

## Article

# Invasion of *Bythotrephes longimanus* and *Cercopagis pengoi* in Lake Champlain: Impacts on the Native Zooplankton Community

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**Abstract:** The zooplankton community of Lake Champlain has been altered over the past decade due to the introduction of two predatory zooplankton species. *Bythotrephes longimanus* Leydig, 1860 was first detected in Lake Champlain in August 2014, and *Cercopagis pengoi* (Ostroumov, 1891) was detected in August 2018. Monitoring for both invasive species at 15 lake sites using whole water tow sampling has been ongoing since 2010 with no detection of either species until 2014. Utilizing data from the Lake Champlain long-term monitoring program, we assessed pre- and post-invasion population dynamics of both invasive species on the native zooplankton community. Our results showed shifts in community structure following invasion, including a reduction in *Diacyclops thomasi* (Forbes, 1882) populations by both invaders and a reduction in *Daphnia retrocurva* Forbes, 1882 following the introduction of *B. longimanus*. Other cyclopoids, bosminids, and rotifers were also reduced, corresponding to both introduced species. The native large-bodied plankton predator *Lepidodora kindtii* (Focke, 1844) appears to be unable to coexist with either invasive predatory cladoceran, displaying seasonal partitioning between *L. kindtii* and the Cercopagidae. These findings suggest that the invasion of both large predators in Lake Champlain have impacted pelagic zooplankton community structure.

**Keywords:** *Diacyclops thomasi*; *Daphnia retrocurva*; community composition; *Bythotrephes longimanus*; *Cercopagis pengoi*; invasive zooplankton



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## 1. Introduction

The introduction of invasive species to North America has led to the alteration of ecosystems and great economic damage [1]. A vast number of invasive species have made their way to the Great Lakes through accidental introduction from vessel ballast water, fish stocking, and recreational fishing or boating [2]. The impact that invasive species have on ecosystem functioning and their invasion to nearby lake systems gives reason for concern of their arrival and the alteration of Lake Champlain. A number of these species that have entered the Great Lakes have already migrated to Lake Champlain most likely via the Champlain Canal. These invasive species have caused lasting alterations to Lake Champlain's planktonic community [3]. The most notable invasive species into Lake Champlain was *Dreissena polymorpha*, which impacted the planktonic food web and resulted in a major decline in rotifers throughout the lake following its invasion in the early 1990s [4,5].

Lake Champlain is among the largest lakes in the United States after the Great Lakes and is an important limnological system in the region. Zooplankton monitoring in Lake Champlain has been conducted since the early 1990s and has been ongoing to the present day, resulting in extensive historical data. This wealth of historical data aids greatly in determining the significance of disturbances, which may impact Lake Champlain's zooplankton community structure. In the past decade, two invasive predatory zooplankton species, *B. longimanus* and *C. pengoi*, have invaded Lake Champlain, both of which have a history of altering the native zooplankton community structure [6,7].

*Bythotrephes longimanus* (spiny water flea) and *C. pengoi* (fishhook water flea) are large generalist planktivorous cladocerans [6,8,9] that originated from the waterbodies of the Palearctic region and the Ponto-Caspian region, respectively [10,11]. Both species are visual predators [11,12]. *B. longimanus* preferentially seeks large bodied prey, such as cladocerans [12], while *C. pengoi* is less selective and consumes smaller organisms [13]. These predatory cladocerans are typically found within the epilimnion and upper metalimnion of invaded lakes [14,15], though *C. pengoi* is more restricted to the epilimnion than *B. longimanus* [16,17]. The first report of *B. longimanus* in the Adirondack region was at Sacandaga Lake in upstate New York in 2008 [18]. Subsequently *B. longimanus* was detected in the Champlain Canal system (2010) and Lake George in 2012 [18], prior to the detection of a small population in Lake Champlain in August 2014. *Bythotrephes longimanus* was detected throughout Lake Champlain in very high densities by September 2014, and levels continued increasing through the following year. *Cercopagis pengoi* was first detected in Lake Champlain 2018 but unlike *B. longimanus* was not previously reported in any adjacent waterbodies.

#### *Potential Impact of the Cercopagidae Invasion*

The invasion of *C. pengoi* and *B. longimanus* to North American lakes typically results in a shift in the zooplankton community composition of these water bodies [19–22]. Both Cercopagidae cause severe density reductions to many key zooplankton species through the summer months when the Cercopagidae are at peak abundance [19,21,22]. *Cercopagis pengoi* typically reaches peak density in July and August in the Great Lakes region [23], and *B. longimanus* typically reaches peak density during July to September, varying depending on the lake [24]. Species that are at high abundance during these months are likely to have reduced peak abundance after either invasion.

*Daphnia retrocurva* is the dominant daphniid in Lake Champlain [4] and is known to decline in abundance in Cercopagidae-invaded lakes [15,25]. Although *D. retrocurva* density is reduced by *C. pengoi* in invaded lakes [25] and *D. retrocurva* shares a similar vertical distribution to *C. pengoi*, its large adult body size makes it difficult to process during feeding for *C. pengoi* [6], which reduces its vulnerability as *D. retrocurva* mature. *Bythotrephes longimanus* on the other hand is a significant predator of *D. retrocurva*; its large body size and slow swimming speed makes *D. retrocurva* highly susceptible to predation throughout its entire lifespan [26]. The second most abundant large-bodied daphniid of Lake Champlain *Daphnia mendotae* (Birge, 1918) [4] may increase in density after *B. longimanus* invasion. The fast escape response of *D. mendotae* decreases the likelihood of capture by *B. longimanus*, and predation on other slower daphnids by *B. longimanus* reduces the competitors of *D. mendotae* [26]. Based on studies in the Great Lakes and the Baltic Sea, the presence of *C. pengoi* leads to a decrease in small-bodied zooplankton biomass, such as *Bosmina longirostris* (Muler, 1776) and *Ceriodaphnia* spp. [9,16]. *B. longimanus* may indirectly increase the population of *Bosmina longirostris* after it establishes a population, as found in Lake Michigan in the years during its initial detection [27].

*Diacyclops thomasi*, the most abundant copepod in Lake Champlain [4], has decreased in abundance following *C. pengoi* invasions in other freshwater systems either through direct predation or competition with *C. pengoi* for prey [12,21]. *D. thomasi* seasonal density dynamics are less commonly impacted by *B. longimanus* along with most other copepods [7,19]. The other two common cyclopoids of Lake Champlain, *Tropocyclops prasinus mexicanus* Kiefer, 1938 and *Mesocyclops edax* (Forbes, 1890), are epilimnetic species like *D. thomasi* [28]. Since both Cercopagidae are predominantly found in the epilimnion, all three cyclopoids are at risk of population density decline by Cercopagidae predation. One of the highest impacted groups in Lake Michigan and Ontario were cyclopoid copepods during high *C. pengoi* density years [22,29].

*Cercopagis pengoi* is known to prey heavily on rotifers, especially when in early instars [30]. Smaller bodied rotifers, such as *Kellicottia* spp. and *Conochilus* spp., increased in dominance, whereas large rotifers, such as *Asplanchna* spp., decreased after *C. pengoi*

introduction in Lake Ontario in the late 1990s [21,31]. *Conochilus* spp., *Keratella* spp., and *Polyarthra* spp. may benefit from high *B. longimanus* density as total rotifer density increased in many Canadian Shield lakes during high *B. longimanus* density [32]. *Bythotrephes longimanus* may increase *Conochilus* spp. density through the suppression of *Leptodora kindtii*, a major predator of *Conochilus* spp. [27].

The invasive Cercopagidae and native *L. kindtii* are generalist predators with overlapping prey size and species preferences, making their coexistence unlikely [33,34]. In Lakes Huron and Michigan, the invasion of *B. longimanus* coincided with the drastic reduction in native *L. kindtii* [34,35], and *B. longimanus* are found to prey upon *L. kindtii* directly [36]. *Leptodora kindtii* is unable to prey upon *B. longimanus* due to its size-limited capturing appendages, while *B. longimanus* are capable of capturing and processing *L. kindtii* [36]. The smaller body size of *C. pengoi* in comparison to the other two predators renders it unable to prey on mature adult *L. kindtii* and *B. longimanus* [33]; however, *C. pengoi* is thought to have caused a decline in *L. kindtii* through competition in Lake Ontario [6,37]. In addition, *L. kindtii* is unable to effectively prey on *C. pengoi* due to its size-limited capturing appendages [12]. There is evidence that *B. longimanus* controls *C. pengoi* population and distribution in the Great Lakes [17]. Thus, years where both species are abundant could see an increase in *B. longimanus* abundance, while *C. pengoi* decreases.

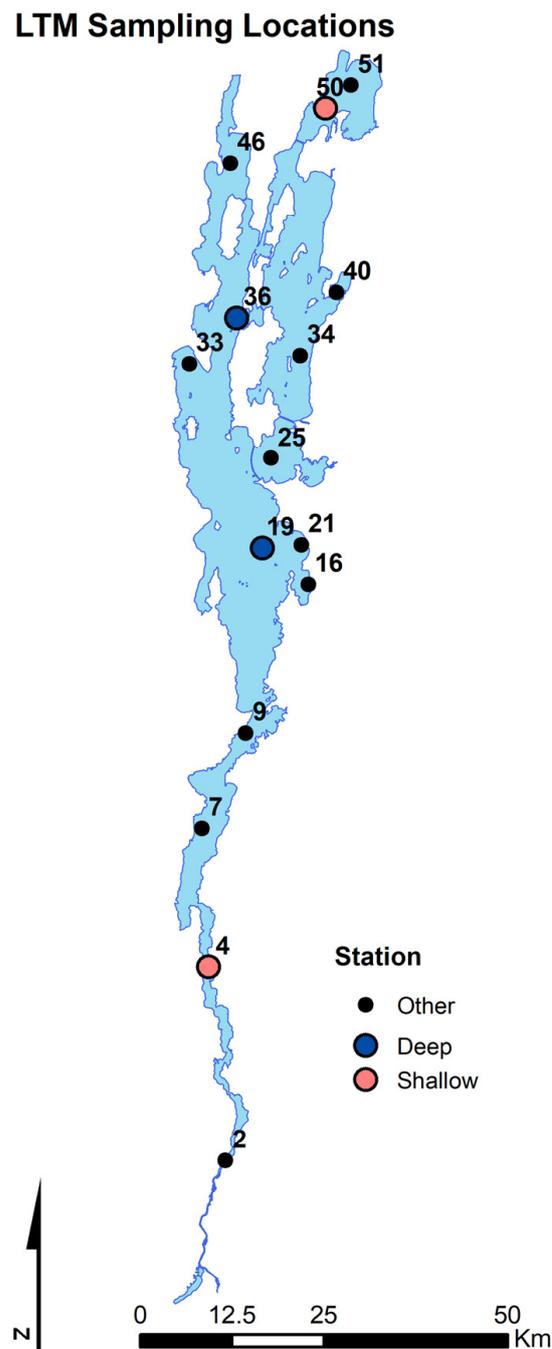
This study was conducted to document the invasion dynamics of *C. pengoi* and *B. longimanus* and determine changes in the zooplankton community composition of Lake Champlain. We hypothesized that *B. longimanus* would reduce the abundance of large-bodied and slow-swimming species, while *C. pengoi* would reduce the abundance of small-bodied species. We also hypothesized that *L. kindtii* may exhibit spatial and temporal partitioning with the Cercopagidae after each invasion.

## 2. Materials and Methods

### 2.1. Zooplankton Community Sampling

Zooplankton samples were collected by the Lake Champlain Monitoring Program (LTMP) using vertical whole water column net tows [38]. Vertical whole water column tows were conducted biweekly during the growing season (May–October). Whole water net tows were taken at midday 1 m from the lake bottom once per date sampled. The time range of the samples used for the present analysis spanned from 2013 to 2019. Samples prior to 2013 were excluded from analysis due to the extreme flooding event that occurred in 2011, which severely altered the zooplankton community during that year and the year following [39]. Samples were generated through the entire field season (May–October) with two samples taken at each station bimonthly, early month (between 1st and 15th) and late month (after 15th) to allow for analysis of seasonal patterns. Zooplankton samples were taken using a zooplankton vertical tow net that was 30 cm in diameter with 153 µm mesh net and retrieved at a rate of 0.5 m per second. The samples were condensed into 125 mL bottles and preserved with 5% formalin-Rose Bengal solution. No correction for net efficiency was used. Subsamples were taken from the 125 mL bottle using a Hensen Stempel pipette measured at 1 mL and viewed using Leica inverted microscopes. Contents of subsamples were counted until the entire slide sample was investigated or until a minimum of 100 total individuals were counted through multiple subsamples. Zooplankton species were identified using *A Revised Key to the Zooplankton of Lake Champlain* [40].

Samples utilized in this study to produce data were collected from 4 LTMP monitoring stations two shallow locations (stations 4 at 10 m and 50 at 5 m) and two deep stratified locations (stations 19 at 99 m and 36 at 50 m) (Figure 1). These stations were chosen as their locations are central to major portions of the lake and are representative of the average environmental conditions to that region. Predatory cladoceran samples were taken at all 15 LTMP stations to determine predatory cladoceran density.



**Figure 1.** Map of Lake Champlain displaying all LTM sampling locations labeled by station number, with the four stations where the zooplankton samples were collected and used in data analysis represented as colored points. Blue points represent deep stations, and red points represent shallow stations.

*Bythotrephes longimanus* and *C. pengoi* sampling was conducted in a similar manner to zooplankton composition sampling using a standard LTMP procedure. A 0.5 m diameter 250  $\mu\text{m}$  mesh net was used to accommodate the large size of the predatory cladocerans and to prevent net avoidance during the tow. Samples were collected through whole water vertical tows retrieved at a rate of 1 m per second. Samples were preserved initially in a 5% formalin-Rose Bengal solution and later transferred to an 80% pure ethanol solution. The sampling of invasive *B. longimanus* and *C. pengoi* was conducted lakewide throughout the study period with no detection of either species in Lake Champlain prior to 2014. Entire

samples were analyzed for *B. longimanus* and *C. pengoi* density using dissecting microscopes. All samples analyzed are archived for long-term storage at the Lake Champlain Research Institute.

## 2.2. Data Analysis

### 2.2.1. Ordination Analysis

In order to determine changes in community composition between pre- and post-invasion communities, multiple non-metric multidimensional scaling (NMDS) ordinations were conducted using relative abundance data calculated from the zooplankton density data. NMDS was chosen due to the highly variable nature of zooplankton populations. Differences between species populations and presence/absence in certain samples or stations do not impact the results of NMDS, which is ideal in the case of zooplankton population dynamics. Two ordinations were conducted using data from differing station depths, one using deep station (19 and 36) data and the using other shallow station (4 and 50) data. Ordinations were run in R Studio [41] using the ‘vegan’ package [42]. The metaMDS function of the vegan package was utilized with the index set to Bray-Curtis dissimilarity and 5 dimensions. NMDS were performed on datasets for deep/shallow groupings using portions of relative abundance data based on timespans. The BVSTEP procedure was used to determine the most influential genera to use for ordination [43]. The BIOENV procedure was utilized to further determine influential genera and the environmental variables with the most influence on the community [43]. The BIOENV procedure was performed using the ‘vegan’ package while BVSTEP were performed using the ‘sinkr’ package [44].

The most influential genera of each major zooplankton taxa (Cladocera, Copepoda, Rotifera) were chosen from the BIOENV procedure. A total of 18 plots were generated from the two ordinations to reduce visual clutter, 6 per major genera, 3 per deep and shallow stations ordinations. The 3 plots per deep/shallow stations category contain points based on the month range the sample was taken, and points were colored based on the specific month. Point size was based on the density of the influential genera found in the sample. The invasive Cercopagidae and *Leptodora kindtii* and any relevant environmental factors determined by the BIOENV procedure were plotted as environmental variables for each ordination.

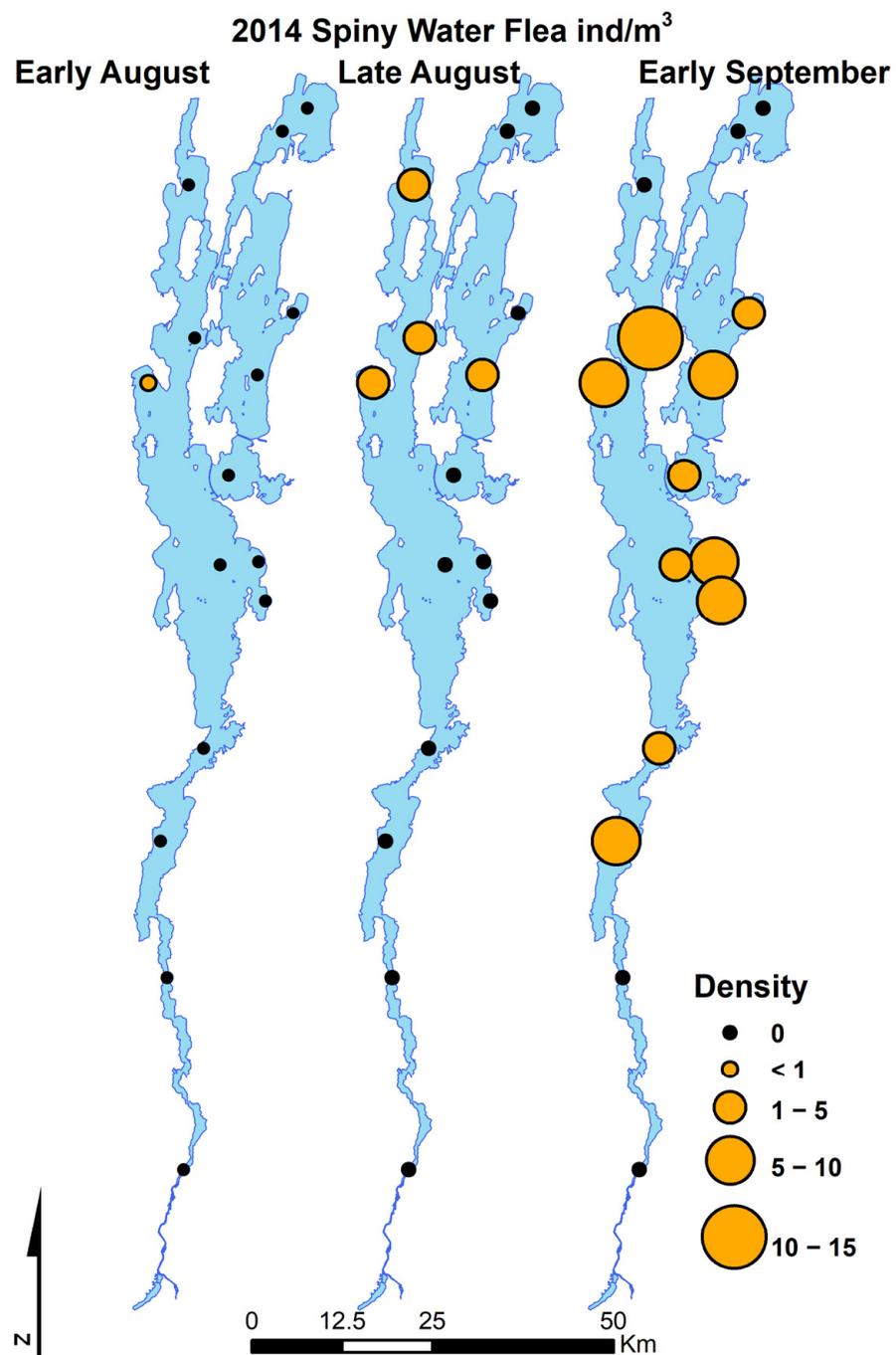
### 2.2.2. Community Structure Analysis

To assess potential changes in community structure before and after invasion, the zooplankton abundance data were rank ordered for each individual sample across all study years. Ranks were then compared among the following categories: before (2013), after *B. longimanus* (2014–2015), and after *C. pengoi* (2018–2019) during July, August, and September for all stations. Ranked data were then used to run Kendall’s  $\tau$  coefficient of concordance to determine community rank order changes before and after invasion.

## 3. Results

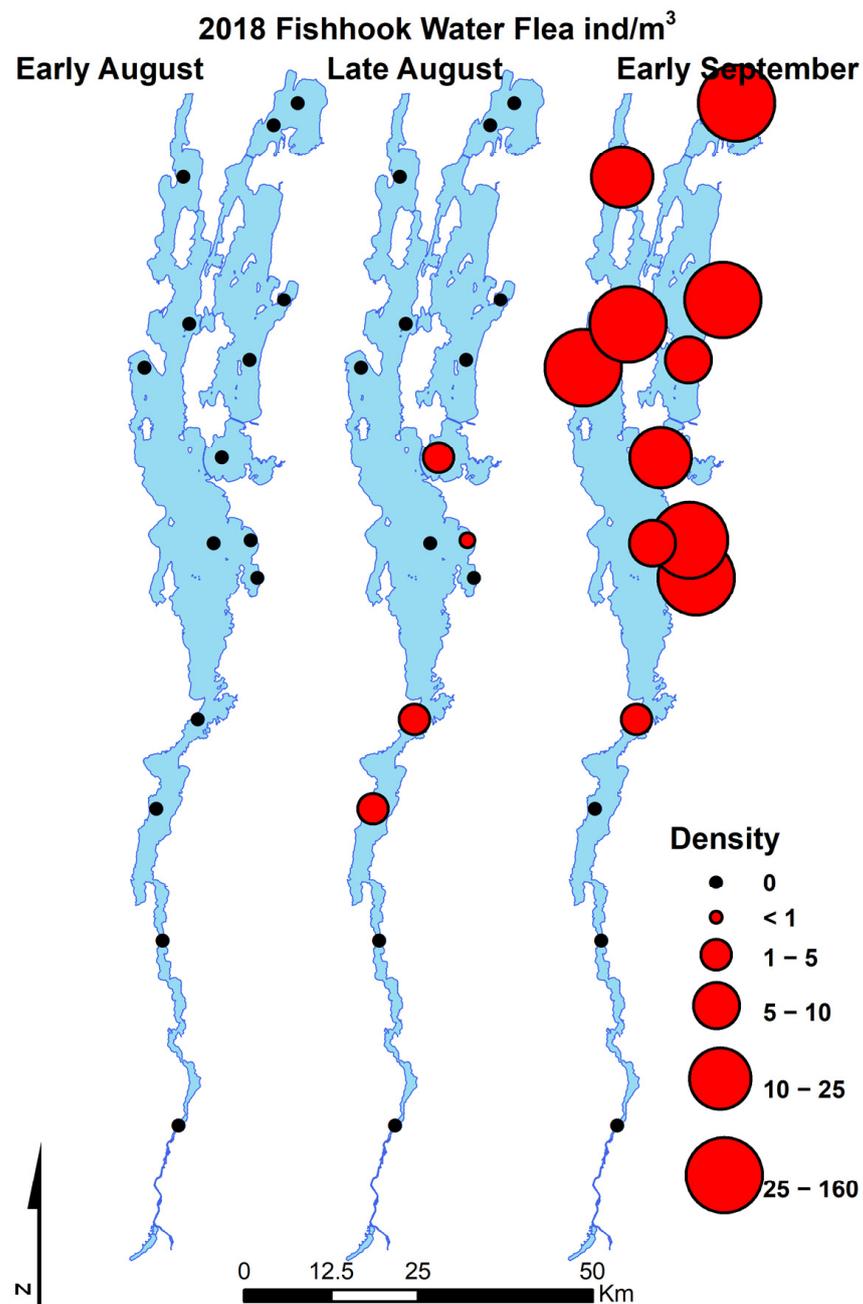
### 3.1. Invasion Dynamics in Lake Champlain

*Bythotrephes longimanus* was first detected in Lake Champlain in early August 2014, and *Cercopagis pengoi* was first detected in Lake Champlain monitoring in late August 2018 (Figures 2 and 3). Neither species was detected in any of the Lake Champlain samples at any monitoring sites lakewide prior to 2014 (*B. longimanus*) or 2018 (*C. pengoi*) despite extensive sampling efforts. *Bythotrephes longimanus* was first detected at low abundance at station 2 (Figure 1) in the southern lake in August 2014. The data collected from net tows illustrate a rapid population expansion from that initial detection throughout most of Lake Champlain to relatively high abundances (>5 per m<sup>2</sup>) lakewide by September–October 2014 (Figure 2). *Cercopagis pengoi* was first detected in samples used for Lake Champlain monitoring in late August at several main lake locations and also exhibited a rapid expansion of populations lakewide within several weeks (Figure 3). Both Cercopagid invaders appear to have spread lakewide very quickly upon initial detection.



**Figure 2.** Map series of Lake Champlain displaying all LTM sampling locations where Cercopagidae were sampled during the initial detection of *Bythotrephes longimanus*.

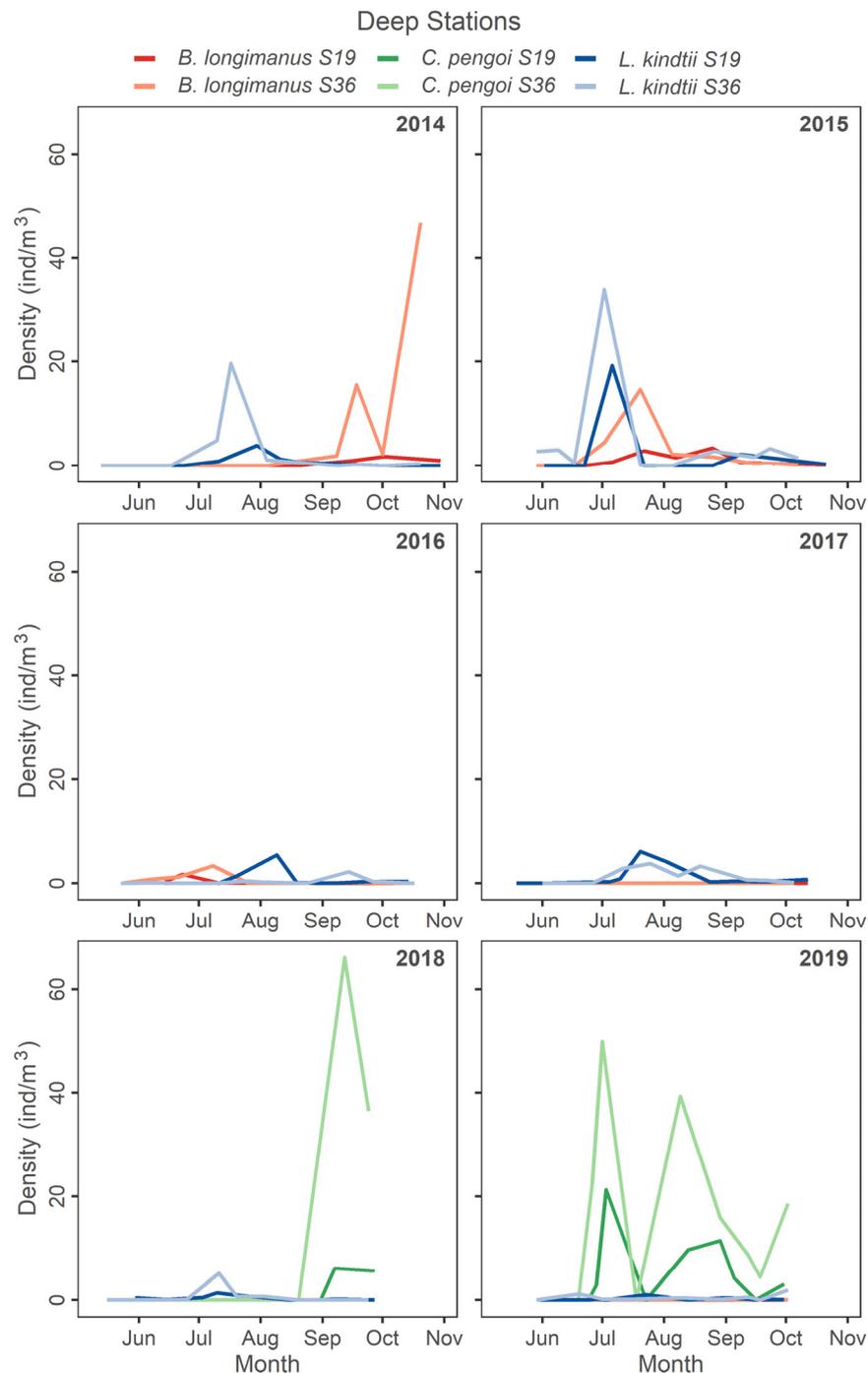
*Bythotrephes longimanus* was detected again in mid-late summer 2015 at relatively high abundance. This was followed by a decline in abundance lakewide in 2016 and subsequent years with no detection at most stations in 2017 and 2018. The population of *C. pengoi* showed a similar invasion dynamic with rapid expansion from a small initial population in August 2018 (Figure 3). *C. pengoi* was abundant from August until October in Lake Champlain in 2019 and has remained at high abundance through 2022 (personal observation).



**Figure 3.** Map series of Lake Champlain displaying all LTM sampling locations where Cercopagidae were sampled during the initial detection of *Cercopagis pengoi*.

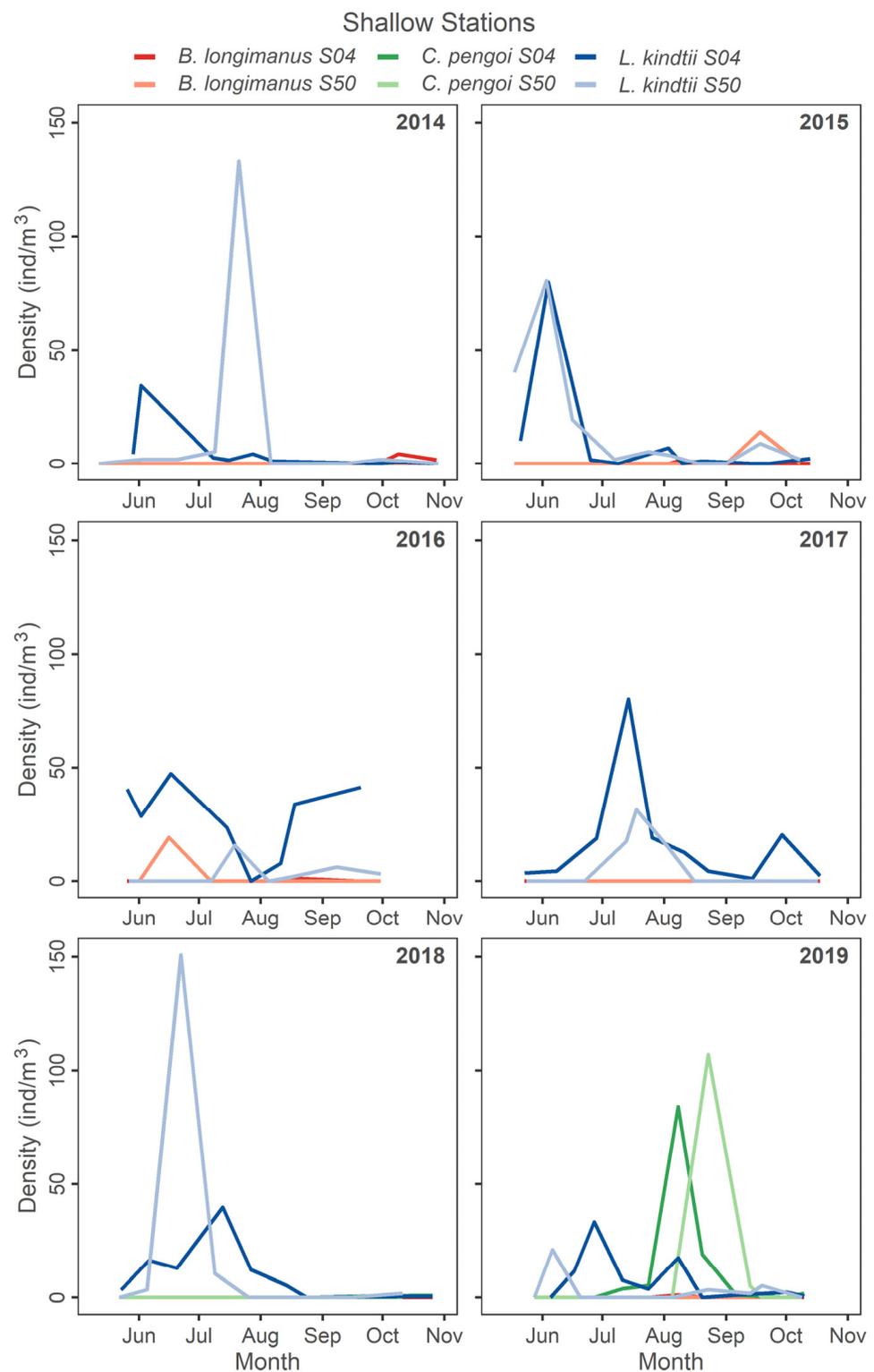
### 3.2. Response of Large Bodied Native *L. kindtii*

At deep stations during the post-2014 *B. longimanus* detection period, *L. kindtii* was typically found at peak seasonal abundance in July (Figure 4). *Bythotrephes longimanus* peaked in October in 2014 and late July 2015, while *L. kindtii* peaked in early July and declined later in the season as *B. longimanus* increased (Figure 4). In 2016 and 2017 *L. kindtii* was found at lower density but peaked later in the season in the absence of *B. longimanus*. In 2018 and 2019, which represent years where *C. pengoi* was in high density, *L. kindtii* was found at low densities (Figure 4). *Cercopagis pengoi* peaked in October 2018 and was abundant, while *L. kindtii* density was low during the entire season in 2019 when *C. pengoi* was abundant (Figure 4).



**Figure 4.** Seasonal density of predatory cladocerans at deep stations in all study years.

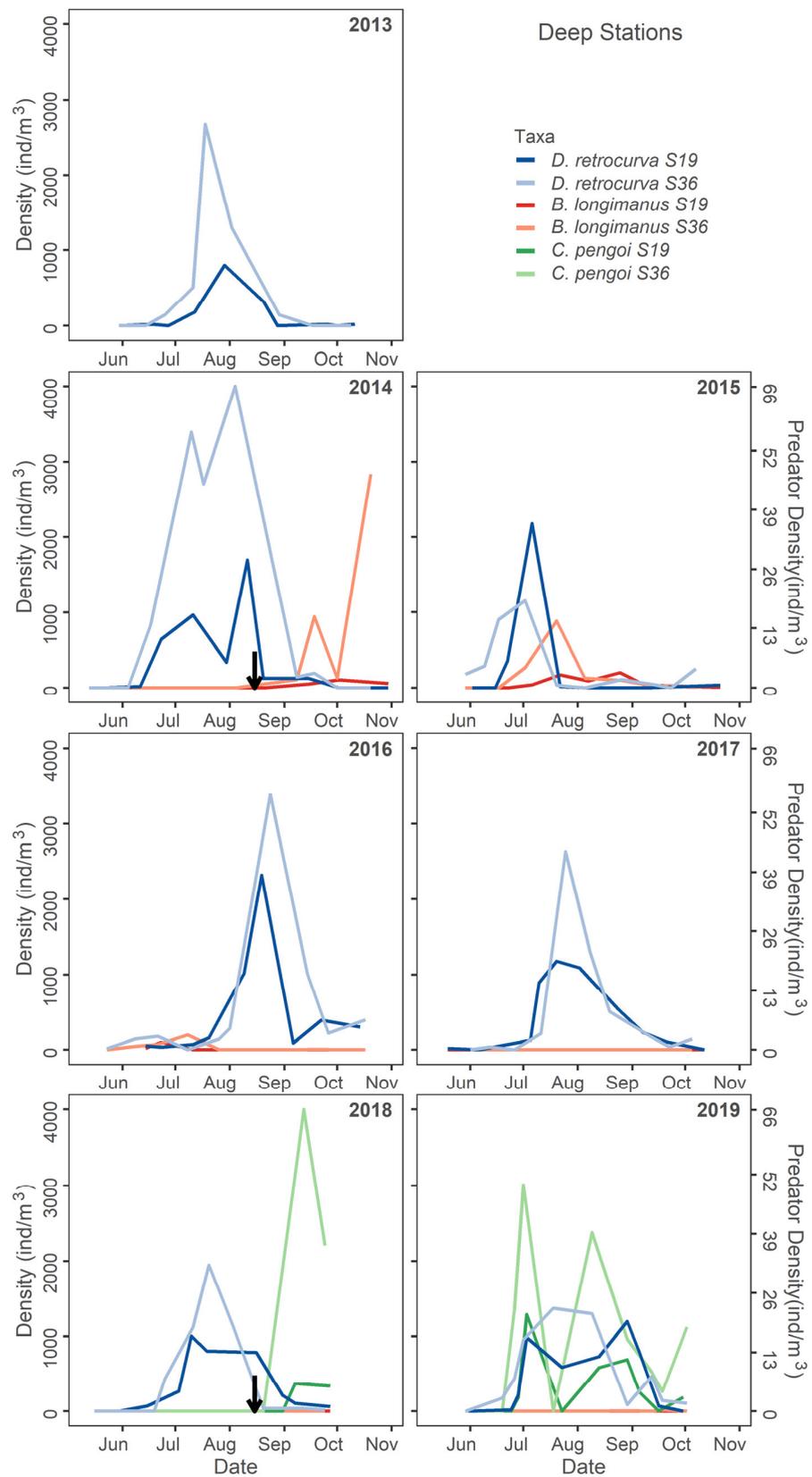
At shallow stations, *L. kindtii* peaked in abundance in June and July with some variability in timing for all years (Figure 5). *Bythotrephes longimanus* was noted at low density in October 2014, present during late September 2015, and peaked in June 2016 (Figure 5). Post *C. pengoi* detection, *L. kindtii* peaked during June and July for both years (Figure 5). In 2019, *C. pengoi* was far more abundant than the year prior and peaked in August and September (Figure 5). In general, the population of *L. kindtii* was found at a low density in Lake Champlain when either Cercopagidae invader was at high density.



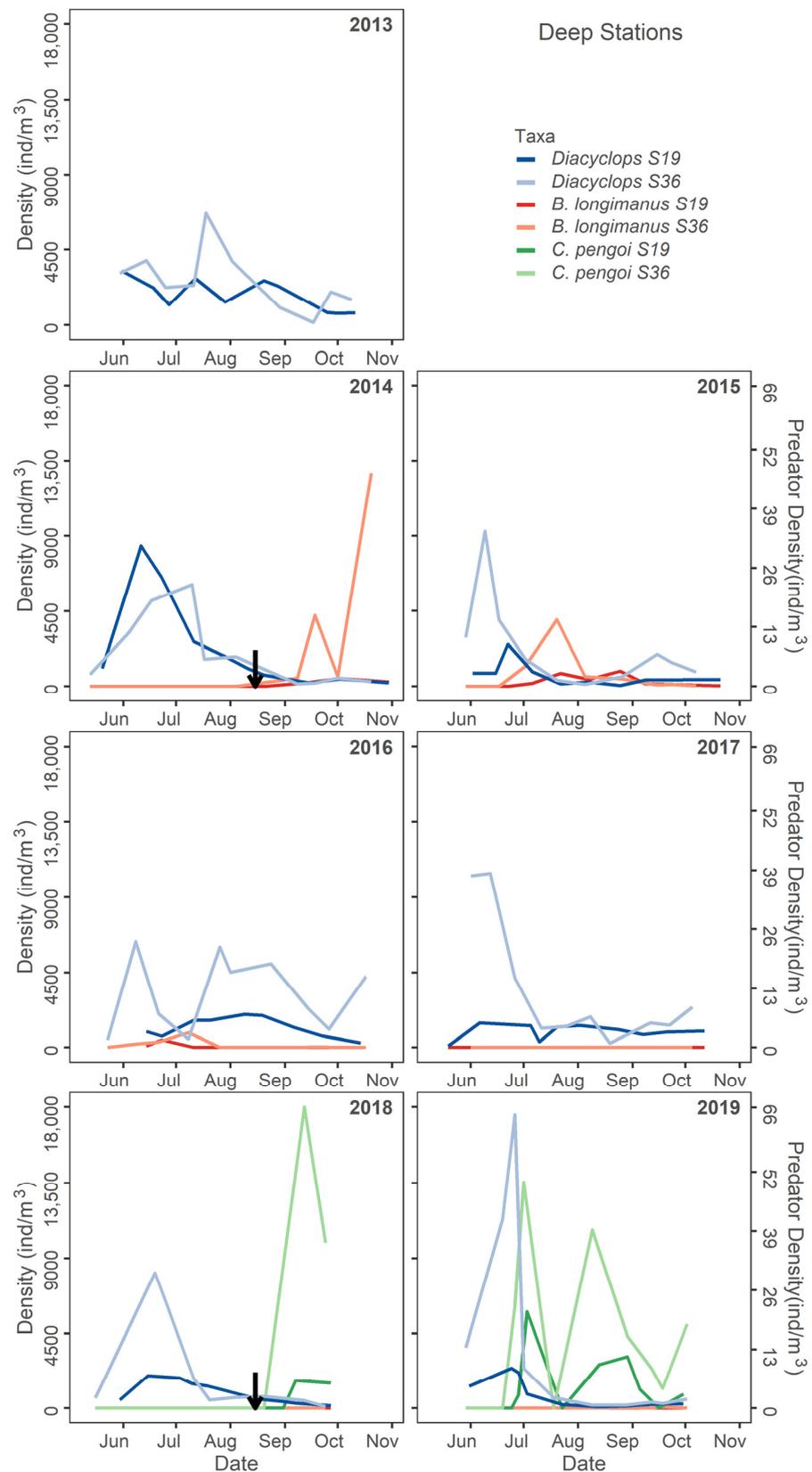
**Figure 5.** Shallow stations seasonal density of predatory cladocerans in all study years.

### 3.3. Zooplankton Abundance Patterns Following Invasion

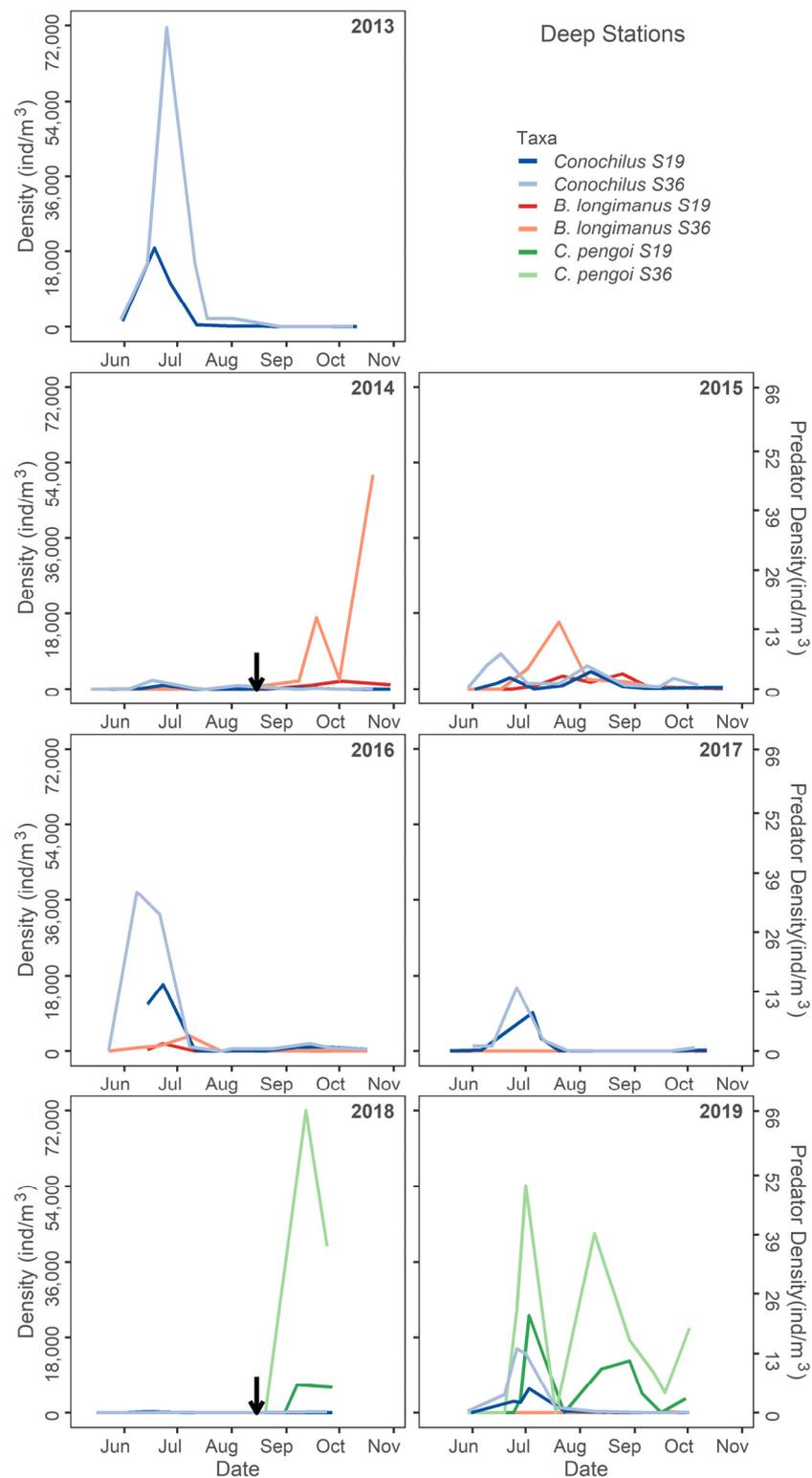
Zooplankton seasonal population dynamics differed between pre- and post-Cercopagidae detection. At both deep and shallow stations, an overall decrease in density occurred for all major zooplankton species following invasion of both Cercopagidae. This change was more pronounced in deep stations; thus, results are presented herein for deep lake stations in response to Cercopagidae invasion (Figures 6–8).



**Figure 6.** Seasonal deep station density of *Daphnia retrocurva* compared to *Bythotrephes longimanus* and *Cercopagis pengoi* in all study years. The black arrow denotes the time when a Cercopagidae was first detected (*B. longimanus* 2014, *C. pengoi* 2018).



**Figure 7.** Seasonal deep station density of *Diacyclops thomasi* compared to *Bythotrephes longimanus* and *Cercopagis pengoi* in all study years. The black arrow denotes the time when a Cercopagidae was first detected (*B. longimanus* 2014, *C. pengoi* 2018).



**Figure 8.** Seasonal deep station density of *Conochilus* spp. compared to *Bythotrephes longimanus* and *Cercopagis pengoi* in all study years. The black arrow denotes the time when a Cercopagidae was first detected (*B. longimanus* 2014, *C. pengoi* 2018).

The seasonality of peak abundance of the most dominant cladoceran, *Daphnia retrocurva*, was most notably altered in 2015 as it shifted from the beginning of August prior to the invasion of *B. longimanus* to early July following the invasion (Figure 6). *Daphnia retrocurva*

peaked earlier in 2015 and then decreased in abundance during the summer peak of *B. longimanus* at deep stations (Figure 6). Minimal changes in the seasonal dynamics of *D. retrocurva* were observed during the *C. pengoi* invasion in 2018–2019 (Figure 6).

The most apparent alteration in seasonal population dynamics amongst the copepods was observed at deep stations for *D. thomasi*, with low abundance occurring during seasonal periods of high density for either Cercopagid (Figure 7). *Diacyclops thomasi* declined during high Cercopagidae density in 2015 and 2019, the years after *B. longimanus* (2015) and *C. pengoi* (2019) were detected in Lake Champlain (Figure 7). During years of high Cercopagidae abundance, *D. thomasi* abundance peaked early in the season and then declined in July (with the onset of peak Cercopagidae summer populations). However, during years with low Cercopagidae abundance (2013, 2016, 2017) *D. thomasi* peak abundance shifted later into the season (Figure 7). There was little discernable change to the *D. thomasi* seasonal population trends during periods of high Cercopagidae abundance at shallow stations.

The seasonal dynamics of the predominant rotifer in Lake Champlain, *Conochilus* spp., showed little response to the *B. longimanus* invasion (Figure 8). The abundance of *Conochilus* spp. was somewhat lower throughout the season during the initial detection years of both predators (Figure 8). During 2019, *Conochilus* spp. density declined when *C. pengoi* densities increased seasonally in both deep and shallow sites (Figure 8).

### 3.4. Zooplankton Community Structure Following Invasion

A summary of community structure patterns from Kendall's  $w$  coefficient of concordance appears in Table 1. Results indicate that zooplankton community structure (rank order of species abundance) differed between pre- (2013) and post-*B. longimanus* invasion samples in August and September and between pre- and post-*C. pengoi* invasion samples in August and September. This illustrates a shift in community composition associated with both invasions.

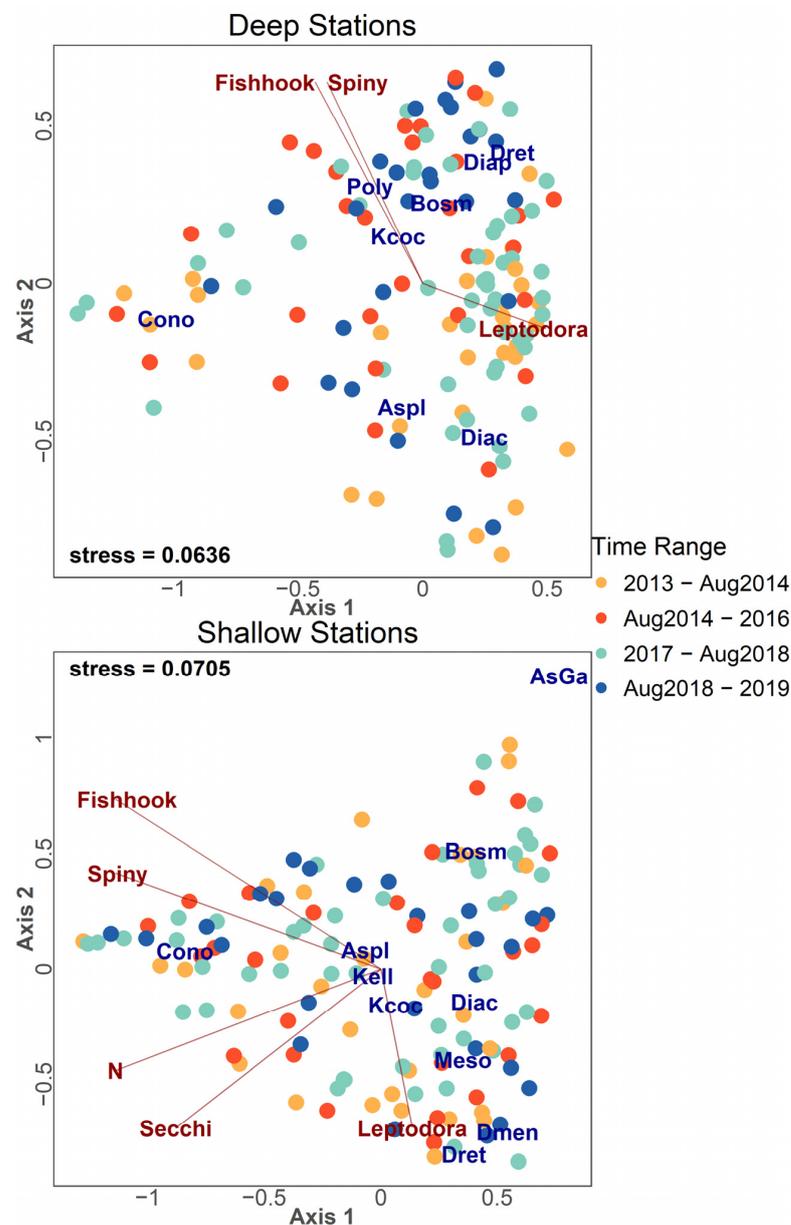
**Table 1.** Results of Kendall's  $w$  statistic for species rank order by month comparing reference species rank order (2013) to Spiny invasion years (2014–2015) and Fishhook invasion years (2018–2019).  $p$  values less than 0.05 indicate that the rank order of species was not similar across the reference and invasion samples. Bold results indicate significance at the 0.05 confidence level.

Station	Month	Fishhook Impact	Spiny Impact
4	July	0.672	0.965
	August	0.029	0.242
	September	0.854	0.107
19	July	0.313	0.864
	August	<b>0.031</b>	0.934
	September	0.134	<b>0.016</b>
36	July	0.429	0.168
	August	0.902	0.221
	September	<b>0.022</b>	0.302
50	July	0.051	0.281
	August	<b>0.012</b>	<b>0.008</b>
	September	0.082	<b>0.005</b>

Community structure change was more prevalent after the *C. pengoi* invasion than the documented changes following the invasion of *B. longimanus* (Table 1). This may be attributed to the shift in rank of *T. prasinus mexicanus*, which decreased rank at all stations in 2018–2019 following the *C. pengoi* invasion. Other species that shifted (>5) in rank following *C. pengoi* invasion are *D. retrocurva*, which declined in community rank at deep stations; *Eubosmina coregoni* (Baird, 1857); and *Asplanchna* spp., which declined at shallow stations. Rank change occurred after *B. longimanus* in *E. coregoni* (declined) and *Conochilus* spp. (increased), which altered community rank at deep stations.

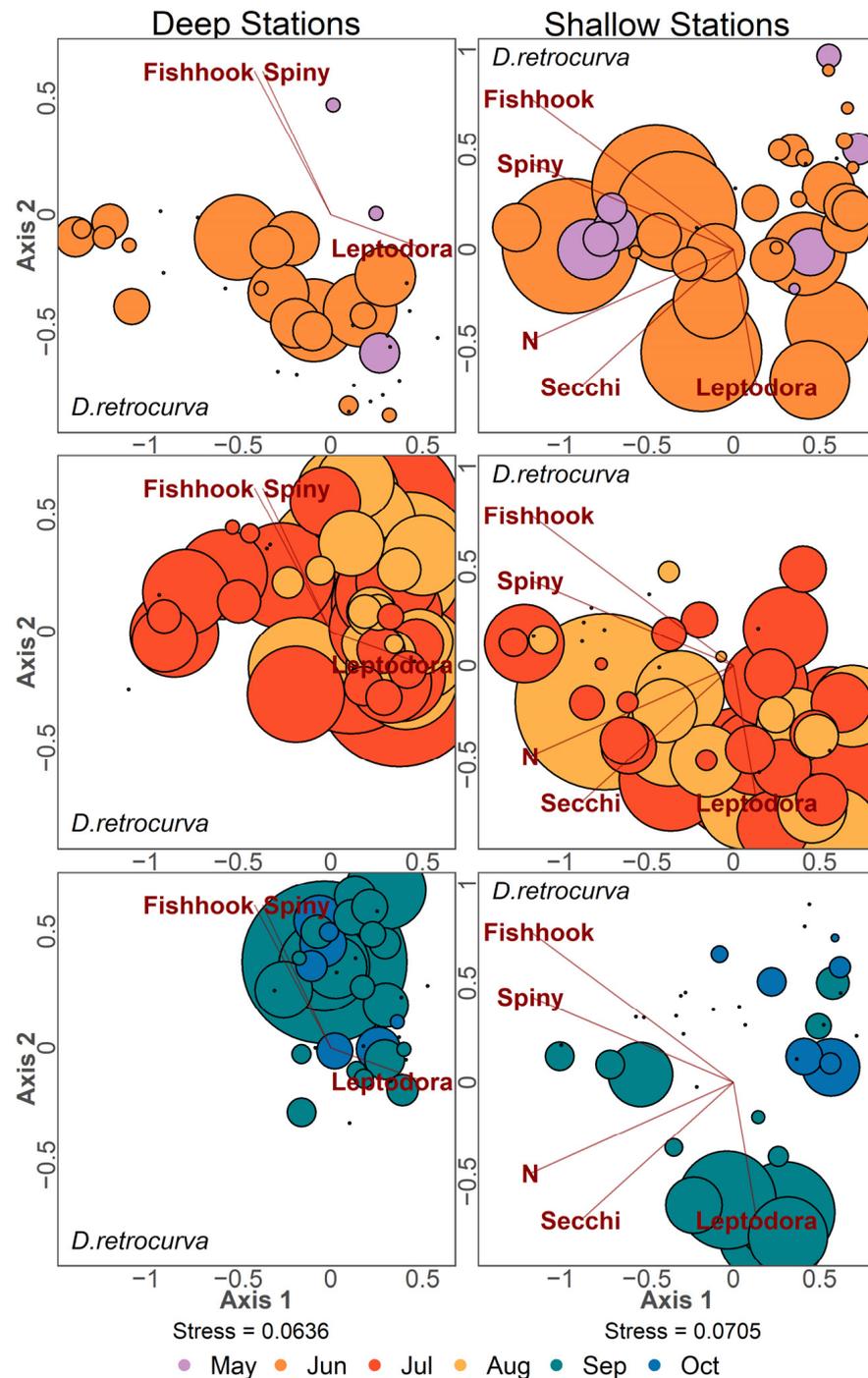
### 3.5. Community Patterns Pre- and Post-Invasion

Community ordination results are found in Figures 9–12 for both deep stations and shallow stations throughout the study period (2013–2019). NMDS ordinations in Figure 9 display the full plots that were used to plot the separated Figures 10–12. Taxa and environmental variables determined to be most influential were plotted on both deep stations and shallow stations panels. Ordination results illustrate the pattern of *Leptodora kindtii*, exhibiting higher abundance in pre-invasion samples and an inverse abundance relationship with both Cercopagid invaders (Figure 9). Samples taken pre-Cercopagidae and during years of low *B. longimanus* density (2016–August 2018) were most similar in community composition in deep stations with shifts in community composition associated with post-Cercopagid invasion periods (Figure 9). *Diacyclops thomasi* was negatively correlated with both Cercopagidae in both deep and shallow stations, more so in deep sites (Figure 9). *Conochilus* spp. were negatively correlated with *L. kindtii* in deep stations and less strongly in shallow stations (Figure 9).

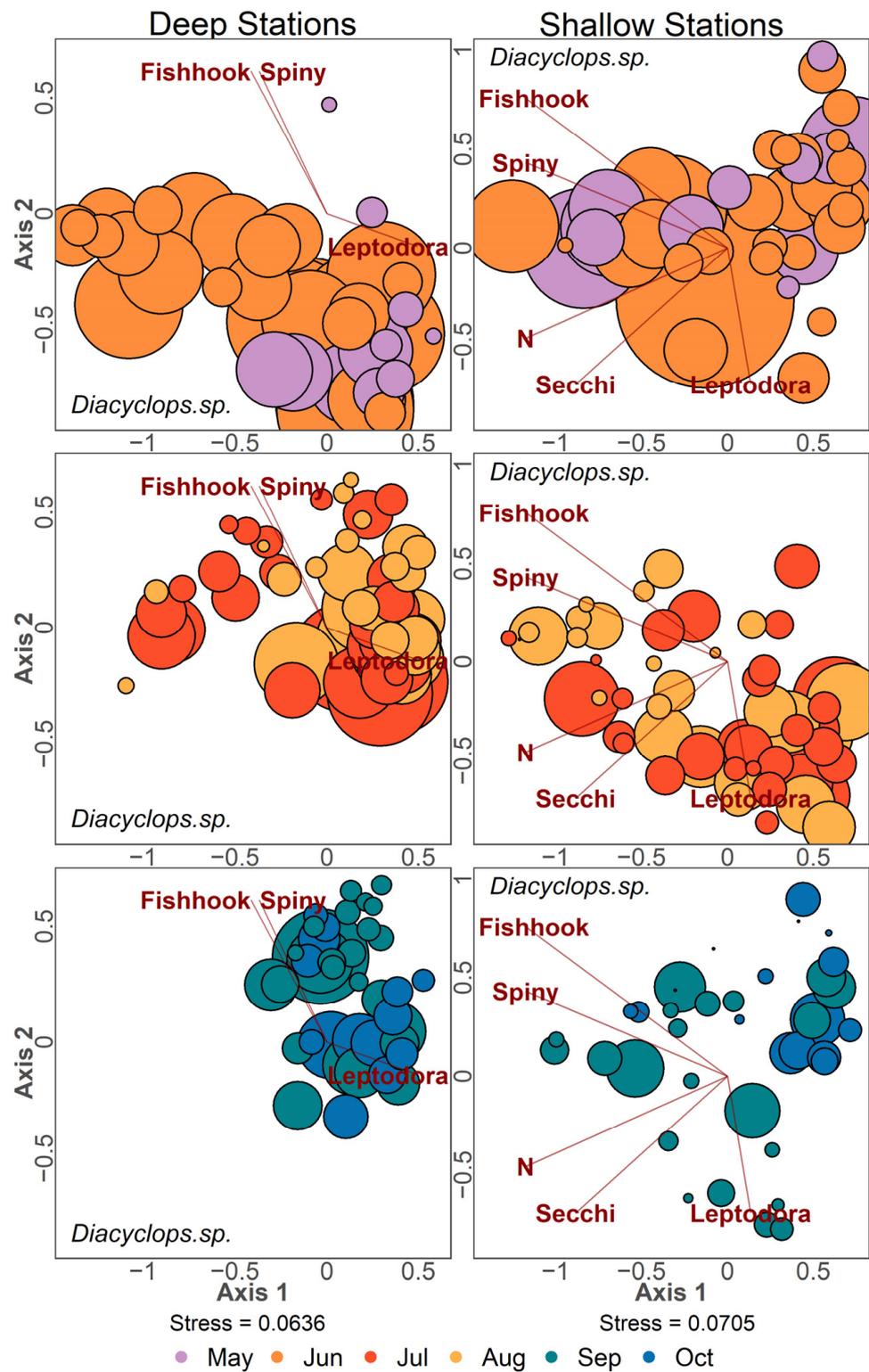


**Figure 9.** NMDS ordinations of zooplankton samples for both deep station and shallow station data. Color of points denotes the time range the sample was taken. The species abbreviations are as follows:

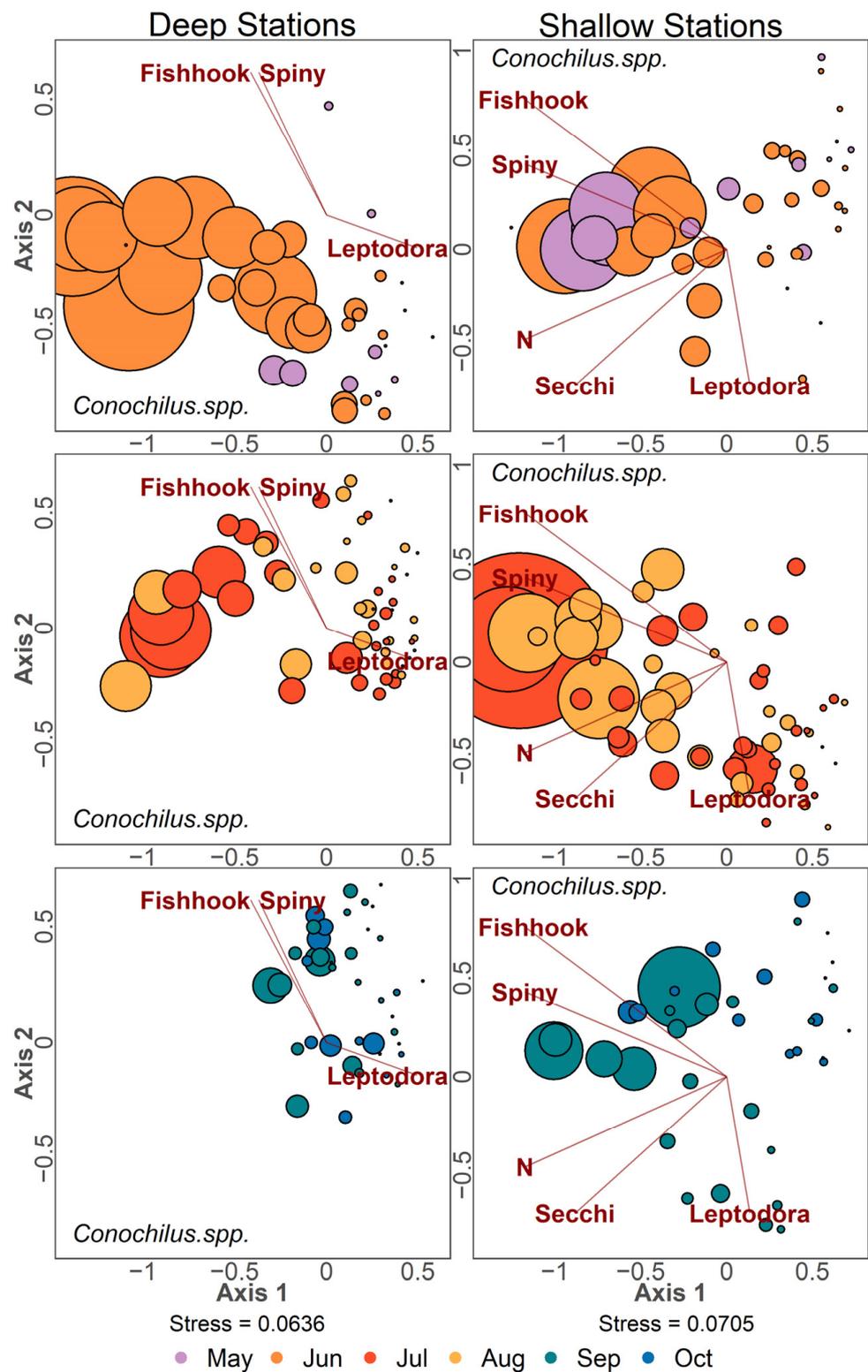
AsGa (*Ascomorpha/Gastropus* spp.), Aspl (*Asplanchna* spp.), Bosm (*Bosmina longirostris*), Cono (*Conochilus* spp.), Diac (*Diacyclops thomasi*), Diap (*Diaptomidae*), Dmen (*Daphnia mendotae*), Dret (*Daphnia retrocurva*), Meso (*Mesocyclops edax*), Poly (*Polyarthra* spp.), Kcoc (*Keratella cochlearis*), and Kell (*Kellicottia* spp.).



**Figure 10.** NMDS ordination of zooplankton samples where point size is based on density of *Daphnia retrocurva* found in the sample. Color of points denotes the month the sample was taken. Left column panels contain data from deep stations and the right column panels contain data from shallow stations. Data points were separated into three panels to reduce visual clutter and contain samples from two consecutive months. Environmental variables are *Leptodora kindtii*, *Bythotrephes longimanus* (Spiny), *Cercopagis pengoi* (Fishhook), nitrogen (N), and Secchi depth (Secchi).



**Figure 11.** NMDS ordination of zooplankton samples where point size is based on density of *Diacyclops thomasi* found in the sample. Color of points denotes the month the sample was taken. Left column panels contain data from deep stations, and the right column panels contain data from shallow stations. Data points were separated into three panels to reduce visual clutter and contain samples from two consecutive months. Environmental variables are *Leptodora kindtii*, *Bythotrephes longimanus* (Spiny), *Cercopagis pengoi* (Fishhook), nitrogen (N), and Secchi depth (Secchi).



**Figure 12.** NMDS ordination of zooplankton samples where point size is based on density of *Conochilus* spp. found in the sample. Color of points denotes the month the sample was taken. Left column panels contain data from deep stations, and the right column panels contain data from shallow stations. Data points were separated into three panels to reduce visual clutter and contain samples from two consecutive months. Environmental variables are *Leptodora kindtii*, *Bythotrephes longimanus* (Spiny), *Cercopagis pengoi* (Fishhook), nitrogen (N), and Secchi depth (Secchi).

NMDS ordinations with point size scaled by density for the three most abundant taxa in Lake Champlain are presented (*D. retrocurva* in Figure 10, *D. thomasi* in Figure 11 and *Conochilus* spp. in Figure 12). Ordination points were plotted separately for 2-month timespans for each panel. *Daphnia retrocurva* was abundant in July and August in all years at all stations and in June for shallow stations (Figure 10). *D. retrocurva* experienced an abundance decline in late season (September and October) most notably in samples containing invasive *B. longimanus* or *C. pengoi* (Figure 10). *Diacyclops thomasi* was at high density in June and July at all stations with late season declines associated with the two Cercopagid invaders (Figure 11). *Conochilus* spp. was most abundant in June and July at deep stations and more spread across May to August in shallow stations (Figure 12). *Conochilus* spp. also exhibited abundance declines mainly associated with the invasion of *C. pengoi* (Figure 12).

## 4. Discussion

### 4.1. Large Predatory Cladoceran Patterns

*Bythotrephes longimanus* was only in high abundance during the first two years (2015–2016) following its first detection in Lake Champlain in late 2014. During this period, it had an evident impact on native large-bodied zooplankton taxa, most notably *L. kindtii* and *D. retrocurva*. The seasonal abundance patterns of *B. longimanus* in Lake Champlain were similar to seasonal patterns found in other comparable lakes. Peak abundance of *B. longimanus* occurs during summer and fall in Lake Michigan [45], and mid-July to October in western Lake Erie after its first detection year [46]. After 2016, *B. longimanus* has remained at a nearly undetectable population level throughout the lake. Despite *B. longimanus* having many advantages over the other predatory cladocerans in terms of feeding efficiency and diet size range [17,47], it remains the least abundant large-bodied predator in Lake Champlain. The possible cause for this near absence may be due to predation from alewife [48] or native fish species, such as cisco [49]. *B. longimanus* were the preferred prey for adult alewife in Lake Michigan, and their consumption rate exceeds the *B. longimanus* production rate [50].

Unlike *Bythotrephes longimanus*, *Cercopagis pengoi* has remained abundant in Lake Champlain following the initial detection. On average, at every lake sampling station, the *C. pengoi* population has been more abundant than the earlier invader, *B. longimanus*. Alewife were found to be far less likely to consume *C. pengoi* over *B. longimanus* at Lake Michigan [50], which may also help to explain why it is still abundant in Lake Champlain. The seasonal population dynamics of *C. pengoi* in Lake Champlain appear to be similar to other invaded North American lakes, where they are found in samples from July to October with their peak abundance occurring in August [6,29,51]. *C. pengoi* populations remain high in Lake Champlain through all post detection years up to 2022 (personal observation), suggesting it will remain a long-term dominant large predatory plankter.

*Leptodora kindtii* appears to be unable to compete with *B. longimanus* in other lake studies [14,27,33,36], and peak densities of *L. kindtii* and *C. pengoi* rarely overlap [33]. Lake Champlain shows similar results to previous studies, where the peak density of *L. kindtii* does not overlap with the peak density of either Cercopagidae. It appears that *L. kindtii* has an advantage over the Cercopagidae at shallow water stations, as their density is not drastically reduced at these locations compared to deep water stations during the years when the Cercopagidae had invaded. For nearly every year, *L. kindtii* has been the dominant predatory cladoceran in shallow lake stations except in 2019, where *C. pengoi* became extremely abundant lakewide in August. Perhaps in shallow sites, higher turbidity may give *L. kindtii* an advantage over the other two sight-based predators [52]. *Leptodora kindtii* displays a similar population trend in the Great Lakes, remaining at high abundance at nearshore environments in Lake Michigan and Erie, locations where *B. longimanus* seems unable to survive [19].

#### 4.2. Zooplankton Invasion Response Trends

Our results suggest that both the *Bythotrephes longimanus* and *Cercopagis pengoi* invasion caused a change in the zooplankton community in Lake Champlain. The density of common species, such as *Daphnia retrocurva* and *Diacyclops thomasi*, were reduced during the years of high Cercopagidae abundance in addition to peak abundance shifting seasonally when compared to years without high Cercopagidae density. These reductions in abundance and the temporal shifting of peak density following the invasions varied between taxa, study years, and deep and shallow lake stations. Most of these changes occurred during the year immediately following first detection of both Cercopagids, especially *B. longimanus* in 2015. Similar high declines of native species during the years of first detection for both Cercopagidae have been found in the Great Lakes as well [6,19,25].

#### 4.3. Filter-Feeding Cladocerans

The decline in *D. retrocurva* during the initial detection years of *B. longimanus* invasion is a common outcome found in the Laurentian region [14,19,53]. *Daphnia retrocurva* was found to have almost no overlap in occurrence with *B. longimanus* in Great Lakes studies [19,54]. This decline has been attributed to the inability of *D. retrocurva* to escape predation by *B. longimanus* [25]. *Daphnia retrocurva* density was not reduced by the *C. pengoi* invasion to the same severity as that noted for the *B. longimanus* invasion in Lake Champlain. Similar results were found at Lake Ontario through PCA analysis, showing similar distributions of *C. pengoi* and *D. retrocurva* in the lake [6]. This similar distribution was attributed to the large body size of *D. retrocurva*, making it less likely to be preyed upon by *C. pengoi* [6].

While *D. retrocurva* had declined due to the presence of *B. longimanus* in Lake Champlain, *D. mendotae* had not increased (see supplemental graphs) as expected based on the outcome of other studies [55,56]. Throughout this study, *D. retrocurva* has remained the most abundant daphniid in Lake Champlain, and *D. mendotae* has remained low in density. *D. mendotae* was seemingly unable to occupy the open niche space available in 2015–2016 when *D. retrocurva* populations were impacted by *B. longimanus*.

*Bosmina longirostris* declined during high Cercopagidae density periods but to a much less severe degree compared to other studies, such as those performed in Lake Ontario [6,22,51] and Lake Huron [55] (see supplemental graphs). *Eubosmina coregoni* appears to have been impacted by both Cercopagid invaders, especially during 2019 when *C. pengoi* density was at its highest (see supplemental graphs). *C. pengoi* has been found to greatly reduce *E. coregoni* abundance when it is at its peak abundance in Lake Ontario [22,51].

Due to the near disappearance of *B. longimanus* in more recent years, it is likely that *D. retrocurva* will remain the dominant daphniid of Lake Champlain because of its large body size, which *C. pengoi* is unable to process [6]. The average body size of *D. retrocurva* may become larger over time as a result of this pressure; however, this is unlikely due to the size pressure exerted by Alewife [4]. *Ceriodaphnia* spp. are smaller bodied than other daphniids and as such are subject to predation from *C. pengoi*, causing their population to remain at low density. Bosminids were in high abundance in years prior to the *C. pengoi* invasion but are likely to remain reduced in years following because of their small average body size.

#### 4.4. Copepods

Changes in seasonal abundance of *Diacyclops thomasi*, the most common copepod in Lake Champlain, occurred in both periods of high Cercopagidae density. During both invasions, the peak abundance of *D. thomasi* shifts to early summer (May–August), and said abundance peak is lower when Cercopagidae are in high abundance. Before either Cercopagidae had invaded it appears *D. thomasi* peak abundance occurred during the early to midsummer (late June–July). This is consistent with other studies, finding that *D. thomasi* reached peak abundance in July before Cercopagidae were detected [22,48]. The density

dynamics of *D. thomasi* were also highly reduced in temporal comparisons between pre and post invasion communities in the lakes at Voyageurs National Park (MN) [57].

*Mesocyclops edax* decreased in density after *B. longimanus* reached detectable density (see supplemental graphs). *Mesocyclops edax* exhibited a highly reduced population throughout the entire study period during high *B. longimanus* density in smaller Laurentian lakes [19,53,56]. This decline was attributed to *B. longimanus* predation upon their copepodid and naupliar life stages [57]. *Mesocyclops edax* was extremely low in years of high *C. pengoi* density as well. *T. prasinus mexicanus* has been impacted by both *C. pengoi* and *B. longimanus* invasions, as their population often decreased during periods of high Cercopagidae density (see supplemental graphs). Due to the small body size of *T. prasinus mexicanus*, they are likely to remain at low density from predation by *C. pengoi*.

While the Cercopagidae invasions have impacted the major cyclopoid species in Lake Champlain, *B. longimanus* and *C. pengoi* appear to have little influence on diaptomid population trends (see supplemental graphs). This outcome has been observed in other lake systems, where overall calanoid abundance did not decrease despite high nauplii consumption in the epilimnion of studied lakes invaded by Cercopagidae [14,19,48,55].

#### 4.5. Rotifers

Rotifera abundance has been reduced in the Great Lakes due to *C. pengoi* presence [21,31]; however, a comparable decline has not occurred in Lake Champlain. High reduction in *Asplanchna* spp. occurred in years where *C. pengoi* is in high abundance in the Great Lakes [21]. *Asplanchna* spp. exhibited a decline, but to a lesser degree in Lake Champlain than the Great Lakes (see supplemental graphs). However, *Conochilus* spp. seem to be much more consistently impacted. It seems that *C. pengoi* preys upon the rotifer *Conochilus* spp. heavily throughout many areas of the lake. Some studies have proposed that an observed decline in rotifer abundance was due to the presence of *C. pengoi*, while others have found no change in the rotifer community following invasion [31]. The population dynamics of other rotifer taxa had little noticeable change in response to either Cercopagidae, likely due to their already small presence in Lake Champlain resulting from the *Dreissena polymorpha* invasion in the 1990s [4].

## 5. Conclusions

The invasion of *Bythotrephes longimanus* and *Cercopagis pengoi* have caused a reduction in the density of key zooplankton species and shifted seasonal peak density in some. The dominant daphniid *Daphnia retrocurva* declined during the initial years where *B. longimanus* reached a detectable density in 2014 and 2015. *Diacyclops thomasi* similarly declined in density during these years as well as after *C. pengoi* reached detectable abundance. *D. thomasi* additionally shifted in seasonal peak abundance to earlier in June. The most dominant rotifer *Conochilus* spp. greatly declined during the years *C. pengoi* reached high density in 2018 and 2019. The changes in the population dynamics of these species occurred most notably at deep water stations, while these changes did not appear to occur at shallow stations.

While the *B. longimanus* population may have become negligible throughout the lake possibly due to high fish predation, the *C. pengoi* population remains strong. *Bythotrephes longimanus* likely has little long-term influence on zooplankton population dynamics, while *C. pengoi* will likely continue to impact the middle food web in the years following. It will be important to continue monitoring the invasive predatory cladoceran population in the years to come with both major invasive species now present in Lake Champlain.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15111112/s1>, Figure S1. Seasonal deep station density of *Daphnia mendotae* compared to *Bythotrephes longimanus* and *Cercopagis pengoi* in all study years. The black arrow denotes the time when a Cercopagidae was first detected (*B. longimanus* 2014, *C. pengoi* 2018), Figure S2. Seasonal deep station density of *Ceriodaphnia* spp. compared to *Bythotrephes longimanus* and *Cercopagis pengoi* in all study years. The black arrow denotes the time when a Cercopagidae was first detected (*B. longimanus* 2014, *C. pengoi* 2018), Figure S3. Seasonal deep station density of *Bosmina*

*longirostris* compared to *Bythotrephes longimanus* and *Cercopagis pengoi* in all study years. The black arrow denotes the time when a Cercopagidae was first detected (*B. longimanus* 2014, *C. pengoi* 2018), Figure S4. Seasonal deep station density of *Eubosmina coregoni* compared to *Bythotrephes longimanus* and *Cercopagis pengoi* in all study years. The black arrow denotes the time when a Cercopagidae was first detected (*B. longimanus* 2014, *C. pengoi* 2018), Figure S5. Seasonal deep station density of *Mesocyclops edax* compared to *Bythotrephes longimanus* and *Cercopagis pengoi* in all study years. The black arrow denotes the time when a Cercopagidae was first detected (*B. longimanus* 2014, *C. pengoi* 2018), Figure S6. Seasonal deep station density of *Tropocyclops prasinus mexicanus* compared to *Bythotrephes longimanus* and *Cercopagis pengoi* in all study years. The black arrow denotes the time when a Cercopagidae was first detected (*B. longimanus* 2014, *C. pengoi* 2018), Figure S7. Seasonal deep station density of Diaptomidae calanoid copepods compared to *Bythotrephes longimanus* and *Cercopagis pengoi* in all study years. The black arrow denotes the time when a Cercopagidae was first detected (*B. longimanus* 2014, *C. pengoi* 2018), Figure S8. Seasonal deep station density of *Asplanchna* spp. compared to *Bythotrephes longimanus* and *Cercopagis pengoi* in all study years. The black arrow denotes the time when a Cercopagidae was first detected (*B. longimanus* 2014, *C. pengoi* 2018).

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