It's like night and day: diel net-effects on Cercopagidae densities in the Laurentian Great Lakes

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Abstract

In the Laurentian Great Lakes, zooplankters are often sampled using standard $\leq 153 \mu\text{m}$ mesh nets without regard to the time of day they are collected. We sampled Cercopagidae during 2013-2014 in northern Lake Huron during day, dusk, and night using two different nets (a 0.5 m wide $153 \mu\text{m}$ mesh “standard” net and a 0.75 m wide $285 \mu\text{m}$ mesh “*Bythotrephes*” net) to determine if there were any differences in their sampled densities. *Bythotrephes* densities with the standard net were approximately 2.07-fold greater when captured at night than during the day. No time of day bias occurred with the *Bythotrephes* net. Nighttime *Bythotrephes* densities did not differ between the two net types. *Cercopagis* densities did not vary with net type or the time of day in this study, but future work should revisit this result given our low sample size and the low occurrence of *Cercopagis* in Lake Huron. To reduce bias and calculate accurate density estimates, Cercopagidae should be sampled at night if using a standard net or any time of day with the *Bythotrephes* net. Given the large impact of invasive predatory cladocerans *Bythotrephes longimanus* and *Cercopagis pengoi* on food webs since their invasion in the Laurentian Great Lakes in the 1980s, proper estimation of their densities is essential.

Keywords: *Bythotrephes longimanus*; *Cercopagis pengoi*; invasive species; predatory cladocerans; zooplankton net; net avoidance

Introduction

Bythotrephes longimanus and *Cercopagis pengoi* (herein *Bythotrephes* and *Cercopagis*) have invaded the Laurentian Great Lakes and surrounding inland lakes in the United States as well as throughout Ontario, Canada (Liebig et al., 2013). Through predation and indirect effects, these two invasive species alter zooplankton community composition (Barbiero and Tuchman, 2004; Warner et al., 2006; Yan and Pawson, 1997), affecting abundance and condition (Bourdeau et al., 2016), and vertical distribution in the water column (Bourdeau et al., 2015; Pangle and Peacor, 2006; Pangle et al., 2007). Their planktivory also causes them to compete with fishes for potentially limited prey (Bunnell et al., 2011; Hoffman et al., 2001). To measure their densities and elucidate their disproportionately large impacts, many monitoring and research programs estimate densities of predatory cladocerans with the same sampling gear (i.e., 0.5-1.0 m diameter net, $\leq 153 \mu\text{m}$ mesh) used to estimate the densities of smaller crustacean zooplankters (e.g., Barbiero and Tuchman, 2004; Bunnell et al., 2011; Lehman and Cáceres, 1993; Vanderploeg et al., 2012). For example, the Great Lakes National Program Office (GLNPO) of the United States Environmental Protection Agency (U.S. EPA) has conducted monitoring on the Great Lakes since 1983 (Barbiero et al., 2001) to capture smaller zooplankton, before the invasion of *Bythotrephes* and *Cercopagis* (Bur et al., 1986; MacIsaac et al., 1999). GLNPO originally used a 0.5 m diameter, $64 \mu\text{m}$ mesh net sampling to a depth of 20 m (or 1 m above bottom at shallow sites), but in 1997, they also began using a 0.5 m diameter, $153 \mu\text{m}$ mesh net to sample down to 100 m (Barbiero et al., 2001).

Sampling for invertebrates with a plankton net can be influenced by the speed at which the net is retrieved as well as different net characteristics (see De Bernardi, 1984; McQueen and Yan, 1993), including the mesh size, mouth diameter of the net, and ratio of mouth-to-net length,

which can influence filtration efficiency (UNESCO, 1968). In general, larger invertebrates are likely to be captured in greater densities when retrieving nets at higher speeds (without induced clogging or malfunction of the flowmeter) with larger mesh sizes and wider net mouths which produce higher filtration efficiencies. As a result, some researchers designed different nets for *Bythotrephes* research. Yan and Pawson (1997) used a 0.75 m diameter net that was 2.5 m in length (1 m long cylinder above a 1.5 m long cone) with a 285 μm mesh. Strecker et al. (2006) used a 0.5 m diameter net that was also 2.5 m in length, but with a 400 μm mesh.

Time of day also can influence probability of biota capture. Shaw and Robinson (1998) established that night to day catch ratios can vary between zooplankton species and that, in general, larger species such as euphausiids are likely to have higher catches at night. Further, some large predatory invertebrates, such as *Mysis*, are associated with the benthic environment during the daytime but migrate up into the water column at night, creating difficulty for daytime collections of these organisms (Beeton and Bowers, 1982). Cercopagidae, however, generally occupy upper water column layers during all times of the day, and undergo limited diel vertical migration (Ptáčníková et al., 2015; Young and Yan, 2008). Hence, these predatory cladocerans should be equally vulnerable to zooplankton nets during either day or night, so long as light does not affect probability of capture.

To understand how the type of zooplankton net and time of sampling influences density estimates for predatory cladocerans, we designed a field study in Lake Huron with a paired tow design, where two different zooplankton net types were used to sample predatory cladocerans during different times of the day. We hypothesized that densities of Cercopagidae sampled at night with a standard zooplankton net would be higher than those sampled during the day (Shaw and Robinson, 1998). We also evaluated whether a similar time of day bias would occur when a

zooplankton net designed to capture *Bythotrephes* (sensu Strecker et al., 2006; Yan and Pawson, 1997) was used.

Methods

Whole water column (WWC) zooplankton samples were collected on six different dates (from July until November) in Michigan waters of Lake Huron in 2013-2014 (Tables 1 and 2) with two different net types using a paired approach. One site close to Hammond Bay (45.79° , -84.25°) was sampled on four separate dates, and the other two sites, nearshore of Cheboygan (45.72° , -84.49°) and offshore of Cheboygan (45.79° , -84.25°), were sampled once each. The net designs included a 0.5 m diameter, 2 m length, 153 µm mesh with a net aspect ratio of 4 (herein called the standard net) and a 0.75 m diameter, 4 m length, closing 285 µm mesh net with a net aspect ratio of 5.3 (similar net designed by Yan and Pawson (1997) for estimating *Bythotrephes* density; herein called the *Bythotrephes* net). One paired replicate included a WWC sample with one net immediately followed by sampling with the other net. To reduce bias, we alternated which net was used first. Multiple pairs of tows (i.e., replicate pairs) were sampled during different times of the day, within twelve hours, on a given date and site (Tables 1 and 2).

WWC samples were collected by lowering each net such that the cod-end was 2 m above the bottom. The net was retrieved at a constant speed of 0.5 m/s. Nets were rinsed down, cod end contents were narcotized with an effervescent tablet, and captured zooplankters were preserved in 5% sugar buffered formalin. In the laboratory, all Cercopagidae were counted by examining subsamples with a dissecting microscope until the whole sample was inspected. Numeric density of *Bythotrephes* and *Cercopagis* were determined by areal densities ($\#/m^2$).

Due to the paired sampling design and our interest in comparing the net type and time of day, we used a linear mixed-effects model from the lmer package (Bates et al., 2015) in the statistics program R (version 3.2.3, R Core Team, 2015) to determine whether the areal densities of each Cercopagidae species varied. For each paired replicate, we first discarded any replicate pairs when 0 individuals for a given species were sampled from both nets. This resulted in 67 replicate pairs where *Bythotrephes* was sampled and 32 replicate pairs for *Cercopagis* out of a total of 69 replicate pairs collected. Density estimates were natural log transformed to normalize the data; a constant of $2/\text{m}^2$ (the smallest density observed) was added to all density estimates prior to transformation to avoid taking the log of 0. For each paired replicate, we calculated the difference of the ln-transformed density estimates, $\ln(\text{density}_{285\ \mu\text{m}}+2) - \ln(\text{density}_{153\ \mu\text{m}}+2)$, then calculated the mean of this difference as the response variable for a given date-site, net type, and time of day. The number of replicate pairs over which the mean was calculated ranged from 1 to 16 (mean = 4) for *Bythotrephes* and 1 to 9 (mean = 4) for *Cercopagis*.

For the linear mixed-effects model for each species, explanatory variables included the fixed-effect of time of day and a random effect of each unique date-site combination. The number of replicate pairs was used as a weighting variable due to more confidence in the estimates with more replicates. We explored models with time of day as either a discrete or a continuous variable, as arguments could be made for the validity of both approaches. Allowing it to be continuous would preserve degrees of freedom, but constrain the relationship from day to dusk to night as linear. We therefore compared the AIC_c values (Akaike's Information Criterion corrected for small sample size, Burnham and Anderson, 2002) for each model to determine whether continuous or categorical was more appropriate. AIC_c was always smaller when time of day was continuous (*Bythotrephes*: $\Delta\text{AIC}_c = 4.21$; *Cercopagis*: $\Delta\text{AIC}_c = 11.92$), indicating that

the time of day effect was approximately linear. Consequently, we report results from the model when time of day was treated as a continuous variable. Given our particular interest in density estimates at night, we assigned $x = 0$ for night ($x = -2$ for day, $x = -1$ for dusk) so that the estimated intercept would reflect the night effect. The significance of the intercept term revealed whether night time density estimates differed between the two net types.

If time of day was significant in the linear mixed-effect model, we followed up with a *post-hoc* linear mixed-effects model for each net type separately. The response variable was $\ln(\text{density}_i + 2)$ for a given species and net type i , date-site remained a random effect, and time of day was, again, evaluated as either a continuous or categorical variable using AIC_c .

Results and Discussion

Bythotrephes

For the initial *Bythotrephes* model, there were two models with substantial support ($\Delta\text{AIC}_c < 2$; Burnham and Anderson, 2002): 1) no effect from time of day and 2) a time of day effect as a continuous variable ($\Delta\text{AIC}_c = 1.84$) on density estimates. In the second model, differences were greater during the day (Fig. 1), and the intercept was not significantly different from zero ($t_9 = -0.106$, $P = 0.92$) indicating the two nets provided similar density estimates at night. These results led to the development of a *post-hoc* model for each net type. For both net types, AIC_c supported time of day as a continuous variable (standard net: $\Delta\text{AIC}_c = 4.36$; *Bythotrephes* net: $\Delta\text{AIC}_c = 4.36$), but *Bythotrephes* densities only showed a marginal time of day difference with the standard net ($t_9 = 2.12$, $P = 0.062$, Fig. 2) and no difference with the

Bythotrephes net ($t_9 = 0.86$, $P = 0.42$, Fig. 2). If there is a density difference between the net types, it is driven by lower estimates during the day with the standard net.

To further investigate the trend that the standard net yielded higher *Bythotrephes* densities at night than during the day, we exploited ten additional WWC samples collected at day and night (also within twelve hours of each other) from Lake Huron in 2012 with the standard net (Table 1). These data were normally distributed (Shapiro-Wilk, $P > 0.1$) and therefore not transformed. We conducted a paired t -test to determine whether the hypothesized time of day bias was supported. *Bythotrephes* densities were greater at night than during the day ($t_{15} = -3.82$, $P = 0.002$, Fig. 3), with average densities 2.07 (± 0.57 , 95% CI) times higher at night. A similar test was done by Keeler et al. (2015) that included samples from Lake Superior in 2011 and these same 2012 Lake Huron samples, and they concluded that *Bythotrephes* densities also were 2.06 times greater at night compared to day. The difference between day and night appears to increase with increasing *Bythotrephes* densities (Fig. 3).

Our results indicate *Bythotrephes* sampled during the day with a standard 0.5 m diameter, 153 μm mesh net can produce density estimates biased low. No time of day bias was revealed with the *Bythotrephes* net. Because nets were retrieved at the same speed, a key factor possibly explaining the differing results between the nets is filtration efficiency, with higher wave pressure likely emanating from the standard net given its smaller mesh, narrower diameter, and smaller surface area (UNESCO, 1968). Young and Yan (2008) determined that a 0.75 m diameter, 4 m length, 300 μm mesh net, similar to ours, used in an oligotrophic lake had a filtering efficiency of 100%. The standard net has been found to have an approximate filtering efficiency of 90% (S. Pothoven, NOAA, 2016, personal communication). However, it remains unclear how putative differences in wave pressure could influence capture efficiency of

Bythotrephes under different light conditions. Previous research on *Bythotrephes* and light levels has revealed reduced feeding at lower light levels (Jokela et al., 2013; Muirhead and Sprules, 2003; Pangle and Peacor, 2009). We hypothesize that the combinations of larger pressure waves and higher light levels improve the ability of *Bythotrephes* to avoid the standard zooplankton net during the day. Although future research will be required to better understand this mechanism, our research suggests previous studies could have been underestimating *Bythotrephes* densities when sampling during the day with a standard 153 μm mesh net.

Cercopagis

For *Cercopagis*, neither time of day ($t_{3,7} = -0.84$, $P = 0.45$) nor the intercept ($t_{4,3} = -0.14$, $P = 0.89$, Fig. 1) was significant in the linear mixed-effects model. Because their densities did not vary between nets and the difference did not vary between day, dusk, and night, the *post-hoc* models were not constructed.

We have less data for *Cercopagis* because they were absent from November 2013 samples, likely because they tend to be more abundant in summer (Cavaletto et al., 2010; Warner et al., 2006). Even though *Cercopagis* has a rapid turning behavior (Pichlová-Ptáčníková and Vanderploeg, 2009), they may not swim fast enough to avoid the net or may not be as visually responsive as *Bythotrephes* because *Cercopagis* have a relatively smaller compound eye. Although *Cercopagis* did not show significant results in our model, we did observe trends of higher densities at night compared to day (Table 2). We recommend replicating our study when and where *Cercopagis* is more abundant to more conclusively determine that no time of day bias exists with the standard 153 μm mesh net.

Conclusions

The accurate estimation of these invasive predatory cladocerans is essential given their potentially large role in the transfer of energy within food webs. They can be the dominant planktivore, competing with fish and other invertebrates for food (Bunnell et al., 2011; Hoffman et al., 2001), along with serving as a prey item themselves for planktivorous and benthivorous fish (Bunnell et al., 2015; Pothoven et al., 2009) as well as *Mysis* (O'Malley and Bunnell, 2014). *Bythotrephes* can change the vertical position of some zooplankton (Bourdeau et al., 2011; Bourdeau et al., 2015; Lehman and Cáceres, 1993), thus affecting their energy costs, reproduction, and probability of being preyed upon (Pangle and Peacor, 2006; Pangle et al., 2007). *Bythotrephes* and *Cercopagis* have both been found to decrease the abundance of small zooplankters such as *Bosmina*, and affect the overall species composition (Barbiero and Tuchman, 2004; Warner et al., 2006; Yan and Pawson, 1997). The many ways that *Bythotrephes* and *Cercopagis* have created ecosystem changes warrants determining their accurate densities crucial for models and descriptive studies so that scientists do not underestimate their impact.

Although there is a history describing the density estimates between net types and day-night sampling for some organisms (Shaw and Robinson, 1998; UNESCO, 1968), this is the first study to compare two specific zooplankton net types while also testing for time of day effects for predatory cladocerans. Estimating the density of zooplankton can be challenging because they are known to have patchy distributions due to diel vertical migration, predator avoidance, concentrating in regions with high food availability, or finding mates (Folt and Burns, 1999). However, between the multiple sampling events and replicates in our study and taking into account the behavior of Cercopagidae (e.g. limited diel vertical migration), this study still demonstrated evidence of a sampling bias for *Bythotrephes* within the Laurentian Great Lakes.

Most researchers within the Laurentian Great Lakes estimate densities of large predatory cladocerans with a standard, 0.5 m diameter, 153 μ m mesh net, usually during daytime. This method underestimates *Bythotrephes* densities and therefore potentially underestimates its ecosystem effects. Our research results suggest that future studies requiring accurate densities of *Bythotrephes* should either sample at night if only a 153 μ m mesh net can be used or sample with the wider and larger 285 μ m mesh net at any time of the day. Changing protocols in a long term monitoring program may not be ideal, and additional sampling with a different net type during field work may not be feasible due to time and cost constraints. If daytime sampling with the standard net must be conducted, one could conservatively apply the correction factor (2.07 times daytime density) derived herein.

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Tables

Table 1. Mean densities ($\#/m^2$) ± 1 SE and N of *Bythotrephes* from Lake Huron using the 0.5 m diameter, 153 μm mesh standard net and 0.75 m, 285 μm mesh *Bythotrephes* net. HB = Hammond Bay, TB = Thunder Bay, Cb = Cheboygan, ns = not sampled.

Date	Depth (m)	Port	153 μm mesh net									285 μm mesh net								
			Day			Dusk			Night			Day			Dusk			Night		
			Density	SE	N	Density	SE	N	Density	SE	N	Density	SE	N	Density	SE	N	Density	SE	N
10 Jul 12	46	HB	79.0	7.6	2	-	-	ns	119.7	22.9	2	-	-	ns	-	-	ns	-	-	ns
11 Jul 12	82	HB	58.6	12.7	2	-	-	ns	201.3	33.1	2	-	-	ns	-	-	ns	-	-	ns
12 Jul 12	18	HB	0	0	2	-	-	ns	15.3	0	2	-	-	ns	-	-	ns	-	-	ns
15 Aug 12	82	HB	137.6	5.1	2	-	-	ns	435.7	53.5	2	-	-	ns	-	-	ns	-	-	ns
19 Aug 12	46	HB	129.9	7.6	2	-	-	ns	430.6	33.1	2	-	-	ns	-	-	ns	-	-	ns
21 Aug 12	46	TB	170.7	48.4	2	-	-	ns	328.7	17.8	2	-	-	ns	-	-	ns	-	-	ns
23 Aug 12	82	TB	137.6	20.4	2	-	-	ns	214.0	15.3	2	-	-	ns	-	-	ns	-	-	ns
6 Sep 12	46	HB	152.9	10.2	2	-	-	ns	236.9	63.7	2	-	-	ns	-	-	ns	-	-	ns
7 Sep 12	82	HB	239.5	5.1	2	-	-	ns	259.9	-	1	-	-	ns	-	-	ns	-	-	ns
9 Sep 12	18	HB	12.7	2.5	2	-	-	ns	15.3	-	1	-	-	ns	-	-	ns	-	-	ns
27 Aug 13	54	Cb	14.7	3.4	9	12.7	2.5	6	23.4	6.6	5	22.4	2.7	9	17	5.6	6	31.3	1.7	5
28 Aug 13	55	HB	45.9	-	1	142.7	-	1	270.1	-	1	108.7	-	1	178.9	-	1	285.4	-	1
29 Aug 13	55	HB	86.6	9.5	4	104.5	22.9	2	158.0	-	1	109.3	19.7	4	106.4	9.1	2	167.6	-	1
19 Nov 13	55	HB	8.0	2.7	7	8.7	0.9	7	12.6	2.7	17	13.9	5.5	7	19.4	5.3	7	15.2	4.3	17
30 Jul 14	55	HB	168.2	45.9	2	-	-	ns	364.3	2.5	2	173.2	10.2	2	-	-	ns	425.8	63.4	2
31 Jul 14	31	Cb	33.1	33.1	2	-	-	ns	12.7	2.5	2	3.4	3.4	2	-	-	ns	6.8	2.3	2

Table 2. Mean densities ($\#/m^2$) ± 1 SE and N of *Cercopagis* from Lake Huron using the 0.5 m diameter, 153 μm mesh standard net and 0.75 m, 285 μm mesh *Bythotrephes* net. HB = Hammond Bay, TB = Thunder Bay, Cb = Cheboygan, ns = not sampled.

Date	Depth (m)	Port	153 μm mesh net									285 μm mesh net								
			Day			Dusk			Night			Day			Dusk			Night		
			Density	SE	N	Density	SE	N	Density	SE	N	Density	SE	N	Density	SE	N	Density	SE	N
10 Jul 12	46	HB	0	0	2	-	-	ns	0	0	2	-	-	ns	-	-	ns	-	-	ns
11 Jul 12	82	HB	0	0	2	-	-	ns	0	0	2	-	-	ns	-	-	ns	-	-	ns
12 Jul 12	18	HB	0	0	2	-	-	ns	0	0	2	-	-	ns	-	-	ns	-	-	ns
15 Aug 12	82	HB	0	0	2	-	-	ns	0	0	2	-	-	ns	-	-	ns	-	-	ns
19 Aug 12	46	HB	0	0	2	-	-	ns	0	0	2	-	-	ns	-	-	ns	-	-	ns
21 Aug 12	46	TB	0	0	2	-	-	ns	0	0	2	-	-	ns	-	-	ns	-	-	ns
23 Aug 12	82	TB	0	0	2	-	-	ns	0	0	2	-	-	ns	-	-	ns	-	-	ns
6 Sep 12	46	HB	0	0	2	-	-	ns	0	0	2	-	-	ns	-	-	ns	-	-	ns
7 Sep 12	82	HB	0	-	2	-	-	ns	0	-	1	-	-	ns	-	-	ns	-	-	ns
9 Sep 12	18	HB	0	-	2	-	-	ns	0	-	1	-	-	ns	-	-	ns	-	-	ns
27 Aug 13	54	Cb	86.1	12.6	9	60.3	9.5	6	436.2	37.3	5	108.7	9.1	9	100.0	14.3	6	445.2	32.6	5
28 Aug 13	55	HB	0	-	1	0	-	1	25.5	-	1	0	-	1	0	-	1	31.7	-	1
29 Aug 13	55	HB	8.9	1.3	4	30.6	15.3	2	66.2	-	1	12.5	2.4	4	10.2	7.9	2	47.6	-	1
19 Nov 13	55	HB	0	0	7	0	0	7	0	0	17	0	0	7	0	0	7	0	0	17
30 Jul 14	55	HB	0	0	2	-	-	ns	0	0	2	0	0	2	-	-	ns	0	0	2
31 Jul 14	31	Cb	35.7	0	2	-	-	ns	56.1	10.2	2	47.6	0	2	-	-	ns	63.4	22.6	2

Figure Captions

Fig. 1. Difference in natural log densities between the 285 μm mesh net and 153 μm mesh net of

Bythotrephes (A) and *Cercopagis* (B) during day, dusk, and night from 2013-2014.

Observed mean differences (± 1 SE) are shown as open circles and predicted values are shown as filled circles with a solid line. The number of sample replicates varied from 1 to 16. Random noise was added in the x-direction to avoid overlapping points.

Fig. 2. Natural log density of *Bythotrephes* collected in 2013-2014 from the standard 0.5 m

diameter, 153 μm mesh net (A) and 0.75 m diameter, 285 μm mesh net (B) during day, dusk, and night. Observed means (± 1 SE) are shown as open circles and predicted values are shown as filled circles with a solid line. The predicted density at night is highlighted by a horizontal line. Random noise was added in the x-direction to avoid overlapping points.

Fig. 3. Mean density ($\#/\text{m}^2$) of *Bythotrephes* collected from the standard 0.5 m diameter, 153 μm mesh net from 2012-2014 during day and night.

(A)

(B)

Density

400

300

200

100

0

Day

Night

Time of Day