 4).

Discussion

The conclusions that one would draw about relationships of these animals to habitat would differ greatly had only daytime samples been collected. Not only were more species present in greater numbers in each habitat at night, but several taxa that were consistently present in the littoral zone appeared in the edge and centre of the pond only at night. Because diel changes in pond animal behaviour are overwhelmingly attributed to the presence of fish, these findings were not expected in a fishless pond. However, Hampton and Friedenberg (2002) reported similar results from a shorter study in other fishless Vermont ponds, suggesting that the phenomenon might be more common than previously thought.

Diel differences in animal abundance and composition

The greater abundance of animals in nighttime samples demonstrated that surface waters in all areas were used more at night. This pattern was clear despite seasonal shifts in the community. The higher nighttime catch might indicate greater swimming activity in general, changes in habitat, or both.

For animals using visual cues, it is possible that the lower daytime catch in traps was due to trap avoidance. We think this is unlikely for several reasons. In a related study (Hampton and Friedenberg 2002), greater nocturnal abundance in surface water samples was similarly apparent in sweep net, trap and column sampler data. In that study, the similarity between sweep and trap samples suggested that trap avoidance does not occur to a large extent. Additionally, some visually orienting animals such as the notonectids and newts often were caught more frequently during the day. Visual avoidance of such traps has not been detected in previous studies (e.g. Holomuzki 1985, 1986; Aiken 1986).

Table 2. Results (*R*-values) from ANOSIM tests for habitat-related differences in sample composition of trap data (Global *R* = 0.194, *P* = 0.0001)Increasing *R*-values signify increasing dissimilarity. *P*-values in parentheses correspond to a test of the hypothesis that *R* is different from zero

	Centre	Day Edge	Littoral	Centre	Night Edge	Littoral
Day						
Centre	–	0.082(0.057)	0.374(0.001)*	0.174(0.001)*	0.464(0.001)*	0.661(0.001)*
Edge		–	0.370(0.001)*	0.303(0.002)*	0.501(0.001)*	0.754(0.001)*
Littoral			–	0.207(0.001)*	0.088(0.059)	0.190(0.001)*
Night						
Centre				–	0.069(0.122)	0.327(0.001)*
Edge					–	0.197(0.002)*
Littoral						–

**P*-values are significant ($\alpha = 0.05$) after Dunn–Šidák correction (*P* = 0.003).

In addition, there are a variety of laboratory experiments and records of diel behaviour for individual taxa that support the interpretation that these pond animals both increase swimming activity and change habitat at night. We collected greater numbers of erpobdellid leeches at night, which is consistent with other diel studies of predatory leeches that found increased nocturnal swimming activity (Elliott 1973; Davies and Kasserra 1989; Davies *et al.* 1996; Angstadt and Moore 1997). Ultimate causes for this periodicity are unknown, although there is some evidence that visual predation by fish and possibly birds poses a greater risk to leeches than invertebrate predation (Young and Spelling 1986).

In the present study, we found greater nocturnal presence of damselfly and dragonfly larvae, the predaceous diving beetles *Dytiscus* and *Hydaticus*, other coleopterans and the large predatory hemipterans *Ranatra* (water stick insects) and *Lethocerus* (belostomatids or giant water bugs). Corbett (1999) summarised the relevant literature on diel feeding patterns of odonate larvae; greater nighttime foraging was common among dragonfly larvae and occurred in some damselfly species. Increased nighttime foraging could be positively correlated with swimming or changing microhabitat. Our finding of higher nighttime numbers of *Dytiscus* adults in traps was consistent with that of Holomuzki (1985, 1986), who found *Dytiscus* almost exclusively in nighttime funnel trap samples from two Arizona ponds. Aiken (1986) found that *Dytiscus* swam more at night in the laboratory and field (as revealed by increased nocturnal funnel trap catch), and they also had more intraspecific interactions in the form of grappling and mounting in the laboratory. Hilsenhoff (1987) speculated that *Hydaticus* and many other coleopterans are primarily nocturnal based on observations. Although we are not aware of reports in the literature on the natural nocturnal activity of the largest hemipterans in our samples, belostomatids (Runck and Blinn 1994) and *Ranatra* (Blinn *et al.* 1993) have been shown to feed equally well under light and dark conditions in the laboratory. This result alone suggests that

foraging, and possibly correlated movements, need not cease at night. Using gut content analysis of field-collected predators, Blinn *et al.* (1993) found that although *Ranatra montezuma* Polhemus consumed more of its preferred prey at night, this was probably a result of higher prey density in its immediate vicinity rather than increased foraging activity.

In the present study, tadpoles, mostly *Rana clamitans* Latreille (green frogs), swam into traps more at night than during the day. The nighttime increase was especially pronounced in the open water of the edge zone and in the central *Potamogeton* stand. Warkentin (1992) reported that *Rana clamitans* in a fishless pond shifted from littoral daytime habitat to occupation of both littoral and open areas at night, although there appeared to be no increase in activity level. Beiswinger (1977) found that *Bufo americanus* (Holbrook) tadpoles avoided the shore at night, due to the cooling of the water there. The *Bufo* tadpoles rested in the warmer water at the bottom of the pond throughout the night, moved back towards the shore as light increased near dawn, and resumed feeding activity. More recently, traps positioned near the bottom of Johnson Pond's centre have caught green frog tadpoles almost exclusively at night (S. E. Hampton, unpublished data). Based on these accounts, it is possible that greater tadpole abundance at night might have occurred as the tadpoles shifted habitats, rather than as the result of a general increase in swimming activity.

Horizontal movement from littoral to centre waters at night

At the community level, diel horizontal movement of animals from the littoral to open water at night (as a habitat expansion, shift or both) is supported by inspection of the MDS plot (Fig. 3) and the ANOSIM results. Edge and centre samples were similar to each other, but distinct from the littoral zone samples during the day. At night, both the edge and centre samples more strongly resembled the daytime littoral community, which suggested horizontal movement from the littoral zone towards the edge and centre.

One can infer from these data either that increased swimming activity caused a general nocturnal increase in

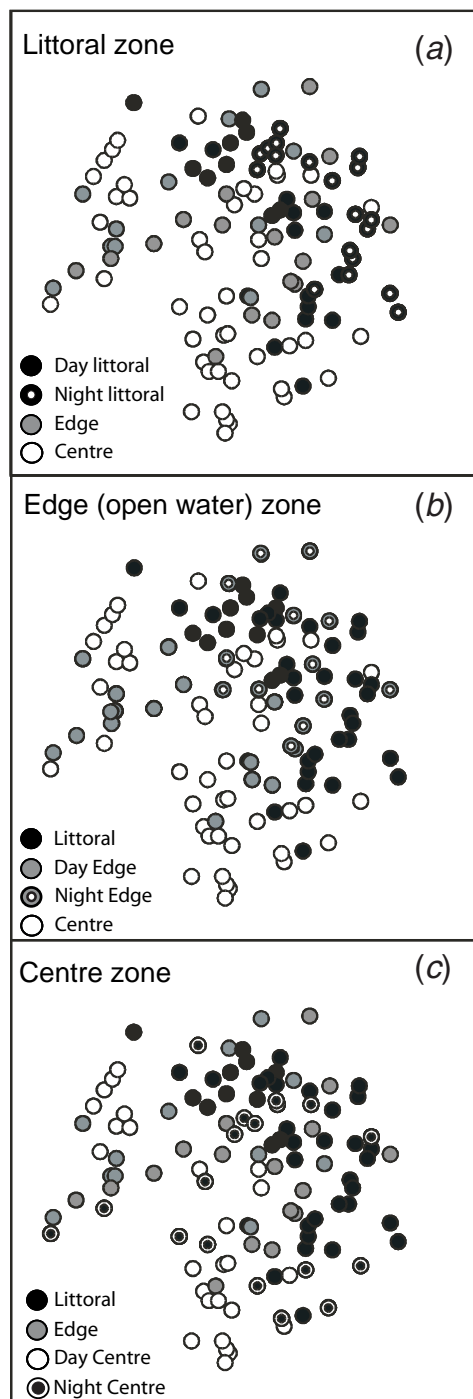


Fig. 3. Multidimensional scaling (MDS) plot of samples showing diel differences in taxonomic composition and abundance among habitats for one area at a time. Habitats are overlaid on the MDS plot as in Fig. 2, but here day and night are separated for the (a) littoral zone, (b) open-water edge zone and (c) the central area. Night samples are marked by a dot in the middle of the circle.

catch, or that transients were caught while changing habitat (to an unmonitored position in the pond), but might not have otherwise increased activity at night. Our own observations

throughout the summer at Johnson Pond suggested that the increased abundance in traps at night was due to greater swimming activity for most taxa. Dytiscids, odonates, mayflies, belostomatids, *Ranatra* and leeches were frequently observed swimming in all areas of the pond throughout the night. Whether our data are indicative of greater swimming activity, habitat shifts or both (as we propose), such striking nocturnal changes in the behaviour of the Johnson Pond community are unexpected in the absence of predatory fish.

Possible reasons for diel behavioural differences in fishless pond communities

Diel habitat shifts and nocturnal increases in activity in aquatic systems are thought primarily to be associated with the presence of a visual predator, specifically fish. Partly to determine whether the behaviour of the Johnson Pond community was aberrant, Hampton and Friedenberg (2002) conducted a separate short-term survey of Johnson Pond, one other fishless pond and a pond with bottom feeding fish. Using three sampling methods (passive bottle traps, sweep nets and a column sampler), Hampton and Friedenberg (2002) found higher nocturnal use of surface waters at night, although they were unable to detect shifts between littoral and open water habitat. Thus, the results presented in the present study are not an aberration and the observed nocturnal changes in habitat use and behaviour were not driven by extant fish predators. We suggest four possible explanations for this phenomenon in fishless ponds.

First, reduced conspicuousness during the day might be favoured in the presence of visually feeding predators such as birds (as suggested by Gilbert *et al.* 1999) or amphibians. In the present study, there were four to seven ducks at any given time on the pond and although we saw them dabbling during the night and day, as well as visually foraging in the open water during the day, these activities were not further quantified. Mallards are known to eat swimming invertebrates, in addition to vegetation, and aquatic invertebrates are particularly important in the diet of ducklings (Cox *et al.* 1998). Although visual prey detection might be compromised at night, ducks can and do still feed on aquatic invertebrates by dabbling (Swanson 1977; McNeil *et al.* 1995; Green *et al.* 1999). Predation pressure by the mallards in Johnson Pond might not be reduced substantially at night, but swimming conspicuously in the open water might have been less dangerous than clinging to shallow vegetation that was still within reach of a nocturnally dabbling predator. Red-spotted newts are also visual predators, but are unlikely to strongly influence the Johnson Pond macroinvertebrates, because this species feeds mostly on littoral microcrustaceans (Strohmeier *et al.* 1989).

Second, increased nighttime macroinvertebrate presence in the near-surface water might possibly have been a response to changes in the distribution of smaller prey not

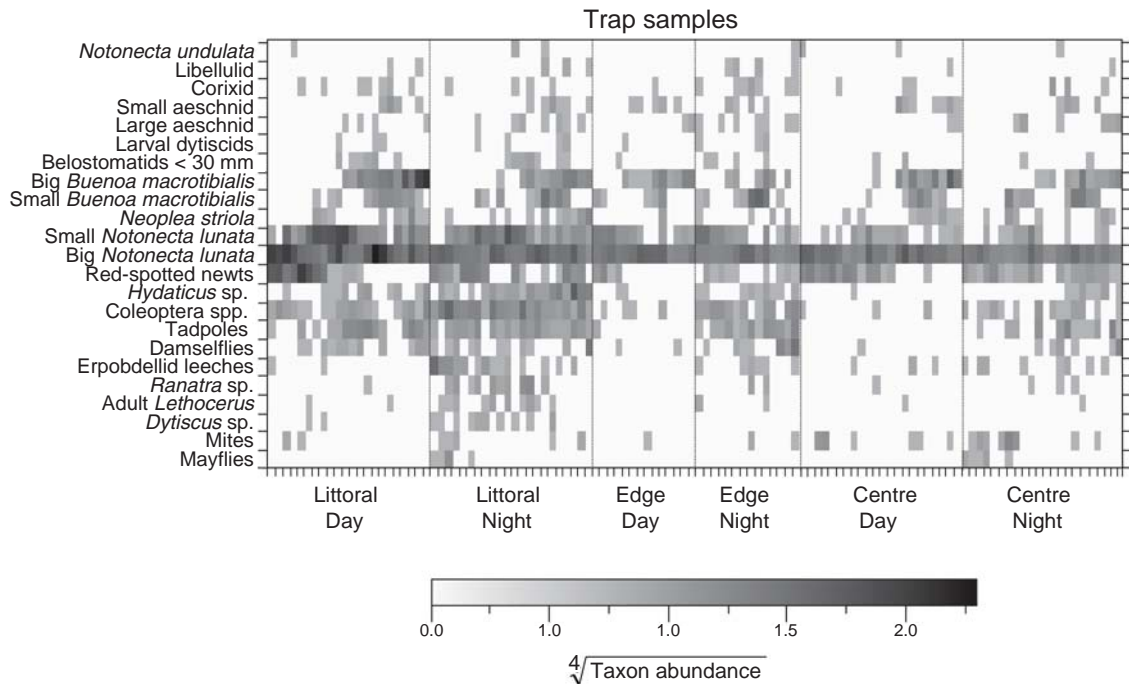


Fig. 4. Shade diagram for taxa and samples divided into habitat and time of day groupings. Darker boxes represent a greater abundance of animals within a sample. On the x-axis, within each habitat-time grouping, the ticks represent sampling dates through the season. Rows and columns of the array are ordered on the basis of cluster analysis and MDS distributions of taxa and samples, such that relative position (of taxa or habitat-time grouping) on each axis indicates similarity or dissimilarity.

examined in this study. However, we think this possibility is unlikely. In another study carried out in August 1999 (Z. M. McLaren and S. E. Hampton, unpublished data), cladocerans, large copepods, amphipods, dipteran larvae and terrestrial prey (caught on the surface) were concentrated in the littoral zone during day and night. Only the rotifers *Hexarthra* (ca. 0.20 mm body length), *Polyarthra* (ca. 0.11 mm body length) and *Keratella* (ca. 0.11 mm body length) were more abundant in the surface water near the *Potamogeton* stand. No significant increases at night were observed. Based on these observations, diel changes in zooplankton availability in the surface waters do not explain macroinvertebrate habitat shifts or increased activity.

A third possibility is that reduction in light forced a change in foraging strategy for many of the predatory macroinvertebrates in our study. Most of the invertebrate taxa that were more active at night are able to navigate both visually and non-visually (Aiken 1986; Blinn *et al.* 1993; Runck and Blinn 1994; Corbett 1999). For example, a sit-and-wait strategy might be appropriate during the day when prey can be visually located and attacked, but at night it may be advantageous to forage more actively to maximise tactile encounters with prey. Movement into the open water of the edge zone might also allow some visual location of prey under moonlight. These questions about profitability of switching foraging strategy are currently under investigation.

A fourth and simple explanation for the increased conspicuousness of most pond animals at night is that it is a non-plastic behaviour that is favoured in most aquatic environments. Many, if not most, pond macroinvertebrates are not necessarily restricted to a single pond from one generation to the next. The adult stages are typically capable of flight (e.g. odonates, aquatic hemipterans, dytiscids). When landing in a new body of water, where the extent of visual predation is unknown (e.g. fish, salamanders, birds), a generally appropriate strategy for large invertebrates might simply be to delay conspicuous activities until night.

In conclusion, in the present study, tadpoles and many macroinvertebrates were caught more frequently at night in passive funnel traps near the surface of both macrophyte-dominated and open water. The expansion or change of habitat, from the littoral zone towards the edge and centre, might be the result of generally greater swimming activity in and around preferred littoral habitat or true migrations to different nighttime habitat.

The reduced conspicuousness of aquatic animals during the day is normally explained by the presence of visually feeding fish. Here the only likely visual predators were four to seven mallard ducks that also foraged by dabbling at night. It is possible that release from visual bird predation in deeper water allows greater macroinvertebrate activity in those areas at night. The nocturnal reduction of light might also

necessitate a change in foraging strategy that results in higher swimming activity. Finally, increased nocturnal swimming activity might simply be a non-plastic behaviour that is generally appropriate for large invertebrates to cope with various visual predators. These proposed explanations are not mutually exclusive.

Changes reported in the present study regarding habitat and activity of pond animals over the diel cycle challenge the assumptions one would make about lentic macroinvertebrate relationships based on daytime observations alone. The impacts of nocturnal behavioural changes on models of aquatic system functioning have been widely recognised for vertically migrating pelagic zooplankton (Williamson and Magnien 1982; Lampert and Taylor 1985; Williamson and Stoeckel 1990) and for stream macroinvertebrates (Johnson and Covich 2000). Even in fishless habitats where dramatic diel differences are not expected, animal abundances might be higher and habitat might overlap much more extensively at night than would be reported during the day. Furthermore, for pond animals that use chemical and mechanical cues in addition to vision for navigating within their environments, interactions might not only continue from day to night, but they might become substantially different during the night, relative to day.

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References

- Aiken, R. B. (1986). Diel activity of a boreal water beetle (*Dytiscus alaskanus*: Coleoptera; Dytiscidae) in the laboratory and field. *Freshwater Biology* **16**, 155–159.
- Angstadt, J. D., and Moore, W. H. (1997). A circadian rhythm of swimming behavior in a predatory leech of the family Erpobdellidae. *American Midland Naturalist* **137**, 165–172.
- Beiswinger, R. E. (1977). Diel patterns of aggregative behavior in tadpoles of *Bufo americanus* in relation to light and temperature. *Ecology* **58**, 98–108.
- Blinn, D. W., Runck, C., and Davies, R. W. (1993). The impact of prey behaviour and prey density on the foraging ecology of *Ranatra montezuma* (Heteroptera): a serological examination. *Canadian Journal of Zoology* **71**, 387–391.
- Burks, R. L., Lodge, D. M., Jeppesen, E., and Lauridsen, T. L. (2002). Diel horizontal migration of zooplankton: costs and benefits of inhabiting the littoral. *Freshwater Biology* **47**, 343–365, doi:10.1046/J.1365-2427.2002.00824.X.
- Clarke, K. R. (1993). Nonparametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117–143.
- Clarke, K. R., and Warwick, R. M. (1994). 'Change in Marine Communities: an Approach to Statistical Analysis and Interpretation.' (Plymouth Marine Laboratory, National Research Council: Plymouth, UK.)
- Cooper, S. D. (1983). Selective predation on cladocerans by common pond insects. *Canadian Journal of Zoology* **61**, 879–886.
- Corbett, P. S. (1999). 'Dragonflies: Behavior and Ecology of Odonata'. (Cornell University Press: Ithaca, NY.)
- Cox, R. R. Jr, Hanson, M. A., Roy, C. C., Euliss, N. H. Jr, Johnson, D. H., and Butler, M. G. (1998). Mallard duckling growth and survival in relation to aquatic invertebrates. *The Journal of Wildlife Management* **62**, 124–133.
- Davies, R. W., Dratnal, E., and Linton, L. R. (1996). Activity and foraging behaviour in the predatory freshwater leech *Nephelopsis obscura* (Erpobdellidae). *Functional Ecology* **10**, 51–54.
- Davies, R. W., and Kasserra, C. E. (1989). Foraging activity of two species of predatory leeches exposed to active and sedentary prey. *Oecologia* **81**, 329–334.
- Dini, M. L., and Carpenter, S. R. (1992). Fish predators, food availability and diel vertical migration in *Daphnia*. *Journal of Plankton Research* **14**, 359–377.
- Elliott, J. M. (1973). The diel activity pattern, drifting and food of the leech *Erpobdella octoculata* (L.) (Hirudinea: Erpobdellidae) in a lake district stream. *Journal of Animal Ecology* **42**, 449–459.
- Flecker, A. S. (1992). Fish predation and the evolution of invertebrate drift periodicity: evidence from neotropical streams. *Ecology* **73**, 438–448.
- Gilbert, J. J., Burns, C. W., and Gilbert, C. C. (1999). Summer distribution patterns of the backswimmer, *Anisops wakefieldi* (Hemiptera: Notonectidae), in a New Zealand pond. *New Zealand Journal of Marine and Freshwater Research* **33**, 661–672.
- Giller, P. S., and McNeill, S. (1981). Predation strategies, resource partitioning and habitat selection in *Notonecta* (Hemiptera/Heteroptera). *Journal of Animal Ecology* **50**, 789–808.
- Green, A. J., Fox, A. D., Hughes, B., and Hilton, G. M. (1999). Time-activity budgets and site selection of white-headed Ducks (*Oxyura leucocephala*) at Burdur Lake, Turkey in late winter. *Bird Study* **46**, 62–73.
- Hampton, S. E., and Friedenberg, N. A. (2002). Nocturnal increases in the use of near-surface water by pond animals. *Hydrobiologia* **477**, 171–179, doi:10.1023/A:1021059108674.
- Haney, J. F. (1988). Diel patterns of zooplankton behaviour. *Bulletin of Marine Science* **43**, 583–603.
- Hilsenhoff, W. L. (1987). Effectiveness of bottle traps for collecting Dytiscidae (Coleoptera). *The Coleopterists' Bulletin* **41**, 377–380.
- Holomuzki, J. R. (1985). Life history aspects of the predaceous diving beetle, *Dytiscus dauricus* (Gebler), in Arizona. *The Southwestern Naturalist* **30**, 485–490.
- Holomuzki, J. R. (1986). Predator avoidance and diel patterns of microhabitat use by larval tiger salamanders. *Ecology* **67**, 737–748.
- Hungerford, H. B. (1933). The genus *Notonecta* of the world (Notonectidae-Hemiptera). *The University of Kansas Science Bulletin* **21**, 5–195.
- Johnson, S. L., and Covich, A. P. (2000). The importance of night-time observations for determining habitat preferences of stream biota. *Regulated Rivers: Research & Management* **16**, 91–99, doi:10.1002/(SICI)1099-1646(200001/02)16:1<91::AID-RRR568>3.0.CO;2-V.
- Kohler, S. L. (1985). Identification of stream drift mechanisms: an experimental and observational approach. *Ecology* **66**, 1749–1761.

- Lampert, W., and Taylor, B. E. (1985). Zooplankton grazing in a eutrophic lake: implications for diel vertical migration. *Ecology* **66**, 68–82.
- McIntosh, A. R., and Townsend, C. R. (1994). Interpopulation variation in mayfly antipredator tactics: differential effects of contrasting predatory fish. *Ecology* **75**, 2078–2090.
- McNeil, R., Díaz, O. D., Liñero, A. I., and Rodríguez, S. J. R. (1995). Day- and night-time prey availability for waterbirds in a tropical lagoon. *Canadian Journal of Zoology* **73**, 869–878.
- Merritt, R. W., and Cummins, K. W. (1984). 'An introduction to the Aquatic Insects of North America.' (Kendall/Hunt Publishing Co.: Dubuque, Iowa, USA)
- O'Brien, W. J., and Vinyard, G. L. (1978). Polymorphism and predation: the effect of invertebrate predation on the distribution of two varieties of *Daphnia carinata* in South India ponds. *Limnology and Oceanography* **23**, 452–460.
- Peckarsky, B. L. (1996). Alternative predator avoidance syndromes of stream-dwelling mayfly larvae. *Ecology* **77**, 1888–1905.
- Peckarsky, B. L., Fraissinet, P. R., Penton, M. A., and Conklin, D. J. Jr (1990). 'Freshwater macroinvertebrates of Northeastern North America.' (Cornell University Press: Ithaca, New York, USA)
- Runck, C., and Blinn, D. W. (1994). Role of *Belostoma bakeri* (Heteroptera) in the trophic ecology of a fishless desert spring. *Limnology and Oceanography* **39**, 1800–1812.
- Streams, F. A. (1982). Diel foraging and reproductive periodicity in *Notonecta undulata* Say (Heteroptera). *Aquatic Insects* **4**, 111–119.
- Streams, F. A. (1992). Age-dependent foraging depths of two species of *Notonecta* (Heteroptera: Notonectidae) breeding together in a small pond. *Aquatic Insects* **14**, 183–191.
- Strohmeier, K. L., Crowley, P. H., and Johnson, D. M. (1989). Effects of red-spotted newts (*Notophthalmus viridescens*) on the densities of invertebrates in a permanent, fish-free pond: a one-month enclosure experiment. *Journal of Freshwater Ecology* **5**, 53–65.
- Swanson, G. A. (1977). Diel food selection by Anatinae on a waste-stabilization system. *The Journal of Wildlife Management* **41**, 226–231.
- Truxal, F. S. (1953). A revision of the genus *Buenoa* (Hemiptera, Notonectidae). *The University of Kansas Science Bulletin* **35**, 1351–1521.
- Warkentin, K. M. (1992). Microhabitat use and feeding rate variation in green frog tadpoles (*Rana clamitans*). *Copeia* **3**, 731–740.
- Williamson, C. E., and Magnien, R. E. (1982). Diel vertical migration in *Mesocyclops edax*: implications for predation rate estimates. *Journal of Plankton Research* **4**, 329–339.
- Williamson, C. E., and Stoeckel, M. E. (1990). Estimating predation risk in zooplankton communities: the importance of vertical overlap. *Hydrobiologia* **198**, 125–131.
- Young, J. O., and Spelling, S. M. (1986). The incidence of predation on lake-dwelling leeches. *Freshwater Biology* **16**, 465–477.
- Zalom, F. G. (1978). A comparison of predation rates and prey handling times of adult *Notonecta* and *Buenoa* (Hemiptera: Notonectidae). *Annals of the Entomological Society of America* **71**, 143–148.

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