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Lake Champlain Zooplankton Community Dynamics Following an Extreme Flood Event

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Abstract: Lake Champlain, the sixth largest freshwater lake in the U.S., is a deep thermally stratified temperate zone lake system. Recently, flood events have impacted the Northeastern U.S. more frequently than in past decades, resulting in increased turbidity and other impacts in northern temperate lakes. This study represents an unprecedented analysis of the impacts of major spring and summer flooding in 2011 on Lake Champlain zooplankton communities. Few studies exist on flood impacts on lake systems, especially in natural un-impounded lakes. Our results illustrate the impacts of large-scale flooding on planktonic communities in deep stratified temperate lakes and the differential responses among species based on autecological traits. Community responses include flood-adapted increase during the flood event (*Ceriodaphnia reticulata* and *Eubosmina coregoni*), a flood-intolerant decline (*Asplanchna* spp. and *Keratella cochlearis*) or a delayed flood intolerance (*Daphnia retrocurva*, *Mesocyclops edax*, and *Polyarthra* spp.). Our results suggest that large, temperate lakes such as Lake Champlain will experience community shifts in zooplankton composition during future extreme flood events associated with climate change-related weather patterns in the Northeastern U.S.

Keywords: Lake Champlain; zooplankton; flooding; stratified temperate lake; flood impacts

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1. Introduction

As extreme flood events are expected to become more common in the Northeastern U.S. due to climate change [1], it is important to understand the possible consequences in large, deep stratified lakes. The influence of flooding on zooplankton communities has been well studied in reservoirs [2–4], estuaries [5] and floodplain lakes [6], but there has been little to no research on temperate natural lakes such as Lake Champlain.

During the spring of 2011, Lake Champlain experienced an extreme spring flooding event with Lake water levels exceeding all recorded data records. As a result of the heavy snowfall during the winter and extensive early-season rain events, Lake Champlain reached its highest recorded water level of 31.45 m (103.19 ft) in 2011 [7], with a 15% increase in surface area and 12.7% increase in volume [8]. The spring flood pulse occurred roughly a month later than the previous year and lasted longer in 2011, into mid-July, than in non-flood years (Figure 1). A second anomalous flood pulse occurred in 2011 when Tropical Storm Irene impacted the Champlain Valley in late August.

The major flooding of 2011 deposited large amounts of sediment into the lake; in one week in April, the Winooski River deposited as much phosphorus as it normally does in six months [8]. Increased turbidity associated with flooding may alter the thermal structure, light availability, and distribution and abundance of planktonic communities of Lake Champlain. Each 2011 flood event can be characterized as a relatively short term "pulse" disturbance in Lake Champlain [9], while the entire 2011 season most likely can be viewed as a "press" disturbance impacting the entire growth season.

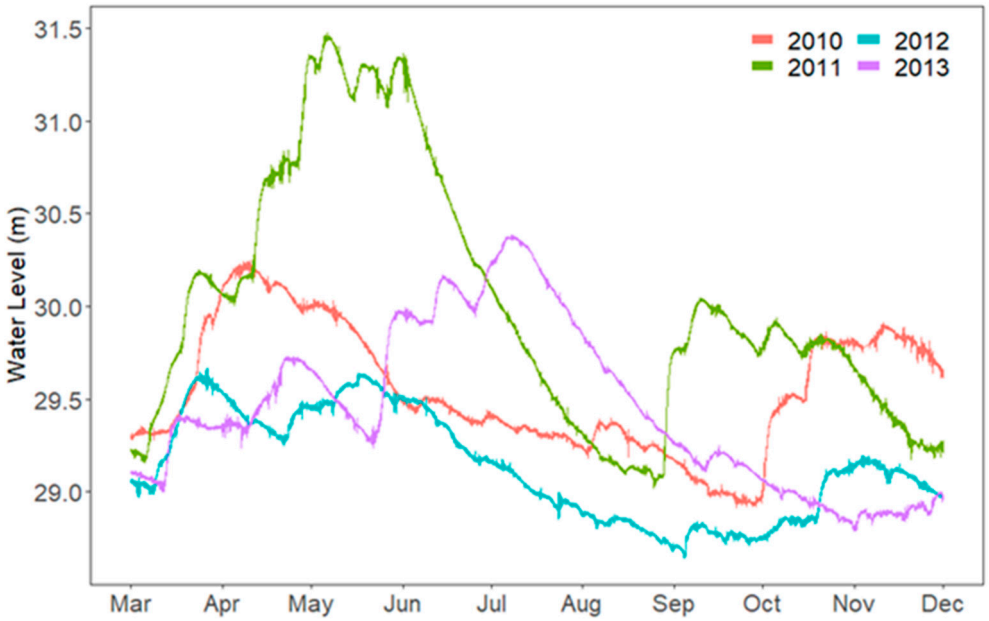


Figure 1. Annual hydrograph of Lake Champlain water level (m) at the USGS Burlington Gage for 2010–2013.

Previous work, conducted mainly in impounded lakes, suggests that floods decrease overall zooplankton density. It is not clear whether this trend is due to decreases in reproduction or zooplankton mortality [4]. Godlewska et al. [4] found that populations of rotifers, such as *Keratella cochlearis*, increased after flood events, whereas copepod and cladoceran populations declined. Of the cladocerans, populations of *Diaphanosoma* spp. fared relatively well during floods, while others such as *Daphnia* spp. populations declined [3]. Because *Daphnia* filter feed indiscriminately, the addition of suspended sediments to water causes the ingestion rates of food items to decrease as they are replaced by sediment [2].

Little is known about how zooplankton communities in large, deep temperate lakes respond to flooding; therefore, we sought to describe the impacts of the 2011 Lake Champlain floods. The objective of this study was to assess the impact of 2011 flooding on the zooplankton community structure in Lake Champlain by comparing seasonal and annual patterns in zooplankton population dynamics between pre-flood, flood and post-flood periods. We also assessed which zooplankton ecological traits were associated with flood conditions and pre-flood or post-flood conditions.

2. Materials and Methods

2.1. Study Sites

Lake Champlain is the sixth largest freshwater lake in the United States. Located between Vermont and New York, it flows 120 miles from the Hudson–Champlain Canal in the south to its outlet, the Richelieu River in the north, with a water residence time of approximately three years. Although it is generally categorized as an oligo-mesotrophic system and has an average depth of 19.4 m, Lake Champlain has several hydrologically distinct basins [10].

Three stations have been selected for this study to represent the condition of the main deep lake (Figure 2). Station 9, the southernmost station, is 87 m deep (Table 1). Station 19, located at the widest portion of the lake outside of Burlington, VT, is 100 m deep. Station 36, located off Grand Isle, is 50 m deep.

Table 1. Zooplankton and water quality sampling stations, their locations, and average depths.

Station #	Station Name	Latitude	Longitude	Depth (m)
9	Split Rock	44°14.53′	73°24.77′	87
19	Main Lake	44°28.26′	73°17.95′	100
36	Grand Isle	44°45.37′	73°21.30′	50

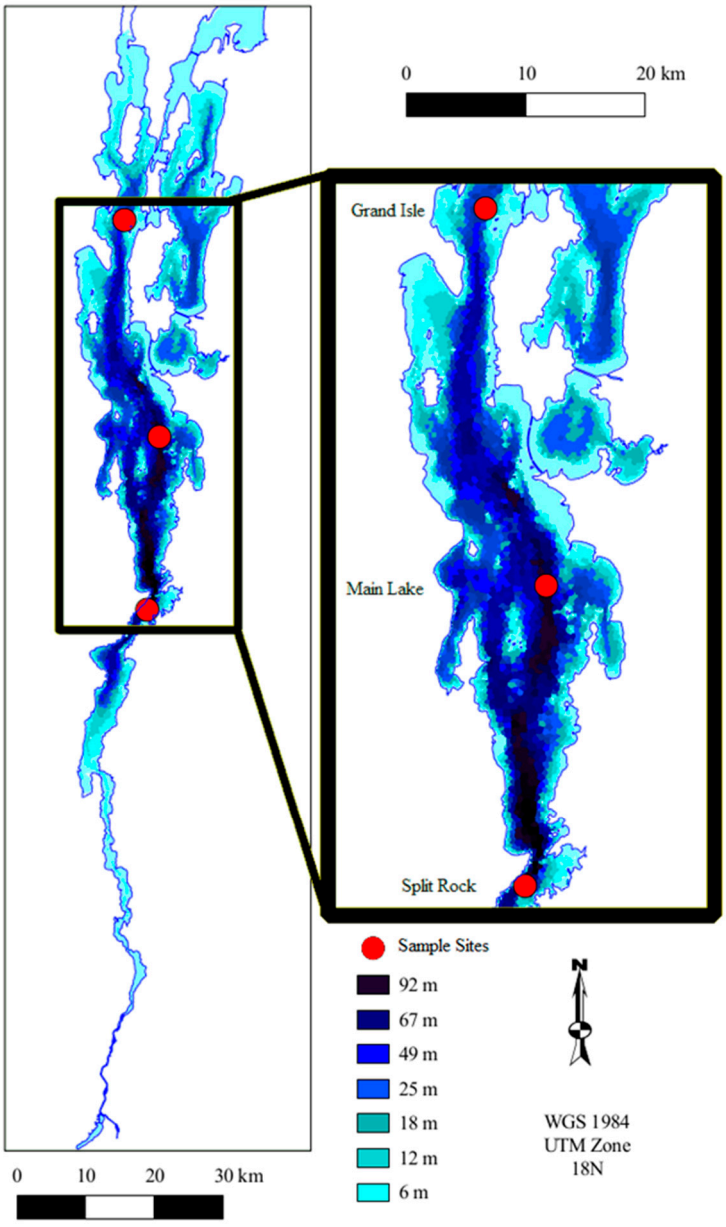


Figure 2. Bathymetry map of Lake Champlain and associated sampling sites, all located within the main lake region along the North-South trench which is 50-100 m in depth.

2.2. Field and Laboratory Methods

All field methods followed procedures from the Lake Champlain Basin Program's Long-Term Monitoring work plan [11,12]. Zooplankton samples were taken as a whole water-column vertical tow with a 153-micron mesh net bi-weekly between May and October in 2010, 2011, 2012, and 2013. All field samples were fixed in 10% formalin. Water clarity was estimated using a Secchi disk reading [12].

In the lab, samples were sub-sampled using a 1 mL Stenson-Hempel pipette and counted in a Sedgwick Rafter cell on an inverted light microscope. Standard keys used to identify the organisms to the lowest taxonomic unit possible include Balcer et al. [13], Stemberger [14], and Grothe and Grothe [15].

2.3. Data Analysis

Because traditional taxonomic categories do not capture all the information about compositional changes, examining functional traits, rather than species, may better detect community shifts. This analysis is already used for other organisms including stream insects [16], phytoplankton [17], and, more recently, crustacean zooplankton [18]. This study contributes qualitative functional information about rotifer ecological traits along with expanded trait information on crustacean zooplankton (see Appendix B).

We ran a nested ANOVA model to test for differences in average Secchi depth and maximum epilimnion depth across years in SPSS [19]. Site was a random factor nested within the fixed factor year, and Secchi/epilimnion depths were the dependent variables. The cutoff value we used was $\alpha = 0.05$.

To determine zooplankton species associations with samples from pre- and post-flood years by season, we used two-dimensional non-metric multidimensional scaling (NMDS) ordinations [20] with a Bray–Curtis dissimilarity index using the R "vegan" package in R.6.1 [21]. Ordination techniques were used to detect broad-scale patterns present in community composition. Species occurring in fewer than 5% of samples overall and within months were eliminated from the ordination to avoid disproportionately affecting the ordinations. We ran ordinations for pre-flood, flood, and post-flood data (2010–2012) by month, June through September, to investigate possible seasonal changes. Data were Wisconsin square root transformed for the analysis.

We created a trait matrix for both crustacean and rotifer zooplankton by conducting a literature search concerning common life-history traits of zooplankton as in Barnett et al. [17]. For example, inferences about the trophic status of the lake were made by observing densities of eutrophic indicator rotifer species (e.g., *Polyarthra* spp., *Conochilus* spp. *unicornis*, *Asplanchna* spp., and *Ploesoma* spp.; and, to a lesser extent, *Keratella cochlearis*, *Polyarthra euryptera*, and *Ploesoma* spp.) [22]. The species–by-sample matrix was transformed into a trait-by-sample matrix by weighting densities with traits and affinities as in Lamouroux et al. [23]. To assess community responses based on ecological traits, we ran trait-based NMDS ordinations for early (June/July) and late (August/September) seasons for the pre-flood (2010), flood (2011) and post-flood (2012) years.

3. Results

Zooplankton taxa richness remained constant throughout the duration of this study. All years had 11 copepod species and 10 cladoceran species; the flood year had 14 rotifer taxa, while the year following had 12. On average, copepods and cladocerans maintained similar densities in 2010 and 2011; in 2012, copepod densities decreased by 35% and cladoceran densities increased by 53%. Meanwhile, rotifer densities decreased by nearly 75% during the 2011 flood year and increased to half of the pre-flood density in 2012. In 2013 rotifer density increased 184% from the density in 2012, copepod density remained the same as the year prior, and cladocerans decreased by nearly 20%.

3.1. Secchi and Epilimnion Depth

A nested ANOVA showed that Secchi depth among the three sites was on average shallower in 2011 than in pre- or post-flood years ($F = 4.566$, $p < 0.0001$; Figure 3). Patterns in Secchi depth suggest that the 2011 flood year was more turbid than other years. The shallower Secchi depths were accompanied by a trend toward a shallower epilimnion ($F = 3.216$, $p = 0.112$). The flooding events of 2011 resulted in reduced epilimnion thickness and a shallower thermocline depth in Lake Champlain during the summer growing season.

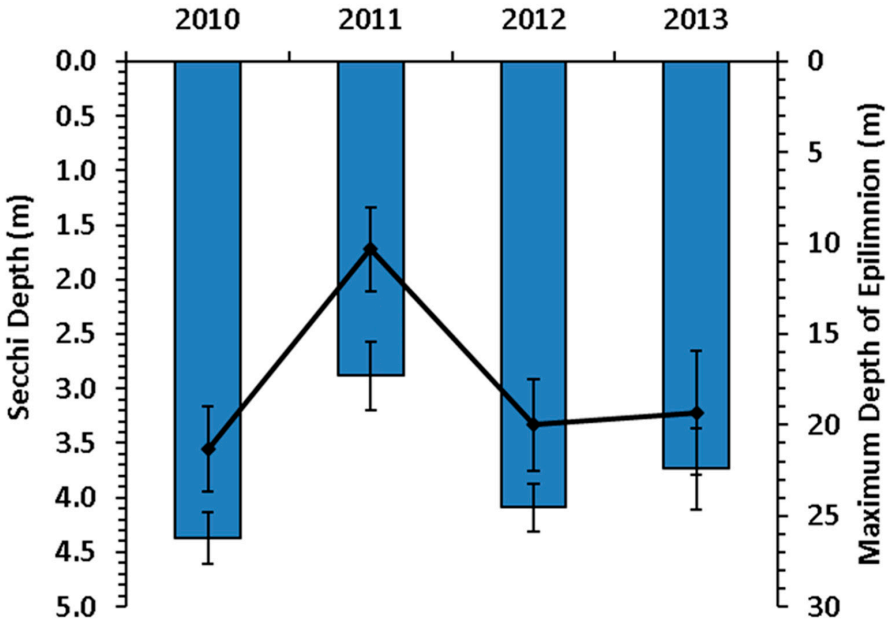


Figure 3. Average Secchi depth (bars, left axis) and average maximum thermocline depth (line, right axis) of Split Rock, Main Lake, and Grand Isle. Error bars represent SE.

3.2. Population Responses to Flooding

Zooplankton densities fluctuated seasonally in Lake Champlain but can be grouped according to their overall trends across the three years of this study. Individual taxa responded differently within groups; responses were either immediate or delayed, and densities decreased, increased, or were consistent across all three years (Table 2).

Table 2. Summary of zooplankton responses to the flooding based on their density trends across the three years. The last three columns indicate a decrease "v", increase "^" or stable trend ">" relative to the density patterns over the course of the study period.

Category	Taxon	Response	2010	2011	2012	2013
Asplanchnid Rotifer	*Asplanchna* spp.	Decrease	^	v	v	v
Brachionid rotifer	*Keratella cochlearis*	Decrease	^	v	v	v
Daphnidae	*Daphnia retrocurva*	Delayed decrease	^	^	v	v
Calanoid copepod	Diaptomidae	Delayed decrease	^	^	v	v
Cyclopoid copepod	*Mesocyclops edax*	Delayed decrease	>	^	v	v
Synchaetid rotifer	*Polyarthra* spp.	Delayed decrease	^	>	v	v
Conochilid rotifer	*Conochilus* spp.	Decrease, recovery	^	v	^	^
Synchaetid rotifer	*Ploesoma* spp.	Decrease, recovery	^	v	^	^
Brachionid rotifer	*Kellicottia longispina*	Decrease, recovery	>	v	^	>
Bosminidae	*Bosmina longirostris*	Neutral	>	>	>	>
Cyclopoid copepod	*Diacyclops thomasi*	Neutral	>	>	>	>
Sididae	*Diaphanosoma birgei*	Neutral	>	>	>	>
Daphnidae	*Ceriodaphnia reticulata*	Delayed increase	v	v	^	>
Bosminidae	*Eubosmina coregoni*	Delayed increase	v	v	^	>
Cyclopoid copepod	*Tropocyclops prasinus mexicanus*	Delayed increase	>	v	^	>

One group, characterized by an immediate decline lasting through 2012, was composed completely of rotifers. *Asplanchna* spp. and *Keratella cochlearis* maintained spring peak abundance in 2011, prior to major flooding, but had no secondary peak during the flood event (Figure 4). *Keratella cochlearis* experienced increased early season declines in 2013, but their overall densities increased with their peak abundance shifting to August

(Figure 4). In addition to a decline in late season densities during (2011) and after (2012) the flood year, *Asplanchna* spp. populations were reduced early in the season during both post-flood years (2012, 2013).

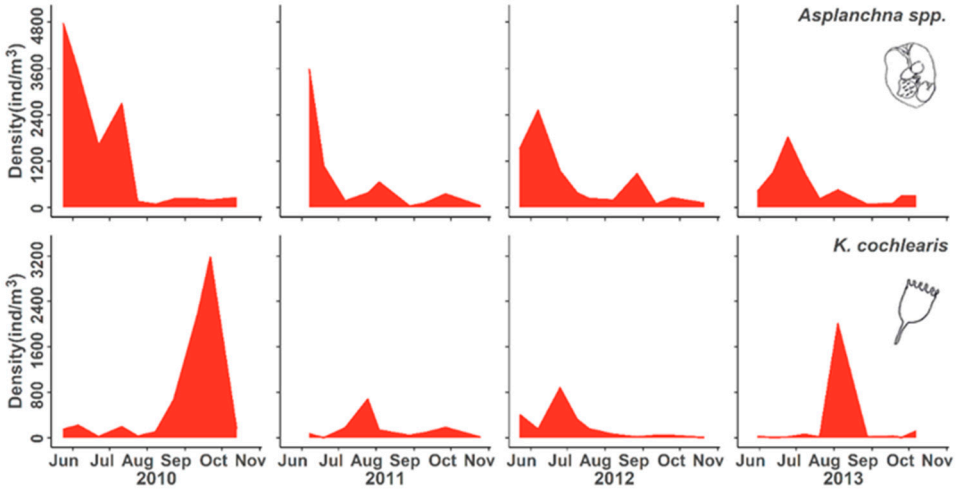


Figure 4. Seasonality of species that showed an immediate lasting decrease in response to the flood event; note the differences in scale on the y-axis.

Taxa that had a delayed decline in 2012 include the cyclopoid copepod *Mesocyclops edax*, the cladoceran *Daphnia retrocurva*, the calanoid copepod family Diaptomidae, and the rotifer genus *Polyarthra* (Figure 5). Population densities of these groups were similar between 2010 and 2011 but were reduced in 2012. *D. retrocurva* density decreased on average by 90% between 2011 and 2012, while the copepods had a more modest decline of roughly 50–60%. Population density of *D. retrocurva* increased in 2013 relative to 2012, while the copepod densities remained similar between the two years after the floods. *Polyarthra* spp. had two short peak density periods during July and September in 2010 and 2011 reaching between 900 and 1200 ind/m^3. In 2012 peak abundance occurred in late June at a 60% decline from previous years (Figure 5).

Several taxa exhibited immediate flood impacts in 2011 followed by immediate recovery in subsequent years. *Kellicottia longispina*, *Ploesoma* spp., and *Conochilus* spp. demonstrated 70–85 percent declines in abundance immediately in 2011 and rebounded to pre-flood densities in 2012 (Figure 6). In 2010, *Ploesoma* spp. density was most prominent in September. The year of the flood, *Ploesoma* spp. peak density was in August, and the year after (2012) it shifted earlier to primarily June and July. *Kellicottia longispina* exhibited a 70 percent decline in peak summer abundance in the 2011 flood year with recovery in 2012 to pre-flood densities. *Conochilus* densities continued to increase in 2013 as *Ploesoma* spp. and *Kellicottia longispina* densities were reduced once again.

Three species responded neutrally to the flood with little to no discernible changes in density. The population densities of the copepod *Diacyclops thomasi* and the cladocerans *Bosmina longirostris* and *Diaphanosoma* spp. remained fairly constant through the pre-flood (2010), flood (2011), and post-flood (2012, 2013) years. *Bosmina longirostris* densities remained similar in 2010, 2011, and 2012 but exhibited a slight increase in the early/mid-season density peak in 2013 (Figure 7).

Two cladocerans, *Eubosmina coregoni* and *Ceriodaphnia reticulata*, and a cyclopoid copepod, *Tropocyclops prasinus mexicanus*, seemed to exhibit a delayed benefit from the flood event, despite density declines of the latter two species during the flood year; populations increased the year following the flood (2012) to greater densities than observed in pre-flood conditions (Figure 8). Post-flood increases in density also occurred primarily during the late season (August–October) in 2012. *Ceriodaphnia reticulata* populations increased 15-fold between 2011 and 2012. These delayed population increases were not maintained in 2013 as densities for all taxa returned to pre-flood levels (Figure 8).

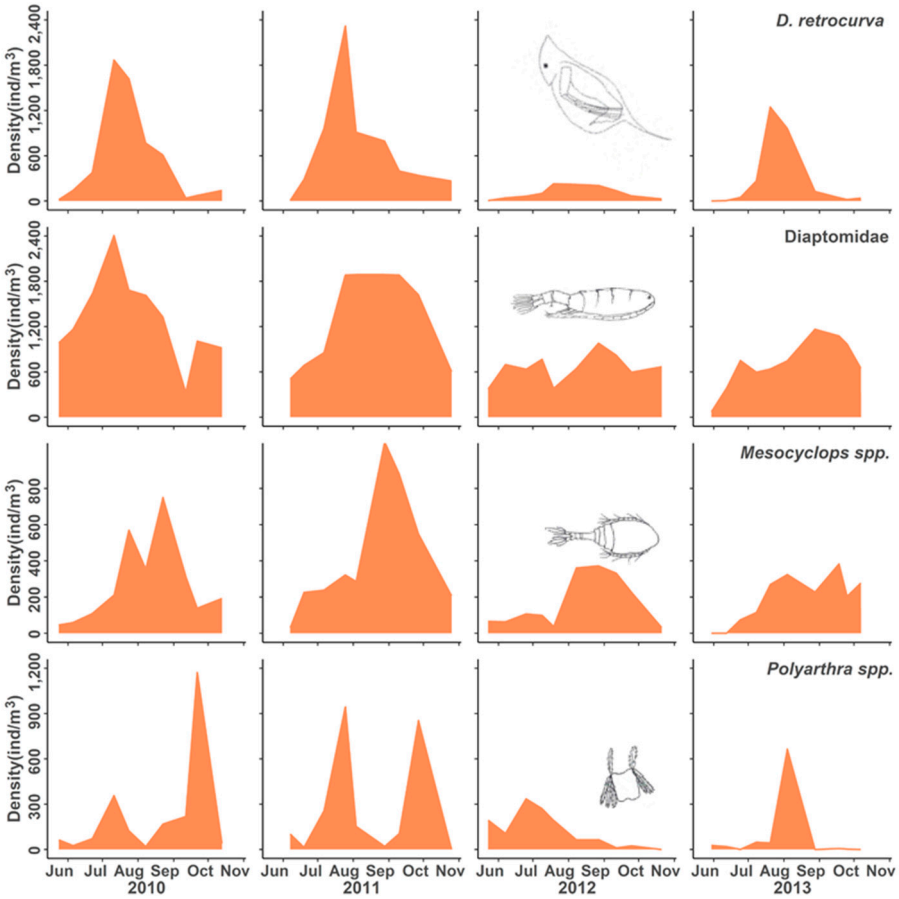


Figure 5. Seasonality of species that decreased in density in 2012, a year after the extreme flooding events in Lake Champlain (2011); note the differences in scale by the y-axis.

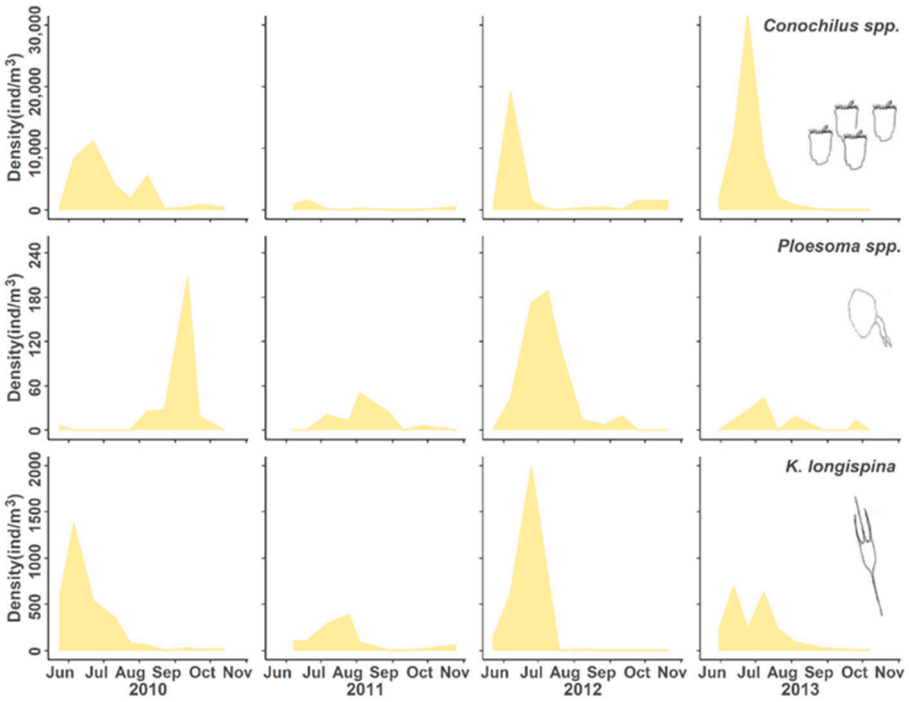


Figure 6. Seasonality of species declining during the flood and recovering after; note the difference in scale on the y-axis.

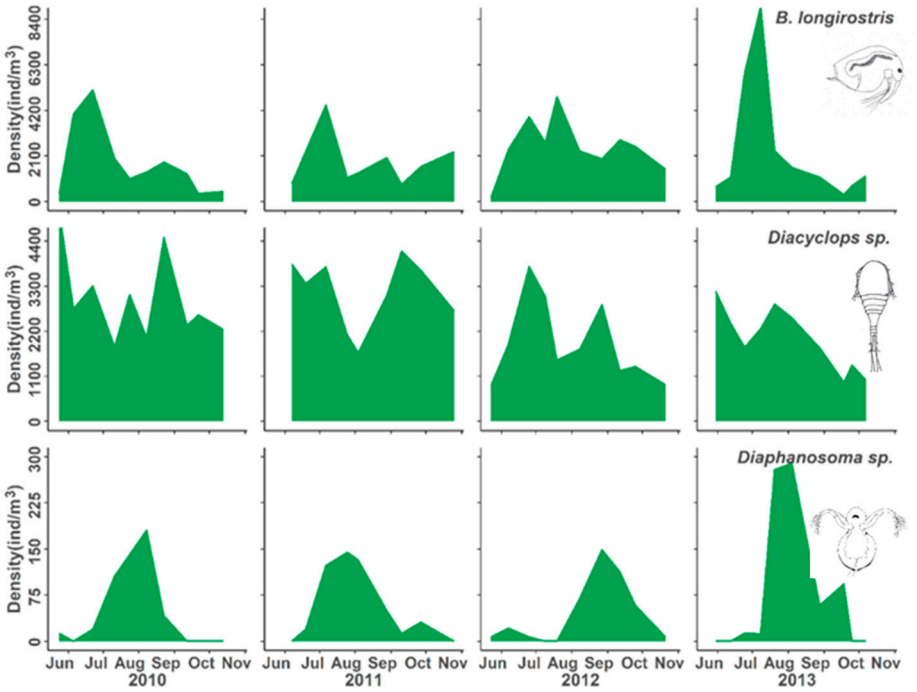


Figure 7. Seasonality of species showing little to no response from the extreme flood events of 2011; note the differences in scale on the y-axis.

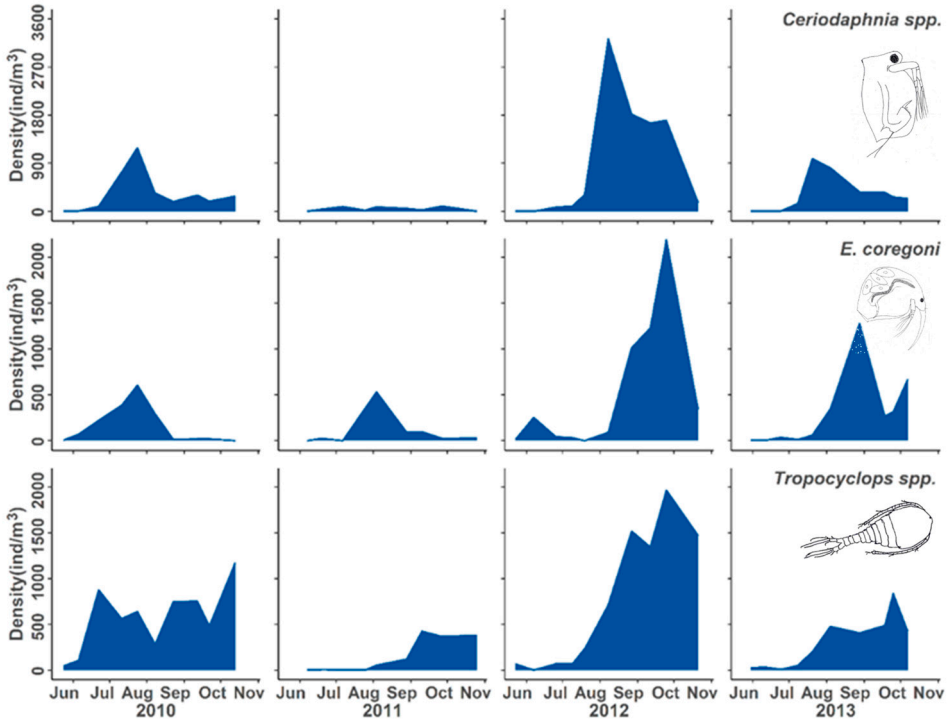


Figure 8. Seasonality of species that increased in density in 2012, one year after the flooding; note the differences in scale on the y-axis.

3.3. Community Composition Ordinations

Shifts in community composition as revealed via NMDS were seasonal in nature, with points clustering by month and year (Figures 9 and 10). June and July showed separation among pre-flood, flood, and post-flood years, particularly in 2012 (Figure 9). August showed less separation between pre-flood, flood, and post-flood years while September illustrated more distinct community shifts between years (Figure 10). The family

Diaptomidae, along with *Mesocyclops edax* and members of the genus *Daphnia* (*D. longiremis*, *D. retrocurva*, and *D. galeata mendotae*) were consistently associated with 2010 and 2011 samples illustrating their low abundance in 2012 following the flood event. *Chydorus* spp., *Ploesoma* spp., *Senecella calanoides*, and *Epischura lacustris* were most associated with 2012. However, some species shifted associations by month. *Keratella* spp. and *Polyarthra* spp. were associated with June 2012 samples only, but in later months were more associated with 2010 and 2011 samples, illustrating a seasonal shift in peak abundance to earlier in the season during the 2012 post-flood year. *Holopedium gibberum*, *Ceriodaphnia*, *Tropocyclops p. mexicanus*, and *Eubosmina* spp. were associated with 2010 and 2011 in June and July, but increased abundance during 2012 in August and September reflecting a post-flood increase and shift to later season peak abundance.

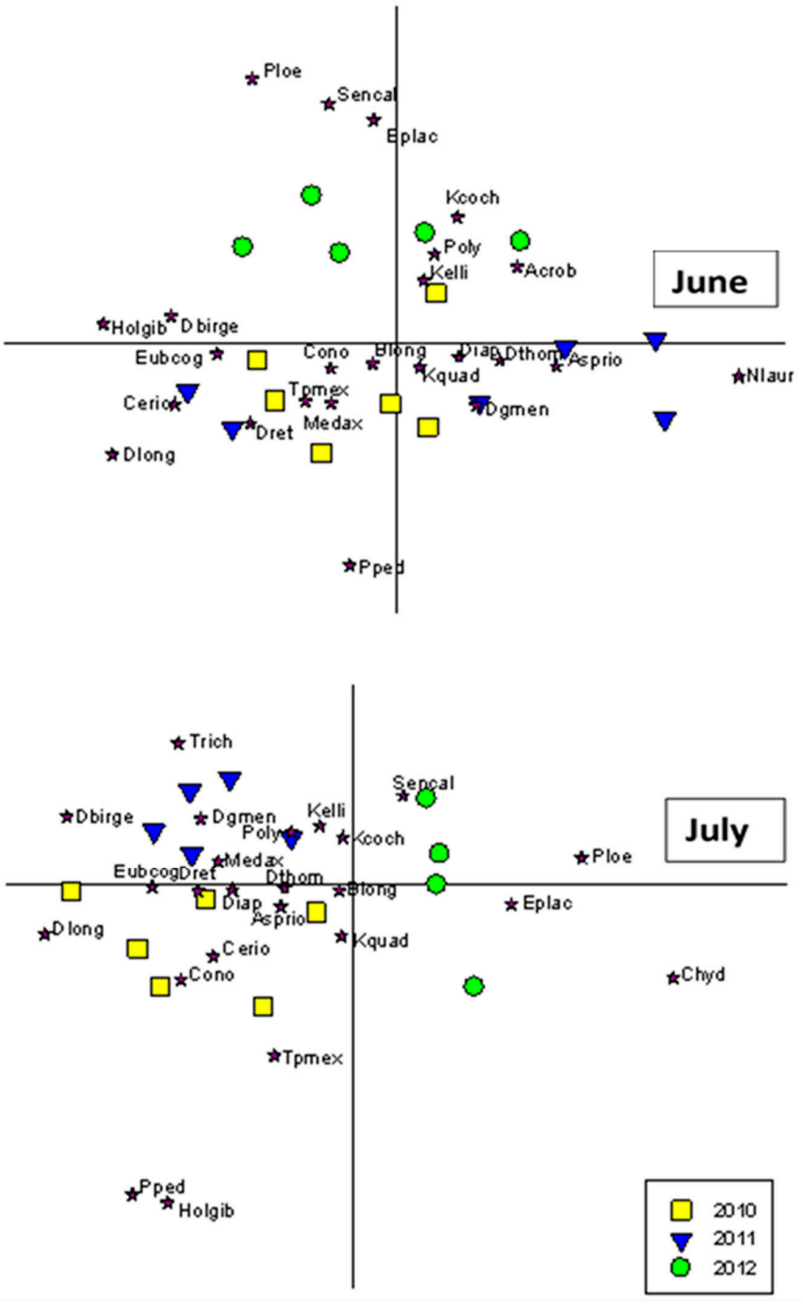


Figure 9. Nonparametric multidimensional scaling (NMDS) ordinations based on zooplankton densities averaged across all sites for June (k = 2, stress = 0.20, 33 tries; **top**) and July (k = 2, stress = 0.15, 4 tries; **bottom**). Taxa names can be found in Appendix A.

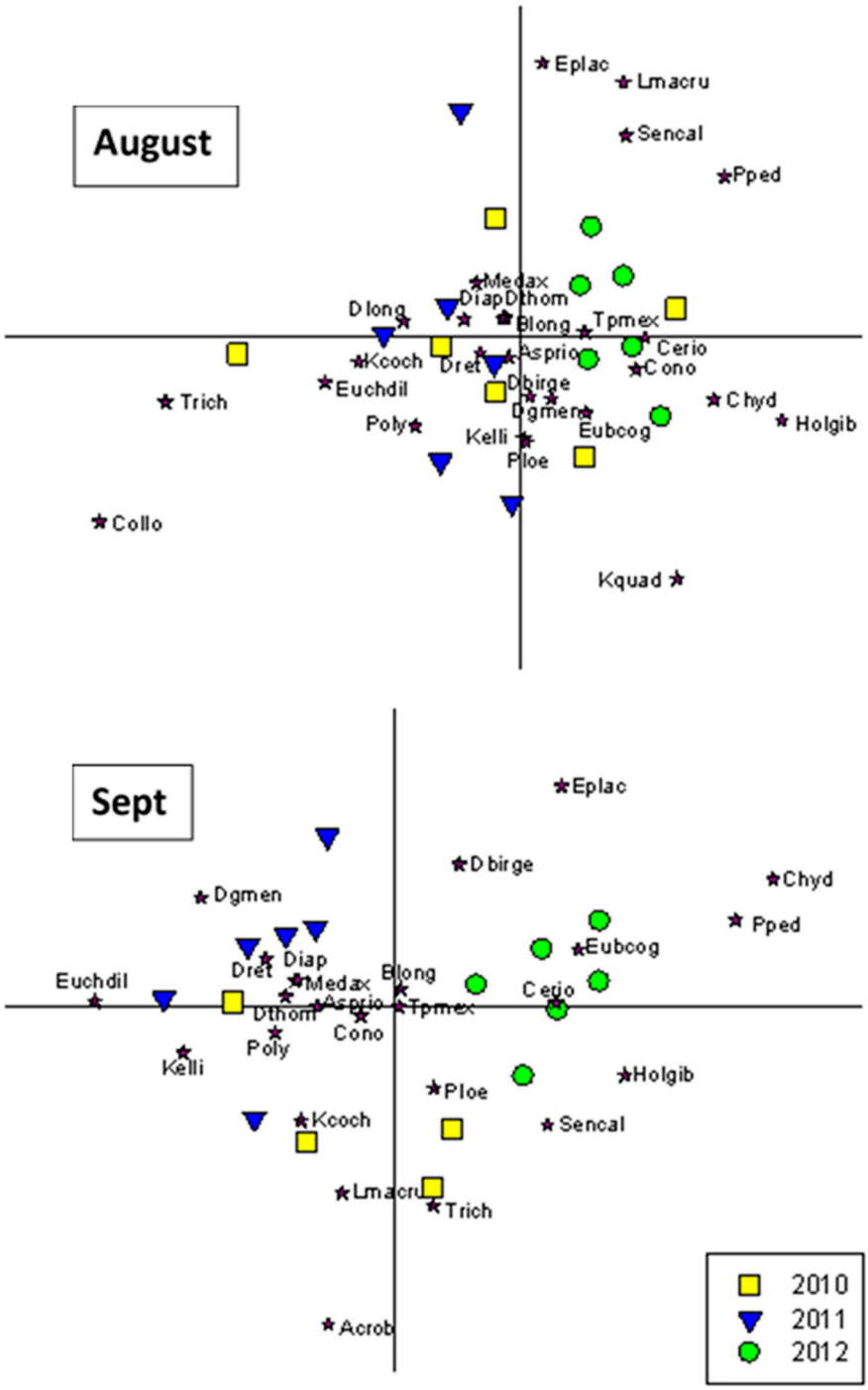


Figure 10. NMDS ordinations based on zooplankton densities averaged across all sites for August (k = 2, stress = 0.21, 24 tries; **top**) and September (k = 2, stress = 0.15, 10 tries; **bottom**). Taxa names can be found in Appendix A.

3.4. Ecological Traits

In an analysis of traits, year correlated with an NMDS axis for the June/July subset (Figure 11; $p = 0.001$; stress = 0.14) and for the August/September subset (Figure 11; $p = 0.044$; stress = 0.16). A summary of traits and trait states used can be found in Table 3. Traits regarding temperature and trophic preferences were centered and not strongly associated with any particular year. Small body sizes, illoricate (soft) bodies, living in both littoral and pelagic areas, and feeding by grasping or sucking, all traits associated with rotifers, were associated most with 2010 and 2011 samples. Helmet presence, a trait pertaining to the

genus *Daphnia*, decreased in 2011 along with presence of a gelatinous sheath. Zooplankton traits that increased the year following the flood event (2012) included omnivory, sexual reproduction, and raptorial feeding (Figure 11).

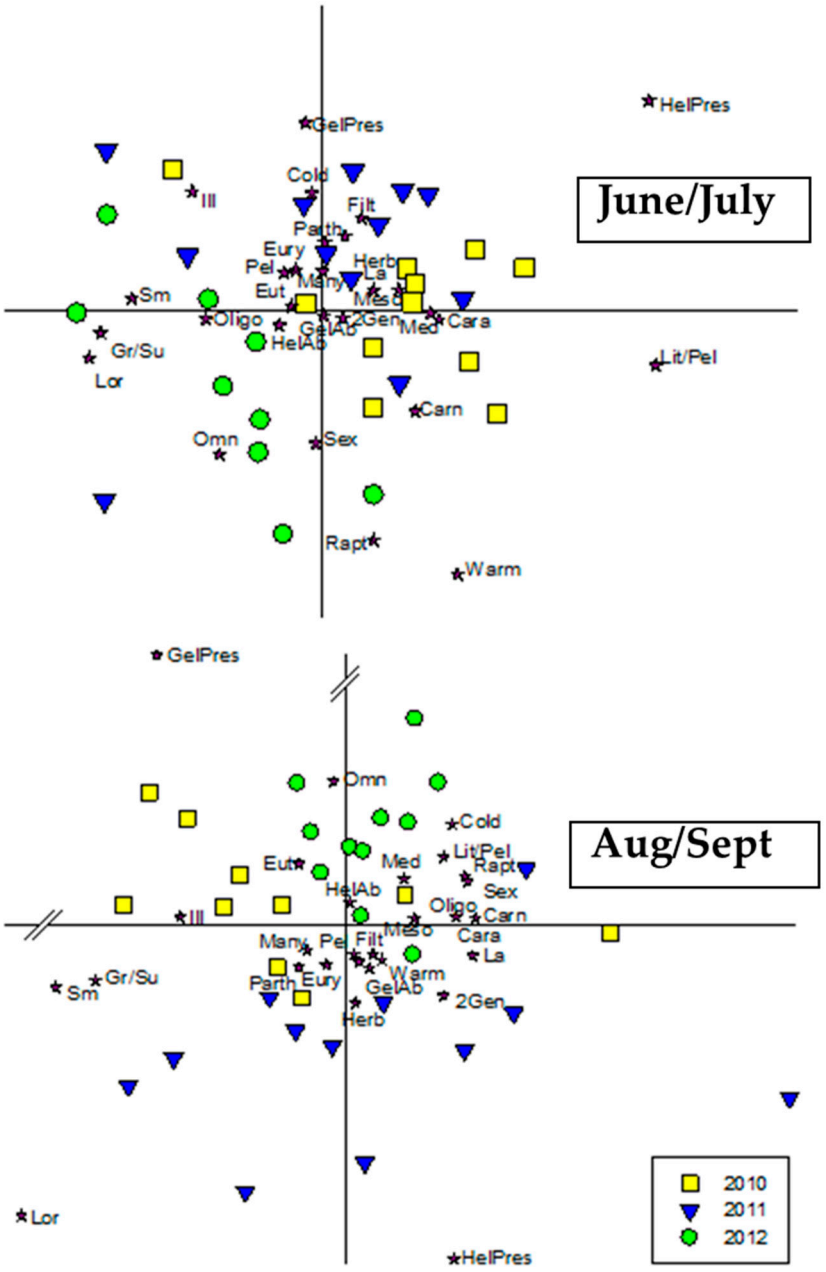


Figure 11. NMDS ordinations of trait-weighted densities for June/July (k = 2, stress = 0.14, 2 tries; **top**) and August/September (k = 2, stress = 0.16, 12 tries; **bottom**). Trait and taxa names can be found in Appendix A.

Table 3. Traits and trait states used in the analysis.

Trait	Trait States
Trophic	herbivore (primary consumer), omnivore, carnivore
Feeding mode	filtration, grasping/sucking, raptorial
Habitat	littoral, littoral/pelagic, pelagic

Table 3. *Cont.*

Trait	Trait States
Thermal	cold, eurytherm, warm
Lake productivity	oligotrophic, mesotrophic, eutrophic
Generations per year	one, two, many
Reproduction	sexual, parthenogenetic
Armor	illoricate, loricate, carapace
Gelatinous sheath	absent, present
Size class	<0.5 mm, 0.5–1 mm, >1 mm
Helmet	absent, present

Note: The traits "trophic", "thermal", and "lake productivity" allowed for intermediates, thereby splitting densities between traits. For example, a cold-adapted eurytherm would have their densities split between the states "cold" and "eurytherm".

4. Discussion

4.1. Population Dynamics

The results of this study suggest that flooding in large lakes may have predictable impacts on zooplankton community structure. Flood responses varied among copepods, cladocerans, and rotifers; therefore, the best categorization in response patterns is in their timing and direction. The floods elicited either an immediate or a delayed response, and either an increase or a decrease in density; in some cases, no response was seen. The timing of responses can likely be attributed to the species' generation times. Sexually reproducing uni- or bivoltine zooplankton (e.g., Diaptomids and *Mesocyclops edax*) may take longer to respond to a disturbance than rotifers reproducing parthenogenetically many times a year (e.g., *Asplanchna* spp. and *Conochilus* spp.). The direction of responses can be attributed to species autecology, which in turn could alter the zooplankton community structure.

4.2. Negative Responses to Flood Event

Individuals exhibiting an immediate and apparently lasting decrease were the rotifers *Asplanchna* spp. and *Kellicottia cochlearis*. Both taxa maintained their early/mid-summer density peaks while losing their mid/late-summer peaks. This suggests that the flooding may have had a negative effect on the later portions of their seasonality. Other work has shown that rotifers and daphnids share the same resources [24] which might explain the lack of a return by *K. cochlearis* and *Asplanchna* spp. What remains to be seen, however, is how these species will respond to repeated, more frequent flood events. Rotifers such as *Conochilus* spp., *Ploesoma* spp., and *K, longispina*, which exhibited an immediate decline followed by recovery, can be expected to suffer during future flood events, but rebound shortly after.

Kellicottia longispina's patterns of spring/early-summer population peaks remained constant across years but was reduced in the 2011 flood year suggesting the floods had a short-term impact on peak density in 2011. Responses of *Asplanchna* spp. and *Polyarthra* spp. suggest that individuals with normal mid- to late-summer density peaks were more affected by the flood event than those with spring density peaks.

Taxa that showed a delayed decrease include the cladoceran *Daphnia retrocurva*, the bivoltine cyclopoid *Mesocyclops edax*, the Rotifer *Polyarthra* spp., and the calanoid copepod family Diaptomidae. Given their longer life cycles, a lag time in response is expected for Diaptomids. Calanoid feeding rates can be reduced in high turbidity, leading to lower egg production rates [25] that likely would not be reflected in the population until the following year. The maintained population decreases observed in *M. edax* and Diaptomids observed in 2013 suggests that population declines associated with floods may extend two or more years for some taxa in temperate stratified lake systems.

Declines in members of the genus *Daphnia* were not immediate; populations decreased by 80–90% the year following the floods (2012). Previous studies have suggested that *Daphnia* species do not fare well in turbid conditions [26,27]. Given that Secchi depths at all sites were significantly shallower in 2011, this may explain the crash of the dominant *Daphnia* in the lake, *D. retrocurva*, as an increase in sediment turbidity inhibits its ability to feed [1]. Simultaneously, populations of *Ceriodaphnia reticulata* saw a 15-fold increase. *Daphnia* and *Ceriodaphnia* are competitors that exploit similar resources [28], making it likely that the latter was allowed to flourish once released from competition with the former. Due to their larger size, *Daphnia* are more efficient filter-feeders than *Ceriodaphnia* and are likely the dominant competitors under normal conditions [29]. The competitive release was short lived as *D. retrocurva* populations recovered in 2013 while *Ceriodaphnia* populations returned to lower abundance levels similar to those observed in 2010.

4.3. Positive Responses to the Flood Event

Few zooplankton populations increased during the 2011 flood year. Populations of *Eubosmina coregoni*, *Ceriodaphnia reticulata*, and *Tropocyclops prasinus mexicanus*, however, increased in the first post-flood year (2012). These species likely increased in abundance due to competitive release associated with *Daphnia* population declines. *Eubosmina coregoni* may possess traits which aid in survival in turbid conditions, as the species showed minimal population declines during the 2011 flood year, while shifting their peak density slightly later in the season.

4.4. Neutral Responses to the Flood Event

A handful of taxa, *Diacyclops thomasi*, *Diaphanosoma* spp., and *Bosmina longirostris*, showed no obvious response in their densities and appeared largely unaffected by the floods. These results suggest that these three species may be well adapted to flood events and are likely to maintain stable populations in future flood years. *Diacyclops thomasi* has long been the dominant copepod in Lake Champlain [10,11,30]. *Bosmina longirostris* likely fared well due to its filtration mechanism which allows it to feed more selectively than *Daphnia* [31], reducing the inhibitory effects of suspended solids on their feeding efficiency. Past work has shown that *Diaphanosoma* are more tolerant of turbidity than other cladocerans and may even increase their population density in turbid conditions [2,32].

4.5. Shifts in Community Composition

The 2011 Lake Champlain floods resulted in variable shifts in zooplankton community composition. We observed an overall decrease in density during and after the flood similar to previous studies in other systems [4]. Overall, copepod densities decreased the year following the flood, likely because of their comparatively long life cycles. *Tropocyclops prasinus mexicanus* densities increased, *Diacyclops thomasi* densities stayed the same, while *Mesocyclops edax* and diaptomid calanoid densities decreased. Cladoceran densities increased overall, largely a product of *Ceriodaphnia* populations increasing during *Daphnia* declines, with *Bosmina longirostris* populations remaining consistent. No rotifers increased during the flood; after several species declined, only populations of *Conochilus* spp., *Ploesoma* spp., and *K. longispina* showed recovery the year following the floods.

4.6. Ecological Traits

Data from traits analysis further support population-level dynamics discussed above. No rotifer species favored flood conditions, which is manifested in the association of rotifer traits with 2010 and 2011. Temperature (“warm”, “eury”, and “cold”) and trophic (“oligo”, “meso”, and “eu”) traits were similarly associated in the ordinations, suggesting that the flooding did not result in major changes in temperature or water quality conditions. The lack of a response from the oligotrophic, cold stenotherm *Notholca laurentiae* corroborates this. In each ordination, having a helmet (a *Daphnia* trait) decreased in 2012, which agrees with the observed population-level collapse of *Daphnia retrocurva*; this is expected as

presence of a helmet is associated with a taxon (*Daphnia* spp.) known to not tolerate turbid conditions [3,26].

Based on the results from this study, we suggest a new suite of traits regarding species' ability to withstand floods (Table 4). Those decreasing during or in the aftermath of the flooding can be considered "flood intolerant." Those not responding are "flood tolerant," and those increasing "flood adapted". Findings from Threlkeld [3] also suggest that flood tolerance varies by species in reservoirs.

Table 4. Suggested traits for ability of taxa to withstand flooding conditions.

Category	Taxon	Flood Adaptation
Asplanchnid rotifer Brachionid rotifer	*Asplanchna* spp. *Keratella cochlearis*	Flood intolerant
Daphnid cladoceran Calanoid copepod Cyclopoid copepod Synchaetid rotifer	*Daphnia retrocurva* Diaptomidae *Mesocyclops edax* *Polyarthra* spp.	Delayed Flood intolerant
Conochilid rotifer Synchaetid rotifer Brachionid rotifer	*Conochilus* spp. *unicornis* *Ploesoma* spp. *Kellicottia longispina*	Flood intolerant Fast recovery
Bosminid cladoceran Cyclopoid copepod Sidid cladoceran	*Bosmina longirostris* *Diacyclops thomasi* *Diaphanosoma birgei*	Flood tolerant
Daphnid cladoceran Bosminid cladoceran Cyclopoid copepod	*Ceriodaphnia reticulata* *Eubosmina coregoni* *Tropocyclops prasinus mexicanus*	Flood adapted

4.7. Ecological Comparison with Other Lakes

The bulk of studies related to the effects of flooding are limited to floodplain lakes and impoundments, producing several confounding factors that would not be present if this study occurred in a natural deep lake [33–36]. Flooding in floodplain lakes causes increased interconnectivity with the river system, altering abiotic conditions associated with their shoreline and littoral zones [33,34]. Floodplain lakes are often in subtropical regions where periods of interconnectivity with surrounding waterbodies is historically frequent [33,35] and are far shallower than Lake Champlain. It is due to these many ecological differences between a temperate stratified lake system, such as Lake Champlain, and other studies of community structure in flood periods in systems such as floodplain lakes or impoundments that caution is advised when comparing this study to others.

5. Conclusions

This study has provided valuable insight into zooplankton community responses to a flood in a large northern temperate lake. Overall zooplankton densities decreased during flooding; response time was likely a product of life cycle length, and response direction was a result of each species' autecology. Turbidity associated with the flood event likely resulted in the delayed decline in the genus *Daphnia*, which released *Ceriodaphnia* from competition and allowed it to flourish in 2012. Taxa either showed a flood-adapted response (*Ceriodaphnia reticulata* and *Eubosmina coregoni*), a flood-intolerant response (*Asplanchna* spp. and *Keratella cochlearis*) or flood intolerance with a delay or fast recovery (Table 4). These results are also reflected in patterns in species traits. This study provides useful information on flood responses among zooplankton in large lakes in addition to previous work on reservoirs, rivers, and estuaries. Large, temperate lakes such as Lake Champlain are likely to exhibit similar zooplankton responses observed herein under future climate change scenarios where extreme flood events are predicted to increase in frequency and intensity.

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Appendix A. Tables of Abbreviations

Table A1. Abbreviations for species in density ordinations.

Abbreviation	Meaning
Acrob	*Acanthocyclops robustus*
Asc	*Ascomorpha* spp.
Asprio	*Asplanchna* spp.
Bcaly	*Brachionus calyciflorus*
Blong	*Bosmina longirostris*
Cerio	*Ceriodaphnia reticulata*
Chyd	*Chydorus sphaericus*
Collo	*Collotheca* spp.
Cono	*Conochilus* spp. *unicornis*
Dbirge	*Diaphanosoma birgei*
Dgmen	*Daphnia galeata mendotae*
Diap	Diaptomidae
Dlong	*Daphnia longiremis*
Dret	*Daphnia retrocurva*
Dthom	*Diacyclops thomasi*
Eplac	*Epischura lacustris*
Erg	*Ergasilus* spp.
Eubcog	*Eubsomina coregoni*
Euchdil	*Euchlanis dilatata*
Fil	*Filinia terminalis*
Holgib	*Holopedium gibberum*
Kcoch	*Keratella cochlearis*
Kelli	*Kellicottia longispina*
Kquad	*Keratella quadrata*
Lec	*Lecane* spp.
Lmacru	*Limnocalanus macrurus*
Medax	*Mesocyclops edax*
Mon	*Monostyla* spp.
Nlaur	*Notholca laurentiae*
Ploe	*Ploesoma spp.*
Poly	*Polyarthra* spp.
Pped	*Polyphemus pediculus*
Sencal	*Senecella calanoides*
Synch	*Synchaeta* spp.
Tpmex	*Tropocyclops prasinus mexicanus*
Trich	*Trichocerca* spp.

Table A2. Abbreviations of traits from trait ordinations.

Abbreviation	Meaning
Herb	Primary consumer (herbivore, bacteriovore)
Omn	Omnivore
Carn	Carnivore
Filt	Filter feeding
GrSu	Grasping/sucking
Rapt	Raptorial feeding
Lit	Littoral
LitPel	Littoral or pelagic
Pel	Pelagic
Cold	Cold
Eury	Eurytherm
Warm	Warm
Oligo	Oligotrophic
Meso	Mesotrophic
Eut	Eutrophic
1Gen	1 Generation per year
2Gen	2 Generations per year
Many	Multiple generations per year
Sex	Sexual reproduction (exclusive)
Parth	Parthenogenetic reproduction
Ill	Illoricate
Lor	Loricate
Car	With carapace
GelAb	Gelatinous sheath absent
GelPres	Gelatinous sheath present
Sm	Small (<0.5 mm)
Med	Medium (0.5–1.0 mm)
La	Large (>1.0 mm)
HelAb	Helmet absent
HelPres	Helmet present

Appendix B. Species Traits Summary Tables

Table A3. Cladoceran trait matrix. Sources are listed in the references [13,14,18,37–55].

Species	Trophic Group	Feeding Mode	Habitat	Thermal	Lake Productivity	Generations Per Year	Reproduction	Armor	Gelatinous Sheath	Size Bin	Helmet
Bosmina longirostris	herbivore [18]	filtration [18]	pelagic [18]	cold-adapted eurytherm [13]	meso-eutrophic [18]	multi [13]	parthenogenetic [13]	carapace [13]	absent [13]	0.5–1 mm	no [18]
Eubosmina coregoni	herbivore [18]	filtration [18]	pelagic [18]	warm-adapted eurytherm [13]	mesotrophic [13]	multi [13]	parthenogenetic [13]	carapace [13]	absent [13]	0.5–1 mm	no [18]
Ceriodaphnia reticulata	herbivore [18]	filtration [18]	both [50]	warm-adapted eurytherm [13]	meso-eutrophic [55]	multi [13]	parthenogenetic [13]	carapace [13]	absent [13]	0.5–1 mm	no [18]
Daphnia longiremis	herbivore [13]	filtration [18]	both [13]	cold stenotherm [13,47,48]	oligo-mesotrophic [13,54]	multi [13]	parthenogenetic [13]	carapace [13]	absent [13]	0.5–1 mm	yes [18]
Daphnia galeata mendotae	herbivore [18]	filtration [18]	pelagic [18]	warm-adapted eurytherm [13]	oligo-mesotrophic [13]	multi [13]	parthenogenetic [13]	carapace [13]	absent [13]	>1 mm	yes [18]
Daphnia retrocurva	herbivore [18]	filtration [18]	pelagic [18]	warm-adapted eurytherm [13]	mesotrophic [13]	multi [13]	parthenogenetic [13]	carapace [13]	absent [13]	>1 mm	yes [18]
Chydorus sphaericus	herbivore [18]	filtration [18]	littoral [18]	Warm	eutrophic [54]	multi [13]	parthenogenetic [13]	carapace [13]	absent [13]	<0.5 mm	no [18]
Diaphanosoma birgei	herbivore [18]	filtration [18]	pelagic [13]	warm-adapted eurytherm [13]	mesotrophic [13]	multi [13]	parthenogenetic [13]	carapace [13]	absent [13]	>1 mm	no [18]
Holopedium gibberum	omnivore [13]	filtration [18]	pelagic [18]	cold [13]	oligo-mesotrophic [13]	multi [13]	parthenogenetic [13]	carapace [13]	present [13]	>1 mm	no [18]
Polyphemus pediculus	carnivore [18]	raptorial [18]	both [13,50]	warm-adapted eurytherm [13]	mesotrophic	two [13]	parthenogenetic [13]	reduced carapace [13]	absent [13]	>1 mm	no [18]

Table A4. Copepod trait matrix. Sources are listed in the references [13,14,18,37–55].

Species	Trophic Group	Feeding	Habitat	Thermal	Lake Productivity	Generations Per Year	Reproduction	Armor	Gelatinous Sheath	Size	Helmet
Diacyclops thomasi Cyclopoid	Omnivore-carnivore [18]	raptorial [18]	pelagic [13]	eurytherm [13]	mesotrophic [13]	two [13]	sexual [13]	carapace [13]	absent [13]	>1 mm	no [13]
Mesocyclops edax	Omnivore-carnivore [18]	raptorial [18]	both [13]	eury-warm [13]	mesotrophic	two [13]	sexual [13]	carapace [13]	absent [13]	>1 mm	no [13]
Tropocyclops prasinus mexicanus	Omnivore-herbivore [18]	raptorial [18]	pelagic [49]	warm-adapted eurytherm [13,38]	mesotrophic	multi [13]	sexual [13]	carapace [13]	absent [13]	0.5–1 mm	no [13]
Acanthocyclops robustus	omnivore [18]	raptorial [18]	both [13,49]	warm-adapted eurytherm [13]	meso-eutrophic [13]	multi [3]	sexual [13]	carapace [13]	absent [13]	>1 mm	no [13]
Ergasilus spp.	ectoparasite [42,49]	grasping	pelagic [42,51]	warm-adapted eurytherm [53]	mesotrophic [42]	one [42]	sexual [13]	carapace [13]	absent [13]	>1 mm	no [13]
Epischura lacustris	omnivore [39]	raptorial [39]	littoral [13]	eury [13]	oligotrophic [13]	one [13]	sexual [13]	carapace [13]	absent [13]	>1 mm	no [13]
Diaptomidae	herbivore [39]	filtration [13]	pelagic [13]	cold-adapted eurytherm [1]	oligo-mesotrophic [54]	two [13]	sexual [13]	carapace [13]	absent [13]	>1 mm	no [13]
Senecella calanoides	omnivore [39]	filtration	pelagic [13]	cold stenotherm [13,54]	oligotrophic [13]	one [38]	sexual [13]	carapace [1]	absent [13]	>1 mm	no [13]
Limnocalanus macrurus	Omnivore-carnivore [39,52]	raptorial [39]	pelagic [13]	cold stenotherm [13,48,54]	oligotrophic [13]	one [38]	sexual [13]	carapace [13]	absent [13]	>1 mm	no [13]

Table A5. Rotifer trait matrix. Sources are listed in the references [13,14,18,37–55].

Species	Trophic Group	Feeding	Habitat	Thermal	Lake Productivity	Generations Per Year	Reproduction	Armor	Gelatinous	Size (µm)	Trophi
Ascomorpha ecaudis	herbivore [45]	sucking [45]	littoral [14]	eurythermal [44]	mesotrophic [40]	multi [45]	parthenogenetic [14]	illoricate [14]	absent [14]	130–200	virgate [14]
Ascomorpha ovalis	herbivore [45]	sucking [45]	littoral [14]	eurythermal [44]	mesotrophic [40]	multi [45]	parthenogenetic [14]	loricate [14]	absent [14]	95–150	virgate [14]
Ascomorpha saltans	herbivore [45]	sucking [45]	littoral [14]	eurythermal [44]	mesotrophic [40]	multi [45]	parthenogenetic [14]	thin lorica [14]	absent [14,45]	100–200	virgate [14]

Table A5. *Cont.*

Species	Trophic Group	Feeding	Habitat	Thermal	Lake Productivity	Generations Per Year	Reproduction	Armor	Gelatinous	Size (µm)	Trophi
Asplanchna spp.	omnivore [14]	grasping [45]	pelagic [46]	eurythermal [41]	eu-mesotrophic [40]	multi [45]	parthenogenetic [14]	illoricate [14]	absent [14]	420–1500	incudate [14]
Brachionus calyciflorus	herbivore [14]	filtration [45]	littoral [14]	eurythermal [41]	eutrophic [40]	multi [45]	parthenogenetic [14]	loricate [14]	absent [14]	180–570	malleate [14]
Collotheca mutabilis	omnivore [14]	trapping [45]	pelagic [37]	eurythermal [41]	mesotrophic [41]	multi [45]	parthenogenetic [14]	illoricate [14]	present [14,45]	178–315	uncinate [14]
Conochilus spp. *unicornis*	herbivore [37]	filtration [45]	pelagic [37]	eurythermal [44]	eu-mesotrophic [41]	multi [45]	parthenogenetic [14]	illoricate [14]	present [14,45]	200–450	malleoramate [14]
Euchlanis dilatata	herbivore [37]	filtration [45]	littoral [37]	warm [44]	eutrophic [14]	multi [45]	parthenogenetic [14]	loricate [14]	absent [14]	200–270	malleate [14]
Filinia terminalis	herbivore [14]	filtration [45]	pelagic [45]	cold [41]	mesotrophic [41]	multi [45]	parthenogenetic [14]	illoricate [14]	absent [14]		malleoramate [14]
Kellicottia longispina	herbivore [37]	filtration [45]	pelagic [37]	cold-adapted eurytherm [14]	oligotrophic [40]	multi [45]	parthenogenetic [14]	loricate [14]	absent [14]	400–860	malleate [14]
Keratella cochlearis	herbivore [37]	filtration [45]	pelagic [37]	eury [43,44]	mesotrophic [40]	multi [45]	parthenogenetic [14]	loricate [14]	absent [14]	115–200	malleate [14]
Keratella quadrata	herbivore [37]	filtration [45]	pelagic [37]	eury [14]	mesotrophic [40]	multi [45]	parthenogenetic [14]	loricate [14]	absent [14]	224–385	malleate [14]
Monostyla spp.	herbivore [37]	filtration [37]	littoral [37]	warm [14]	eutrophic [14]	multi [45]	parthenogenetic [14]	loricate [14]	absent [14]	78–142	malleate [14]
Notholca laurentiae	herbivore [45]	filtration [45]	pelagic [14]	cold [14,37,41]	oligotrophic [40]	multi [45]	parthenogenetic [14]	loricate [14]	absent [14]	192–250	malleate [14]
Ploesoma spp.	omnivore [37]	grasping [45]	pelagic [37]	warm [41]	oligotrophic [40]	multi [45]	parthenogenetic [14]	loricate [14]	absent [14]	150–600	virgate [14]
Polyarthra spp.	herbivore [37]	grasping [45]	pelagic [37]	eury [41]	mesotrophic [14]	multi [45]	parthenogenetic [14]	illoricate [14]	absent [14]	72–200	virgate [14]
Synchaeta spp.	herbivore [37]	grasping [45]	pelagic [37]	eury [41]	mesotrophic [40]	multi [45]	parthenogenetic [14]	loricate [14]	absent [14]	90–600	virgate [14]
Trichocerca spp.	omnivore [14]	sucking [45]	littoral [14]	eury [41]	eu-mesotrophic [14]	multi [45]	parthenogenetic [14]	ill/lor [14]	absent [14]	85–310	virgate [14]

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