



Nocturnal increases in the use of near-surface water by pond animals

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Abstract

We assessed diel animal habitat use in three shallow ponds, using unbaited funnel traps, a large column sampler, and sweep net collections in the upper stratum (0–0.3 m) of littoral and open habitats. In all three ponds, more animals were caught at night than during the day, indicating that use of near-surface waters was greatest at night, particularly in the fishless ponds. All methods yielded similar patterns. Our results demonstrate that nocturnal observations of pond animals are necessary to describe their ecology, even in fishless ponds where diel differences in habitat use or behavior might not be anticipated.

Introduction

For logistical reasons, most assessments of animal habitat use, population densities and activities are done in the daytime, but there is growing evidence that dramatic nocturnal differences in aquatic animal behavior are common and thus worthy of incorporating into population and community models (Lampert & Taylor, 1985; Johnson & Covich, 2000). Diel differences in behavior are known to occur among certain aquatic animals, such as fish (Levy, 1990; Piet & Guruge, 1997), pelagic zooplankton (Pennak, 1944; Haney, 1988; Levy, 1990; Neill, 1990), and some groups of macroinvertebrates (Waters, 1962; Pierce, 1988; Van Buskirk, 1992; Johnson, 1995; Peckarsky, 1996; Holomuzki & Hoyle, 2000; Johnson & Covich, 2000). Nocturnal behavior of lentic macroinvertebrates is less well studied than that of fish and stream macroinvertebrates, but the ability of many macroinvertebrates to use both vision and mechanoreception to navigate the environment implies that important activities need not cease at night. Observations that the community of one fishless Vermont pond changed habitat use at night (S.E. Hampton & I.C. Duggan, unpublished manuscript) led us to question whether such

nocturnal habitat shifts were common among pond communities.

Simultaneously determining diel changes in behavior and habitat use for more than one group of pond organisms is logistically problematic, and relatively rarely done. Each sampling method suffers from taxonomic bias depending upon behavior, habitat use, and body size. A combination of methods increases the accuracy of a community survey by averaging method-specific sampling biases. In a diel study, simultaneous use of several methods may be particularly important, since it is possible that some taxa may avoid certain sampling apparatus more during day or night.

Our primary purpose in this study was to assess the diel changes in habitat use of the macroinvertebrate and vertebrate communities of three ponds, focusing on the differences between near surface water use in vegetated and non-vegetated areas of the pond. We increased the accuracy of our assessment by using three different sampling methods, enabling us to compare the effectiveness of the three methods in capturing various taxa.

Materials and methods

Study sites

All three ponds are located on privately owned land in Vermont, U.S.A. Sylvester Pond and Johnson Pond are shallow (ca. 1.5 and 2 m maximum depth, respectively) and fishless. Sylvester Pond is relatively small (0.05 × 0.05 km) and macrophytes (mainly *Typha*) are regularly removed by the land owners. The littoral zone is thus very sparse and primarily composed of water lilies and sedges. In contrast, the Johnson Pond (0.1 × 0.05 km) littoral zone is dense and dominated by *Typha*, and the center of the pond has a well-developed *Potamogeton* stand. Childs Pond is shallow (ca. 3 m maximum depth) but comparatively large (0.25 km × 0.20 km). Macrophytes are almost solely water lilies that grow sparsely along all shores. Fish are present in Childs Pond, mainly brown bullheads (*Ameiurus nebulosus*) although some larger carp may also occur there (M.A. McPeck, pers. comm.).

Collection methods

We sampled each pond intensively over a 48-h period within a 9-day period, such that comparisons among ponds could be made with relatively little consideration paid to seasonal changes. Collections were made 14–16 September 1999 in Childs Pond, 17 and 18 September 1999 in Sylvester Pond, and 21–23 September 1999 in Johnson Pond. All collections were made from a boat in open water and littoral zones. Vertebrates were identified and released, whereas the remainder of each sample was preserved in ethanol.

We took 'sweep' samples with a rectangular (16 × 19 cm) aquatic net fitted with a 0.5-mm mesh. We swept an approximately 1 m transect 30 cm below the water surface back and forth three times. The net was inverted into a bucket and contents washed through with pond water. We concentrated this sample using a 0.21-mm mesh-lined bucket and preserved it with approximately 70% ethanol. Three replicate sweep collections were done in open and vegetated water at approximately noon (day samples) and midnight (night samples).

A column ('ring') sampler was constructed and used as described by Streams & Shubeck (1982). A cylinder of 0.5 mm mesh net was held open by an inflated bicycle inner tube on one end, and a weighted bicycle rim on the other. The entire cylinder was collapsed and thrown from the boat for open water

samples, but had to be dropped more carefully over macrophytes in the littoral zone. We then used a 0.5-mm mesh sweep net to remove all visible animals within the column, and swept up and down the inner surface for approximately half a minute once no animals were visible in the column. These sweeps from the column were then preserved as described above. We took three replicate ring samples from open and vegetated water at approximately noon and midnight.

We constructed clear plastic unbaited funnel-traps as described by Streams (1992) with a few modifications. We riveted clear 15 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. Traps were suspended horizontally on a rack constructed of PVC pipe. A rope was drawn through a 1.5-m vertical PVC pipe with an anchor at the bottom and a float at the top. Four horizontal arms could be fitted at any depth by drilling holes at the desired height on the pipe. 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. As we set the traps, we allowed a pocket of air to remain in the traps, both to reduce mortality of air breathing animals and to provide buoyancy. Traps were thus oriented at right angles in four directions 30 cm below the surface on each rack. Three racks were placed in the littoral as well as in the open water. After a 12-h period, we emptied all four traps from each rack into a bucket and preserved the contents as described above, such that each of the racks was a replicate sample. For day samples, we set the traps at 7 am and emptied them at 7 pm. We re-set the traps, and night samples were collected at 7 am.

Sample enumeration

We sorted and counted all animals that were plainly visible to the naked eye, working together to minimize researcher variation. This criterion included, for example, *Chaoborus* and amphipods, but excluded all copepods and the smallest mayflies. We then counted all animals in the samples primarily using identification keys in Peckarsky et al. (1990), Merritt & Cummins (1984), Hungerford (1933), Truxal (1953), and Cook (1956).

Analysis of diel patterns within pond

All count data were log_e-transformed to fit ANOVA model assumptions of normality and homoscedasticity. We included only those taxa that comprised 2%

or more of the community. We analyzed the data separately for each lake with a 3-way ANOVA using JMP (SAS Institute), to determine effects of time of day (day and night), habitat (littoral and open water), and collection method (sweep, ring, and trap samples) and interactions among these effects. Where Method was significant, we used a Tukey's test to help determine how the methods differed from each other.

Comparison of methods and communities across ponds

All community analyses were performed with the General Linear Models procedure in SAS (SAS Institute). To reduce the number of data points with no individuals, replicates for each method were pooled for each sampling bout (time of day within date), resulting in twelve replicates for each method: two night and two day samples in each pond. This condensed data set was used to compute taxon richness and Fisher's alpha as a diversity index (Fisher et al., 1943). Fisher's alpha, α , is a parameter estimated from community census data such that:

$$\frac{N}{S} = \frac{(e^{S/\alpha} - 1)}{S/\alpha},$$

where e is the natural exponent, N is the number of individuals in a sample and S is the number of species (Fisher et al., 1943). Simply, α is a constant related to the rate of decay of a log-series distribution so that the probability of the first, second, third, and r th terms of the series is:

$$\alpha, \frac{\alpha\theta^2}{2}, \frac{\alpha\theta^3}{3} \cdots \frac{\alpha\theta^r}{r},$$

where theta is a parameter of the distribution and has a value less than one. The parameters alpha and theta can be estimated simultaneously using the iterative algorithm suggested by Birch (1963) to fit a log series to species abundance data. Importantly, Fisher's alpha is a measure of diversity that is independent of sample size.

The slope of an ordinary least-squares linear regression through a \log_e -transformed species rank-abundance curve describes the evenness of a community (Tokeshi, 1993). A shallow slope indicates high evenness, while a steep slope is indicative of a community dominated by a few abundant species. The slope is also closely related to Fisher's alpha. A one-way ANOVA of Fisher's alpha across methods therefore tests whether our perception of community

diversity, both in terms of richness and evenness independent of sample size, is affected by the sampling method we use.

Results

Diel animal abundance and distribution within ponds

In all three ponds, many taxa were significantly more abundant in night and littoral samples (Fig. 1, Table 1). No taxon was significantly more abundant in the day or the open water. In most cases, higher order interactions were also significant (Table 1), complicating the interpretation of the Time or Habitat effect alone. However, closer inspection of the significant interactions, discussed below, also showed that most animals were more abundant at night and were primarily found in the littoral zone.

Significant Time*Habitat interactions were typically caused by abundance increases in only one habitat at night (Fig. 1). In both Johnson Pond and Sylvester Pond, *Notonecta lunata* Hungerford was more abundant in the littoral zone at night, although its abundance was consistent from day to night in the open water. Collembolans were caught in the open water of Childs Pond only during the day, while collembolan littoral abundance was similar from day to night. *Chaoborus* demonstrated the opposite pattern in Johnson Pond, peaking in abundance in the open water at night. In Sylvester Pond, *Hesperocorixa*, *Peltodytes*, and *Hydaticus* were more abundant during the night than day, but found almost exclusively in the littoral zone.

Significant interactions involving Method did not appear to indicate that a collection method was differentially effective in a habitat or time of day. In every case, inspection of the data showed that this interaction could be explained by the fact that a taxon was rarely or never collected with one or two methods and a strong effect of Time or Habitat was apparent.

Comparison of methods within ponds

Table 1 shows the results of Tukey's pairwise comparisons of methods for individual taxa. In Childs Pond, traps collected a significantly higher number of fish and the non-perching notonectid *Buenoa* than the other methods. Sweeps and the ring often captured similar abundances of taxa, and were frequently more effective than traps. The only animals that were most effectively gathered by sweeps were the surface-dwelling collembolans.

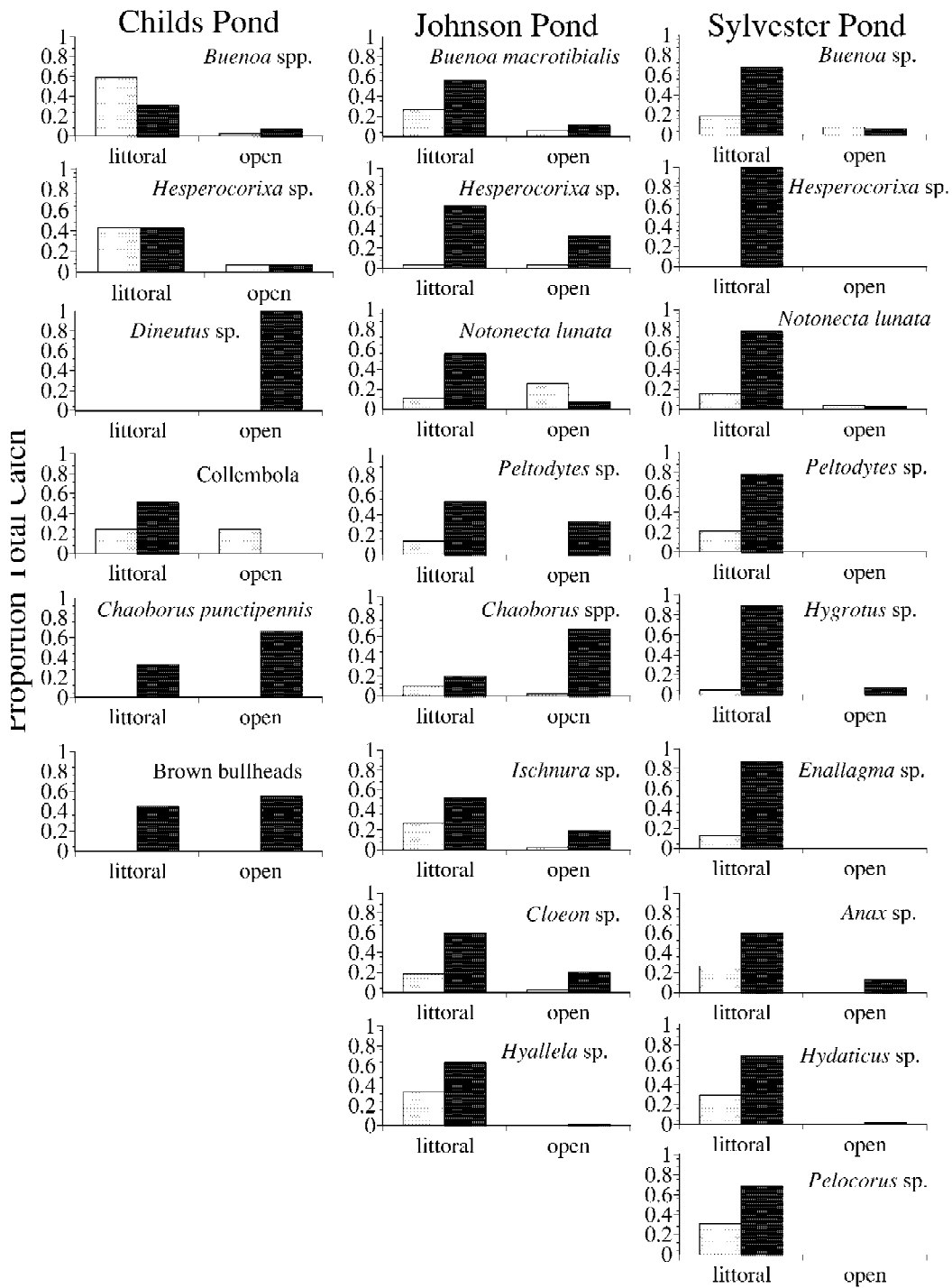


Figure 1. Proportions of total individuals caught in the littoral and open water of each pond by day (light bars) and night (dark bars), for those taxa comprising 2% or more of each pond community.

Table 1. Results from 3-way ANOVAs on pond animal abundances from day and night (Time), littoral and open areas (Habitat), using 3 techniques (Method): a large column sampler (ring=r), sweep nets (s), and unbaited passive funnel traps (t). Significant or nearly significant *P*-values are shown, and those greater than 0.05 are indicated by NS (non-significant). Relationships in parentheses represent results of Tukey's tests to determine differences among methods – '>' indicates significant differences, while commas indicate similarity

Taxon	Time*Habitat*Method	Time*Habitat	Habitat*Method	Time*Method	Time	Habitat	Method
Childs Pond							
<i>Buena</i>	NS	NS	0.0594	NS	NS	<0.0001	0.0017(T>R,S)
<i>Hesperocorixa</i>	NS	NS	NS	NS	NS	0.0003	NS
<i>Dineutus</i>	NS	NS	NS	NS	NS	NS	NS
Collembola	0.0364	0.0214	NS	NS	NS	NS	0.0121(S>T)
<i>Chaoborus</i>	NS	NS	NS	0.0314	0.0018	NS	0.0314(R,S>T)
Brown bullheads	NS	NS	NS	<0.0001	0.0006	NS	<0.0001(T>R,S)
Johnson Pond							
<i>Buena</i>	NS	NS	0.0201	NS	NS	<0.0001	NS
<i>Hesperocorixa</i>	NS	NS	NS	0.0024	0.0042	NS	0.0007(R>T,S)
<i>Notonecta</i>	NS	0.0075	0.0612	0.0552	NS	NS	NS
<i>Peltodytes</i>	NS	NS	NS	0.018	0.0012	<0.0001	<0.0001(R>T,S)
<i>Chaoborus</i>	0.0611	0.0097	0.0435	0.0011	<0.0001	NS	<0.0001(S,R>T)
<i>Ischnura</i>	NS	NS	NS	0.0582	0.0161	<0.0001	<0.0001(S,R>T)
<i>Cloeon</i>	NS	NS	NS	NS	<0.0001	<0.0001	<0.0001(R>T,S)
<i>Hyalalea</i>	0.0412	NS	NS	NS	NS	0.0005	NS
Sylvester Pond							
<i>Buena</i>	NS	NS	0.0165	NS	NS	0.0002	NS
<i>Hesperocorixa</i>	NS	0.0343	NS	NS	0.0343	0.0343	NS
<i>Notonecta</i>	NS	0.0312	NS	NS	0.0453	<0.0001	NS
<i>Peltodytes</i>	0.0104	0.0394	<0.0001	0.0104	0.0394	<0.0001	<0.0001(R>T,S)
<i>Hygrotus</i>	0.0061	NS	0.0382	0.0002	0.0017	0.0072	0.0017(R>T)
<i>Enallagma</i>	NS	NS	NS	NS	NS	0.0022	NS
<i>Anax</i>	NS	NS	NS	NS	NS	0.0071	NS
<i>Hydaticus</i>	NS	0.0551	0.0127	NS	0.0214	<0.0001	0.0481(R,S>T)
<i>Pelocorus</i>	NS	NS	0.0279	NS	NS	0.0018	0.0279(R>T,S)

Comparison of methods and communities across ponds

Richness and number of individuals were compared across sampling methods and pond habitats using 2-way ANOVAs. Both richness and number of individuals were higher in the littoral than open water ($P<0.001$ and $P<0.0071$, respectively) regardless of method. While the different methods yielded similar estimates of richness, rings caught more individuals per sampling bout than sweeps or traps (Fig. 2). Estimates of Fisher's alpha did not differ across methods (Fig. 3), indicating that the analysis of richness is valid regardless of the differences in individuals caught by each method.

The Spearman rank correlation coefficient comparing taxon abundance across methods was 0.75 between rings and sweeps, 0.58 between rings and traps, and 0.55 between traps and sweeps. While the different methods ranked species differently, they yielded similar estimates of richness. All three methods produced the typical non-linear three-phase \log_e rank-relative abundance curve expected in communities of high species richness (Tokeshi, 1993). That is, abundant species were very abundant, rare species were very rare, and intermediate species were more similar to each other in relative abundance across ranks. The statistical similarity of Fisher's alphas among methods suggests that the three rank- \log_e relative abundance curves are drawn from the same statistical population and can be pooled to create a single profile of com-

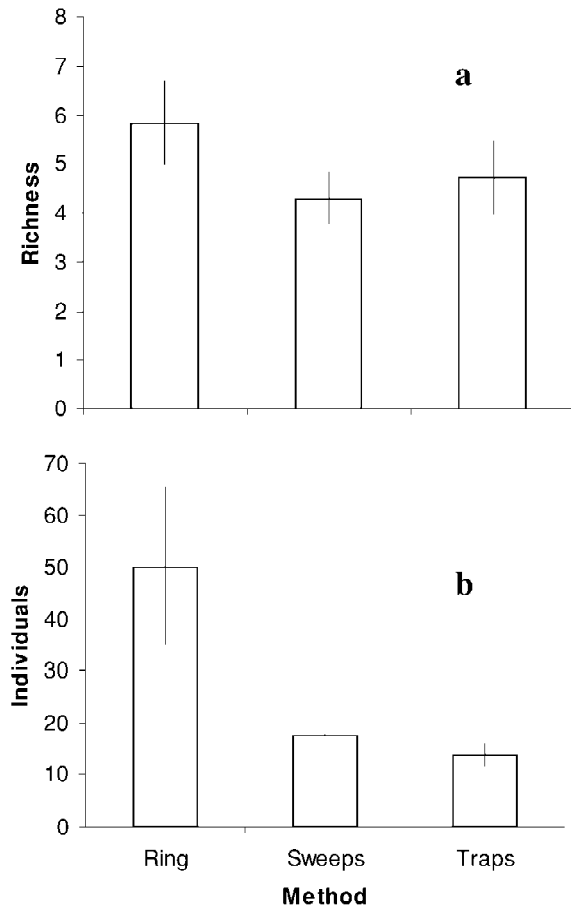


Figure 2. Mean (± 1 SE) richness and number of individuals in each sampling bout using different sampling methods. (a) There is no statistical difference among methods (ANOVA, $P=0.20$). (b) The ring method caught significantly more individuals than the other sampling techniques used (Scheffe Test, $P<0.01$).

munity diversity. An ordinary least-squares regression through the pooled rank-abundance data visually summarizes species abundance and evenness (Fig. 4).

To investigate differences among the methods in their sensitivity to taxon abundance, we divided taxa into categories of common and rare. Common taxa each represent more than 1% of individuals sampled and collectively account for more than 95% of all individuals counted. Rare taxa each represent less than 1% of individuals sampled and collectively account for less than 5% of all individuals counted. A one-way ANOVA of residuals from the pooled regression across methods suggests that methods did not differ in their estimates of the relative abundance of common taxa ($P<0.624$). Among rare taxa, however, the ring method yielded lower average \log_e

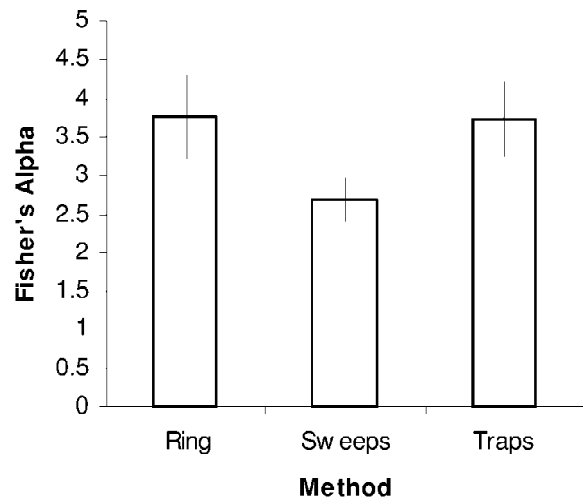


Figure 3. Mean (± 1 SE) estimates of Fisher's alpha as calculated for the different methods. There is no statistical difference among methods (ANOVA, $P=0.28$).

relative abundance than did sweeps and traps, a trend that is evident in Figure 4. Rings estimated the average \log_e relative abundance of rare taxa to be -6.38 ($SD=0.861$), whereas sweeps and traps estimated means of -5.46 ($SD=0.595$) and -5.12 ($SD=0.669$), respectively. While these means are all small, there is a three-fold difference between the untransformed means of rings and the other methods.

Discussion

Diel animal abundance and distribution

The animal communities of all ponds exhibited much higher nocturnal than diurnal abundance in near surface samples, particularly those of the two fishless ponds (Fig. 1). Higher night-time abundance in these samples may be due to microhabitat shifts – animals move closer to the surface at night – or higher swimming activity, neither explanation being mutually exclusive. While a variety of studies have described diel changes in zooplankton (Pennak, 1944; Haney, 1988; Levy, 1990; Neill, 1990) and fish (Hall et al., 1979; Bohl, 1980; Levy, 1990; Allison et al., 1996; Piet & Guruge, 1997) distribution in lakes, and macroinvertebrate drift or distribution in streams (Waters, 1962; Brittain & Eikeland, 1988; Holomuzki & Hoyle, 2000; Johnson & Covich, 2000), there are fewer reports of the nocturnal activity of lentic macroinvertebrates. Because many aquatic macroin-

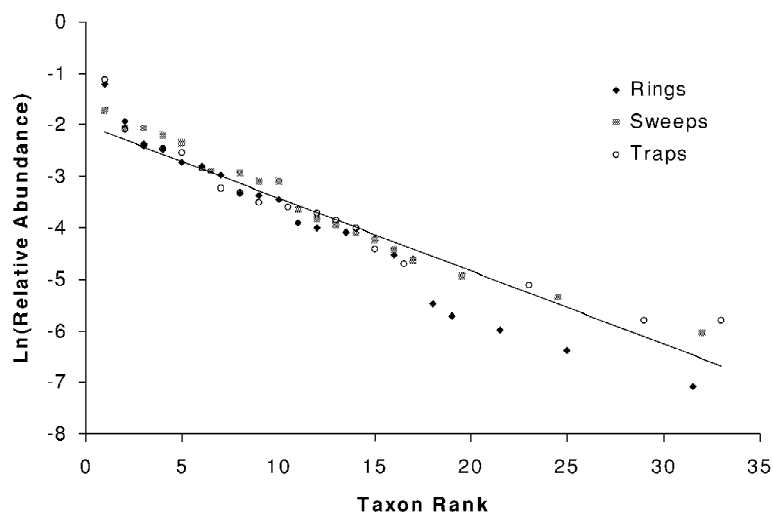


Figure 4. Taxon rank-abundance data for ring, sweep, and trap sampling methods based upon the sum of all observations. Although the curve is characteristically non-linear, a linear regression visually summarizes the study ponds' natural log-series community profile. The slope of the line is -0.1419 ($R^2=0.91$, $P<0.00001$).

vertebrates use both mechanoreception and vision for navigating their environments, diel changes in their activity are especially interesting as predators can hunt throughout the night, but the loss of vision may change foraging strategy and relationships between predators and prey. Our results demonstrate that nocturnal observations of pond animals are necessary to understand habitat use and overlap of macroinvertebrate communities.

This report of greater near-surface water use by animals in ponds regardless of fish presence is novel and counterintuitive. Visual predation by fish is often invoked to explain increased nocturnal conspicuousness of animals in aquatic systems (Zaret & Suffern, 1976; Haney, 1988; Levy, 1990; Dini & Carpenter, 1992; Flecker, 1992; Cowan & Peckarsky, 1994). In this study, fish predation was absent in Sylvester Pond and Johnson Pond, where macroinvertebrates showed the highest increase in nocturnal activity. Red-spotted newts occur in Johnson Pond, but those present at the time of this study were in low abundance and also demonstrated higher nocturnal activity (S.E. Hampton & I.C. Duggan, unpublished manuscript). In Childs Pond, brown bullheads were in the water column at night. The comparatively small night-time increase in macroinvertebrate abundance in Childs Pond may be a response to the greater night-time pelagic presence of these fish, or may simply reflect lower insect abundance in the pond overall due to the low productivity of the pond. A few mallard ducks reside in

Johnson Pond, and bird abundance in the other two ponds is mostly unknown. It is possible that pressure by such non-aquatic visual predators favors increased nocturnal activity (see Gilbert et al., 1999), but this hypothesis is untested. Finally, nocturnal increases in activity could simply be a behavior that is favored in most environments where various visual predators are present, and may not be a plastic trait.

The greater animal abundance in the littoral zones of all ponds is not surprising, given the widely recognized correlation of aquatic macroinvertebrate with macrophyte abundance (Marchant, 1982; James et al., 1998; Ó Hare & Murphy, 1999), and habitat complexity with animal diversity and abundance in general (Dean & Connell, 1987a, b; O'Connor, 1991; Martin-Smith, 1993; Caley & St. John, 1996). In this study, there was little evidence for night-time switching between littoral and open habitat, as most Time*Habitat interactions could be explained by increased nocturnal abundance in the single habitat a taxon primarily occupied. One exception was *Chaoborus* in Johnson Pond, which may have been horizontally or vertically migrating, consistent with previous reports of diel changes in *Chaoborus* distribution (Wood, 1956; Teraguchi & Northcote, 1966; Voss & Mumm, 1999). In another study, Hampton & Duggan (unpublished manuscript) reported horizontal movements of several macroinvertebrates into open water at night in Johnson Pond throughout the summer. Gilbert et al. (1999) found that the South-

ern Hemisphere notonectid *Anisops* moved from the littoral toward open water at night. Perhaps a longer time frame is necessary to observe this pattern of horizontal movement, more intensive sampling is needed to observe relatively subtle abundance changes over this short time period, or the behavior has ceased to occur by autumn.

Comparison of methods

Sweeps and rings were particularly useful in collecting animals that are strongly associated with a substratum. In contrast to the traps, both animals clinging to vegetation and those actively swimming are gathered. The ring captured the highest abundance of animals overall. Given the high rank correlation between sweeps and rings, it seems possible that simply increasing the number of sweeps at a site would yield the same results as a ring sample.

The benefit of the ring is mainly that a sampling location may be randomly chosen and a discrete column of water quantitatively sampled. However, its usefulness is limited to areas with relatively sparse vegetation. In addition, in any emergent vegetation, it is impossible to randomly throw it to a location and let the ring settle from a distance as one would in open water. The ring also tended to yield very high numbers of the most common taxa and comparatively low numbers of the rare taxa, in contrast to sweeps and traps.

The horizontally oriented traps used here are especially good for capturing actively swimming animals in a particular stratum of water (Streams, 1992). However, these traps are not effective in catching animals that are inactive, swim consistently below or above the trap level, or travel vertically like *Chaoborus*. In Childs Pond, traps were most effective in capturing fish and the non-perching notonectid *Buenoa*. Beetle researchers have found similar traps useful in collecting Coleoptera adults (Aiken & Roughley, 1985; Hilsenhoff, 1987), and baited minnow traps of comparable design are widely employed. For collection of swimming animals, traps may be set at various depths and left in the field for any period of interest. In addition, when paired with sweep net or column sampler data, traps can provide an indicator of changes in swimming behavior rather than simply data on distribution.

Conclusions

Our results emphasize the need for including temporal variability in studies of the spatial distribution of pond animals (*sensu* Resh & Rosenberg, 1989). Daytime sampling may underestimate abundance of animals in a particular habitat, leading to erroneous conclusions about habitat use and the strength of species interactions in an environment. Our result that increased use of the near-surface water was not related to fish presence may indicate that other visual predators, such as birds, also drive the phenomenon; alternatively, the behavior may simply not be plastic for many pond animals. The three sampling methods yielded qualitatively similar results, but some differential effectiveness in collecting certain taxa was apparent. We recommend that studies of pond animal distribution include both day and night collections and that a combination of sampling methods be used. A combination of passive and active collection methods can not only increase the accuracy of distribution assessments, but the comparison can also provide information on swimming behavior of animals.

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