Should we be sampling zooplankton at night?

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Scientific Significance Statement

Sampling zooplankton in the pelagic zone of lakes during the day is standard practice in limnology. However, zooplankton commonly exhibit diel vertical and horizontal migration, which may lead to biases in zooplankton demographic estimates collected during the day. We analyzed almost 900 paired night–day samples from the literature and found night crustacean zooplankton density and biomass estimates exceeded day estimates by approximately 255% and 125% on average, respectively, suggesting a potential systematic bias in such estimates and, by extension, rate processes derived from day sampling.

Abstract

Limnologists generally sample during the day. Consequently, many estimates of lake ecosystem processes are derived from daytime samples. Zooplankton, which play critical roles in many such processes, are typically sampled during the day in the pelagic zone, although they commonly exhibit diel vertical and horizontal migration. Demographic estimates using day pelagic sampling may be biased depending on the type and extent of migration. We compiled 870 paired night-day zooplankton samples from the literature and found that crustacean zooplankton had, on average, 255% and 125% greater density and biomass, respectively, at night compared to day. Although limnologists have been aware that night zooplankton estimates are often higher than day estimates, our results provide quantitative estimates of the differences. Such underestimates from daytime sampling are alarming and call into question ecological rate processes derived from sampling zooplankton during the day.

Fundamental to science are the sampling procedures by which representative estimates of the phenomena under investigation are measured, whether from a laboratory beaker or the open ocean. In limnology and oceanography, plankton sampling is the backbone on which estimates of community demographics are based. Such estimates form the foundation for downstream inferences on plankton communities and their influence on ecosystem properties, be they population estimates or global biogeochemical rates (Carpenter et al. 1987; Jeppesen et al. 2011; Archibald et al. 2019).

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Zooplankton behavior and sampling design and methods influence demographic estimates. For example, water column density of *Bythotrophes longimanus* in Lake Huron was ×2 higher at night than day with a 153-μm mesh net, but no different using a 285-μm mesh (Armenio et al. 2017). Daytime sampling limited to surface layers can also lead to biased population estimates due to diel vertical migration (DVM) (Zaret and Suffern 1976). Similarly, day sampling limited to open water (i.e., pelagic) habitat may bias demographic metrics because zooplankton can exhibit diel horizontal migration (DHM) (Burks et al. 2002). Night estimates of zooplankton are often greater than day estimates, even when the entire water column is sampled (Lampert and Taylor 1985; Doubek et al. 2018). However, day sampling in the pelagic zone of lakes is a long-standing practice in limnology (Birge and Juday 1922). Consequently, such estimates could be biased, and thus fundamentally alter our inferences on ecological processes such as food web interactions (Brooks and Dodson 1965), carbon cycling and methane efflux (Bastviken et al. 2003; Devlin et al. 2015), energy transfer (Lindeman 1942; Cole et al. 2011), and seasonal succession (SOMMER et al. 1986).

If the default practice in limnology is to sample zooplankton during the day, then day estimates should accurately represent zooplankton populations and should be no different than night estimates. We tested this hypothesis by compiling and comparing published data for paired night-day zooplankton density and biomass estimates. We expected night estimates to be greater than day estimates. Because DHM is likely more prevalent in small and shallow lakes, we also expected night-day differences to be negatively related to lake surface area and station depth.

**Methods**

**Literature review**

Web of Science (v.5.32, 1982 to 18 May 2019) was used to find articles that reported day and night zooplankton density and biomass by

(zooplankton dens * OR zooplankton biomass*) AND (night AND lake).

All flagged articles were screened to determine if they met the following criteria: (1) freshwater lakes or reservoirs; (2) day and night samples collected within the same 24-h period with the same gear; (3) entire water column samples in the pelagic or open water zone; and (4) density, biomass, or both reported or extractable from figures. Samples had to be collected from ≥80% of the station depth to be considered entire water column samples. If zooplankton were collected with a discrete depth sampler, samples had to be taken at least every 2 m to estimate mean water column density and biomass. We chose 80% because only 2 studies and 18 individual observations were excluded at this cutoff (Doubek et al. 2019). Using more conservative cutoffs of 90%, 95%, or 100% of the water column did not affect results.

We included cladocera, copepods (adults, copepodites, and nauplii), and rotifers in our analyses. We did not include invertebrates that commonly migrate into or on lake sediments (e.g., *Mysis* and *Chaoborus*), ostracods, and dreissenid veligers. We also did not include data from size spectrum analyses (e.g., Bruet et al. 2010) or from acoustic devices (e.g., Vanderploeg et al. 2009) because we tested taxa-specific differences.

Another Web of Science (v.5.32, 1982 to 31 May 2019) search was conducted using slightly different terms to more comprehensively search the literature:

(zooplankton AND day AND night) AND (lake OR reservoir).

All flagged articles were screened as outlined above. The reference lists from relevant articles were examined for additional studies that met our criteria but were missed by Web of Science (e.g., articles published before 1982).

We recorded the following information: lake name, country, lake surface area, maximum depth, trophic state, station depth, sampling gear, sampling date, day and night density and/or biomass of reported zooplankton taxa, and the distance from the bottom of the lake for sample collection (Supporting Information Table S1; Doubek et al. 2019). WebPlotDigitizer (v4.2) was used to extract data when only accessible in figures. Density and biomass were standardized to individuals L⁻¹ and μg dry weight (DW) L⁻¹. Studies that reported only carbon or wet weight were not included.

**Statistical analyses**

We assessed night-day differences across broad taxonomic groups because of ecological variability across such groups: *Daphnia*, other cladocera (mostly smaller cladocera taxa such as *Bosmina* and *Ceriodaphnia*), predatory cladocera (*Bythotrophes*, *Cercopagis*, and *Leptodora*), copepods (adults + copepodites), nauplii, and rotifers. We also used crustacean zooplankton (cladocera + adult and copepodite copepods [but not nauplii]) as a composite group.

The number of paired observations was variable among studies. In some cases, many observations for one taxon were available from the same study within short-time frames. Inclusion of each observation violated nonindependence, but paired night-day observations also represented the focus of our study. Consequently, we ran analyses at three different levels of data aggregation: each paired observation (“all observations”); mean values by lake-year-month for each group (“monthly”); and mean values by lake-year for each group (“annual”). The monthly aggregation assumed that a month is longer than a generation time for many taxa (Allan 1976) and thus reduced impacts of nonindependence. We assumed the annual aggregation removed nonindependence, but at a cost of reduced sample size. Consistency of results across all
three levels of aggregation would provide more confidence in findings.

**Analysis 1: Instances of higher density and biomass at night compared to day**

First, we broadly assessed the number of occurrences where night or day had greater density and biomass. We expected a 50 : 50 distribution of points above and below a 1 : 1 line, if on average, no diel differences in density or biomass existed. We examined the paired observations by plotting a 1 : 1 line and comparing the observations above, on, and below the line.

**Analysis 2: Percent change in diel population estimates**

We next calculated the relative change of each paired observation for each zooplankton group for density and biomass across the three levels of data aggregation to standardize estimates across the diversity of taxa and lake trophic states. For example, a doubling of a predator zooplankton might be orders of magnitude less in density than a doubling of herbivorous zooplankton. Relative change was calculated as percent difference:

\[
\frac{(\text{OBS}_N - \text{OBS}_D)}{\text{OBS}_D} \times 100 \text{ if } \text{OBS}_N > \text{OBS}_D,
\]

\[
-\frac{(\text{OBS}_D - \text{OBS}_N)}{\text{OBS}_N} \times 100 \text{ if } \text{OBS}_D > \text{OBS}_N,
\]

where OBS is the observed density or biomass, N is night, and D is day. The different equations were used to keep increases or decreases between night and day on the same scale (i.e., no change = 0%), with a positive percent difference indicating an increase at night and a negative percent difference indicating a decrease at night.

We performed a one-sided single-sample t test to test if the percent difference in density and biomass was greater at night compared to the day for each group. We took a conservative

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**Fig. 1.** Relationships between paired day-night zooplankton density (A–C) and biomass (D–F) using all (A, D), monthly (B, E), and annual (C, F) data. The numbers in bold indicate the number of observations when night zooplankton density and biomass were higher (above the 1 : 1 line), when day zooplankton density and biomass were higher (below the 1 : 1 line), and when day and night zooplankton density and biomass estimates were the same (on the 1 : 1 line). Note that each axis is in logarithmic scale. A zero for any density or biomass value was replaced with the minimum observed density or biomass value for plotting purposes.
approach by only including paired night–day density and biomass estimates that had values greater than zero, so that zero values would not have an exaggerated effect on results. We did not apply a correction measure for these analyses because the dependent variable values were different in each test (all observations, monthly, and annual), thereby representing a different family of tests (Kutner et al. 2005).

Analysis 3: Relationship between lake surface area and station depth and percent change
Lastly, we tested for relationships between the percent difference in diel zooplankton density and biomass at the annual data aggregation and lake surface area and station depth using linear regression. Surface area and station depth were log10 transformed prior to analysis to meet assumptions of normality and equal variance.

For all statistical analyses, a p value at $\alpha \leq 0.05$ was considered significant. All analyses were performed in R v.3.6.0 (R Core Team 2019).

Results
Forty-eight studies met our criteria. The studies included 60 lakes and reservoirs and 870 paired night–day zooplankton observations: 692 of just density, 73 of just biomass, and 105 of both. Lakes were in 25 countries and ranged from 0.001 to 59,600 km$^2$ surface area and from 1.2 to 1470 m maximum depth (Supporting Information Table S1).

Analysis 1: Instances of higher density and biomass at night compared to day
Zooplankton estimates were more often higher at night compared to day. Paired samples were approximately $\times 2$ more likely to be above the 1 : 1 line for density and biomass (Fig. 1A,D). Furthermore, zooplankton density and biomass were about $\times 2.5$–3 more likely to fall above the 1 : 1 line, respectively, after averaging by month (Fig. 1B,E) and year (Fig. 1C,F).

Analysis 2: Percent change in diel population estimates
Mean ($\pm$ 1 SE) crustacean zooplankton density and biomass estimates were 257 ± 32% ($t_{661} = 8.07; p < 0.0001$) and 168 ± 40% ($t_{156} = 4.18; p < 0.0001$) higher at night compared to day (Fig. 2; Tables 1 and 2), respectively, for all observations. Similarly, Daphnia, predatory cladocera, and copepods had higher density ($p \leq 0.0001$) and biomass ($p \leq 0.01$) at night compared to day (Fig. 2A,D; Tables 1 and 2). Other cladocera had higher densities at night compared to day.
Rotifers and nauplii did not differ in density between night and day (\( p \geq 0.36 \)), and nauplii did not differ in biomass (\( p = 0.72 \); Fig. 2A,D). No biomass data were available for rotifers. Crustacean zooplankton density was also higher at night than day using monthly (228\% and 70\% annually) means (\( p < 0.0001 \); Fig. 2B,C; Table 1), as was crustacean biomass (105\% for each of monthly and annual means; \( p \leq 0.0005 \); Fig. 2E,F; Table 2). Daphnia and copepods had consistently higher density (\( p \leq 0.01 \)) and biomass (\( p \leq 0.03 \)) at night than during the day for monthly and annual means (Fig. 2; Tables 1 and 2). Predatory cladocera had higher density (\( p \leq 0.004 \)) at night compared to day after monthly and annual averaging and had higher biomass at night compared to day after monthly averaging (\( p = 0.05 \); Fig. 2B,C,E). However, predatory cladocera biomass was only marginally higher at night compared to day after annual averaging (\( p = 0.08 \); Fig. 2F), but the sample size was low (\( n = 4 \); Table 2). Likewise, other cladocera had significantly, or marginally, greater density at night compared to day after monthly or annual averaging (\( p \leq 0.06 \)), but no differences existed for other cladocera biomass (\( p \geq 0.14 \); Fig. 2; Tables 1 and 2). No differences between night and day densities existed for rotifers or nauplii (\( p \geq 0.22 \)) or nauplii biomass (\( p \geq 0.62 \); Tables 1 and 2) for monthly or annual means.

When we calculated each group’s mean percent change at night relative to day across the three levels of data aggregation, predatory cladocera were about 715\% and 380\%, Daphnia were about 240\% and 125\%, copepods were about 115\% and 95\%, and other cladocera were about 210\% and 45\% higher at night compared to day for density and biomass, respectively. Overall, crustacean zooplankton were 255\% and 125\% higher at night compared to day for density and biomass, respectively.

### Table 1. Sample sizes, means ±1 SE, and one-sided t-test statistics (degrees of freedom [df] for each test are in parentheses) of the percent differences in zooplankton density at night compared to day; \( p \) values in bold indicate statistical significance at \( \alpha \leq 0.05 \).

| Taxa               | \( n \) | Mean ± 1 SE (%)   | \( t \) Statistic (df) | \( p \) Value |
|--------------------|--------|-------------------|------------------------|--------------|
| **All observations** |        |                   |                        |              |
| *Daphnia*          | 176    | 273.8 ± 69.4      | 3.95 (175)             | \textbf{<0.0001} |
| Other cladocera    | 155    | 136.8 ± 48.4      | 2.82 (154)             | \textbf{0.003} |
| Predatory cladocera| 100    | 774.7 ± 132.3     | 5.86 (99)              | \textbf{<0.0001} |
| Copepods           | 231    | 102.0 ± 25.0      | 4.08 (230)             | \textbf{<0.0001} |
| Nauplii            | 42     | 11.0 ± 29.9       | 0.37 (41)              | 0.36         |
| Rotifers           | 40     | −41.6 ± 71.8      | −0.58 (39)             | 0.72         |
| Crustaceans        | 662    | 257.4 ± 31.9      | 8.07 (661)             | \textbf{<0.0001} |
| **Monthly**        |        |                   |                        |              |
| *Daphnia*          | 64     | 225.5 ± 65.2      | 3.46 (63)              | \textbf{0.0005} |
| Other cladocera    | 63     | 203.4 ± 109.5     | 1.86 (62)              | 0.03         |
| Predatory cladocera| 30     | 624.0 ± 160.4     | 3.89 (29)              | \textbf{0.0003} |
| Copepods           | 84     | 107.9 ± 26.2      | 4.11 (83)              | \textbf{<0.0001} |
| Nauplii            | 24     | 36.4 ± 45.9       | 0.79 (23)              | 0.22         |
| Rotifers           | 12     | −14.2 ± 44.8      | −0.32 (11)             | 0.62         |
| Crustaceans        | 241    | 228.3 ± 41.0      | 5.57 (240)             | \textbf{<0.0001} |
| **Annual**         |        |                   |                        |              |
| *Daphnia*          | 31     | 218.1 ± 92.3      | 2.36 (30)              | \textbf{0.01} |
| Other cladocera    | 37     | 288.7 ± 182.3     | 1.58 (36)              | 0.06         |
| Predatory cladocera| 14     | 752.7 ± 242.6     | 3.10 (13)              | \textbf{0.004} |
| Copepods           | 38     | 140.1 ± 42.9      | 3.26 (37)              | \textbf{0.001} |
| Nauplii            | 13     | 66.2 ± 84.1       | 0.79 (12)              | 0.22         |
| Rotifers           | 9      | −26.4 ± 59.1      | −0.45 (8)              | 0.67         |
| Crustaceans        | 120    | 277.6 ± 69.8      | 3.98 (119)             | \textbf{<0.0001} |

(\( t_{154} = 2.82; \ p = 0.003 \)), but not biomass (\( p = 0.11 \)). Rotifers and nauplii did not differ in density between night and day (\( p \geq 0.36 \)), and nauplii did not differ in biomass (\( p = 0.72 \); Fig. 2A,D). No biomass data were available for rotifers.
for the percent difference in zooplankton biomass at night compared to day and station depth ($p = 0.05$; $R^2 = 0.11$; Fig. 3D; Supporting Information Table S2).

**Discussion**

A recurring theme in zooplankton ecology is that many, if not most, taxa exhibit DVM (Pearre 2003). Diel density and biomass estimates should be similar if migrations occur within the water column and the entire water column is sampled. However, we found proportionally large increases in zooplankton density and biomass at night, suggesting that the standard procedure of sampling zooplankton during the day needs to be reconsidered.

Larger-bodied groups (*Daphnia*, predatory cladocera, and copepods) exhibited the largest percent increases at night relative to day while the smallest-bodied groups (nauplii and rotifers) showed no differences, consistent with expectations of size-selective predation by visual predators (Brooks and Dodson 1965). The percent change, however, was higher for density than biomass, which at first appeared inconsistent with expectations of size-selective predation pressure. However, 80% ($n = 692$) of the paired night–day density observations did not have a concurrent biomass to evaluate size-frequency comparisons. Direct comparisons where both density and biomass observations were available ($n = 105$) revealed a much greater percent change at night for biomass than density (226% vs. 58%), consistent with size-selective pressure on larger-bodied zooplankton to migrate.

The question remains, where do zooplankton go during the day? Zooplankton may migrate close to the sediment where water column sampling is difficult. However, we did not detect a decrease in night–day differences even when analyses were restricted to observations that reportedly sampled 100% of the water column. Future research on potential zooplankton subsidies to the water column at night from the sediment–water interface may benefit from multiple approaches including discrete pump sampling, benthic grab samples, acoustics, and high-resolution video.

Zooplankton may also exhibit DHM. Lake depth and surface area are considered major drivers in the extent of zooplankton DHM (Burks et al. 2002). We did not find a relationship between lake surface area and percent change in diel zooplankton density or biomass, and only a weak negative association between percent change in biomass (not density) and station depth, suggesting DHM alone cannot explain night–day discrepancies. As a postanalysis, we tested if lake trophic state could explain night–day differences and found that crustacean zooplankton biomass was higher at night compared to the day in eutrophic vs. oligotrophic lakes ($F_{2,44} = 4.44$; $p = 0.02$; Supporting Information Fig. S1). Consequently, zooplankton may exhibit more DHM vs. DVM in eutrophic compared to oligotrophic lakes.

Table 2. Sample sizes, means ±1 SE, and one-sided t-test statistics (degrees of freedom [df] for each test are in parentheses) of the percent differences in zooplankton biomass at night compared to day; $p$ values in bold indicate statistical significance at $p \leq 0.05$.

| Taxa                | $n$ | Mean ± 1 SE (%) | t Statistic (df) | $p$ Value |
|---------------------|-----|-----------------|------------------|-----------|
| **All observations**|     |                 |                  |           |
| *Daphnia*           | 26  | 118.2 ± 49.3    | 2.40 (25)        | 0.01      |
| Other cladocera     | 32  | 65.5 ± 52.2     | 1.26 (31)        | 0.11      |
| Predatory cladocera | 38  | 362.5 ± 135.3   | 2.68 (37)        | 0.005     |
| Copepods            | 61  | 120.6 ± 44.9    | 2.68 (60)        | 0.005     |
| Nauplii             | 7   | −25.6 ± 40.6    | −0.63 (6)        | 0.72      |
| Crustaceans         | 157 | 167.5 ± 40.1    | 4.18 (156)       | <0.0001   |
| **Monthly**         |     |                 |                  |           |
| *Daphnia*           | 15  | 147.9 ± 73.3    | 2.02 (14)        | 0.03      |
| Other cladocera     | 21  | 23.2 ± 36.7     | 0.63 (20)        | 0.27      |
| Predatory cladocera | 6   | 401.7 ± 206.5   | 1.95 (5)         | 0.05      |
| Copepods            | 27  | 78.8 ± 32.2     | 2.45 (26)        | 0.01      |
| Nauplii             | 4   | −22.6 ± 70.1    | −0.32 (3)        | 0.62      |
| Crustaceans         | 69  | 105.0 ± 30.7    | 3.42 (68)        | 0.0005    |
| **Annual**          |     |                 |                  |           |
| *Daphnia*           | 12  | 112.2 ± 52.4    | 2.14 (11)        | 0.03      |
| Other cladocera     | 15  | 44.2 ± 38.6     | 1.14 (14)        | 0.14      |
| Predatory cladocera | 4   | 378.0 ± 208.7   | 1.81 (3)         | 0.08      |
| Copepods            | 16  | 88.5 ± 33.0     | 2.68 (15)        | 0.009     |
| Nauplii             | 3   | −25.6 ± 6.9     | −3.69 (2)        | 0.97      |
| Crustaceans         | 47  | 105.0 ± 29.0    | 3.62 (46)        | 0.0004    |
oligotrophic lakes because of lower hypolimnetic dissolved oxygen (DO) concentrations (e.g., Doubek et al. 2018), increased fish predation pressure (e.g., Bachmann et al. 1996), or larger taxa, which exhibit more migration than smaller taxa, because of increased phytoplankton availability (e.g., Ger et al. 2014). Future research could focus on diel zooplankton estimates across productivity gradients with attention to explanatory variables not resolved in our data set, such as DO concentrations, fish biomass, and community size structure, and invertebrate predators.

Net avoidance during the day is another possibility to explain night–day differences. Such an effect was evident in the predatory cladoceran *Bythotrephes* (Fig. 2; Armenio et al. 2017). However, night–day differences were consistent in groups that are not as strong swimmers as predatory cladocera, and thus net avoidance cannot explain our results. We also did not find a positive relationship between diel zooplankton population estimates and mesh size for studies that used vertical net tows in our data set ($p \geq 0.34$). Collectively, our results suggest that after more than a century of zooplankton sampling, research is still needed to understand biases in night vs. day zooplankton estimates.

Our results are cause for concern regarding how zooplankton demographics in freshwater lakes are used to estimate ecosystem processes. For example, nitrogen (N) and phosphorus (P) excretion rates based on daytime zooplankton assemblages can vary from 1.4 to 24.5 mg N m$^{-2}$ d$^{-1}$ and from 0.1 to 4.0 mg P m$^{-2}$ d$^{-1}$ (Axler et al. 1981; Urabe et al. 1995; Vanni 2002). Excretion rates at night can be similar to day (e.g., Macedo and Pinto-Coelho 2000), which suggests a mean night time percent increase in crustacean zooplankton biomass of 125% could more than double daytime-based zooplankton N and P excretion estimates (3.2–55.1 mg N m$^{-2}$ d$^{-1}$ and 0.2–9.0 mg P m$^{-2}$ d$^{-1}$). By extension, other rates of zooplankton-mediated processes in lake food webs and ecosystem metabolism could also be biased low. Therefore, we performed another Web of Science search (1982 to 2 July 2019) using:

"secondary production" OR "zooplankton production"

AND (lakes OR reservoirs),

to evaluate how zooplankton production estimates may be affected by day zooplankton samples. From the 547 resultant

![Fig. 3. Percent change in annual zooplankton densities (A, B) and biomass (C, D) at night compared to day as a function of lake surface area (left) and station depth (right). Note that x-axes are in logarithmic scale.](image-url)
studies, we randomly examined 55 (10% of the studies) that sampled zooplankton in situ. Of the 55 studies, 27% were derived from daytime samples, 4% from night samples, 7% from both day and night samples, and 62% did not report time of sampling. Most of the studies that did not report time of day likely sampled during the day, in which case, upward to 90% of conducted studies on zooplankton production may be underestimated.

The linear relationships between night and day zooplankton estimates suggest the potential for corrections to adjust density and biomass estimates from those collected during day samples. We provide regressions to estimate night values from day values (Supporting Information Table S3) but suggest caution in their use; we may have insufficient understanding of which environmental factors predominantly drive diel differences across different lake types.

In conclusion, limnologists cannot ignore night–day differences in zooplankton demographic estimates, particularly for larger-bodied taxa, and at a minimum should evaluate possible biases in estimates of ecological rate processes when they rely on daytime zooplankton samples. Limnologists have known for a long time that night estimates of zooplankton are often higher than day estimates, but now we have quantitative estimates of the differences. The role of larger–bodied taxa such as Daphnia in many ecological concepts and ecosystem-level processes, and the range in sampling designs from repeated sampling of single lakes (Winder and Schindler 2004) to large-scale studies that sample many lakes once as “snapshots” (Mantzouki et al. 2018), necessitates an evaluation to better understand what we are sampling and what it means for estimates of ecological processes.

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