Hidden Beneath the Ice: Actively Overwintering Zooplankton Populations

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Abstract

Freshwater lakes in winter are a historically uncharted territory. Scientists have failed to acknowledge the importance of winter limnology, and thus, a blatant knowledge gap needs to be filled. To understand the uniqueness of freshwater lakes requires studying the aquatic food web from the bottom up by identifying zooplankton species present in winter. This meta-analysis was conducted by analyzing data regarding the taxonomy and abundance of actively overwintering zooplankton species. Temperate and alpine lakes, or those above 45°N latitude were included in this meta-analysis. To compare winter-to-summer abundances, a ratio was produced and then correlated with abiotic factors associated with the data. Results showed that actively overwintering zooplankton communities were present in freshwater lakes; however, as expected, these communities were of lower abundances in winter than in summer. Future research should synthesize these results and correlate them with causal factors. Additionally, this meta-analysis shows that zooplankton overwinter in the water column and should contribute to winter food webs. Whether winter food webs are identical to summer food webs remains to be addressed.

INTRODUCTION

Conventional thought is that freshwater lakes are teeming with life in summer and desolate in winter. To the contrary, growing evidence suggests that winter food webs exist under the ice that scientists have simply failed to recognize (Karlsson and Säwström 2009). Considering that temperate and alpine lakes are frozen on average a quarter of the year, a large portion of the year is not being observed. The current literature is lacking abundant data on winter months, especially when it comes to zooplankton assemblages. The prevailing belief is that the majority of the zooplankton community enters **diapause** during the winter to avoid unfavorable conditions such as low light, decreased temperature and food availability (Wetzel 2001). However, researchers found evidence for overwintering zooplankton decades ago (Elgmork 1959; Hall 1964); furthermore, recent studies suggest that zooplankton are actively overwintering as adults in some temperate and alpine lakes, and are not limited to a particular trophic state (Chen and Folt 1996; Horn 2003; Mariash et al. 2017). The popular belief that active zooplankton assemblages disappear during winter does not match studies described within this article. The blatant lack of literature exploring under ice aquatic communities stems primarily from the iconic initial findings of the Plankton Ecology Group (PEG) model (Sommer et al. 1986).

Diapause: a period of suspended development in an invertebrate, especially during unfavorable environmental conditions

The PEG model describes the seasonal succession of lower trophic levels (i.e. primary producers and consumers) and firmly states that winter is a reset on the planktonic biota in an aquatic ecosystem. More specifically, the PEG model forecasts that zooplankton populations decrease in density to a winter minimum and rebound when favorable conditions return in spring (Fig 1; pink line). Recently, a modified PEG model (Sommer et al. 2012) stressed the importance of overwintering zooplankton communities and their possible effects on other seasons (Fig 1; blue line). The recreated image of the original PEG model does not include the seasonality of specific zooplankton genera but rather focuses on the lack of detail in regards to the winter months.

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Understanding the composition of the winter zooplankton community would begin to investigate the mystery of winter food webs. Based upon which zooplankton species are present in winter would indicate how energy is transferred through the lake ecosystem. Without surprise, there is a limited amount of primary literature on winter zooplankton assemblages.

The focus of this meta-analysis is to catalog the zooplankton species that have been shown to actively overwinter as adults. Additionally, winter abundances will be recorded and compared relative to summer abundances in freshwater lakes. Only lakes located in temperate and alpine environments or those above 45°N latitude were included in the present study.

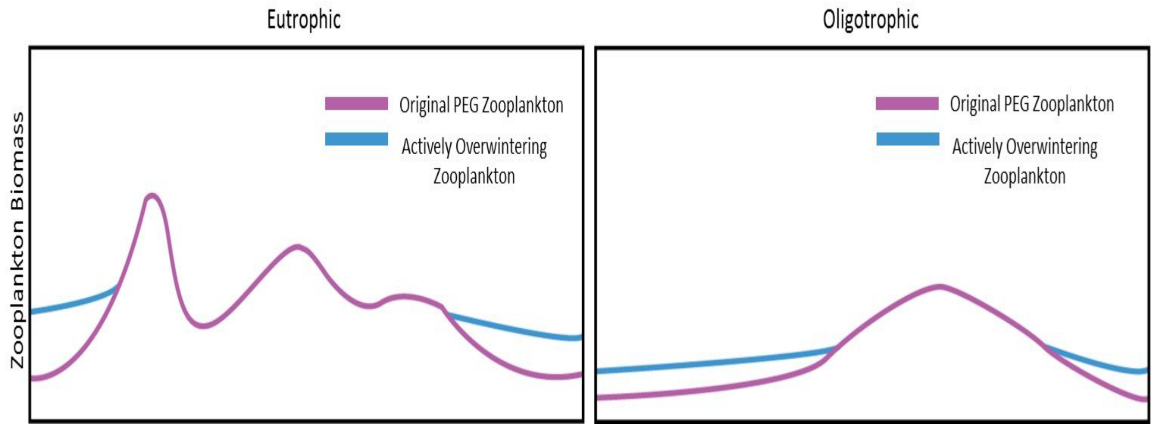

Figure 1. The Plankton Ecology Group (PEG) Model. The x-axis represents a calendar year beginning in January and ending in December. The seasonal succession of zooplankton in terms of biomass (pink line). The revised PEG model considers the importance of overwinter zooplankton (blue line). Reimaged from Sommer et al. (2012)

Freshwater Food Webs

Food webs are models created to organize the flow of energy through organisms within an ecosystem (Lindeman 1942). Energy and nutrients travel from the bottom of the food web up to higher trophic levels. Most commonly, organisms are grouped together into the trophic levels of producers, consumers, and detritivores based on how they obtain energy. The base of the food web carries the weight of the higher trophic levels, such as the socioeconomically important fish like walleye and bass. Phytoplankton, such as algae, are the base of the **pelagic** aquatic food web, and obtain energy directly from the sun. Zooplankton, including cladocerans (Fig 2A) and copepods (Fig 2B), represent primary consumers, ingesting algae for energy. The majority of cladocerans are herbivorous, while some are predatory such as *Bythotrephes, Leptodora, and Polyphemus*. Similarly, not all copepods are herbivorous with some being either carnivorous or omnivorous. In turn, the zooplankton are eaten by planktivorous fishes, often juveniles, who themselves are food for higher trophic level organisms. Zooplankton are a vital group of organisms that transfer energy from the lowest trophic levels, the algae, to the higher trophic levels such as fish.

Pelagic Zone: Any water in a sea or lake that is neither close to the bottom nor near the shore

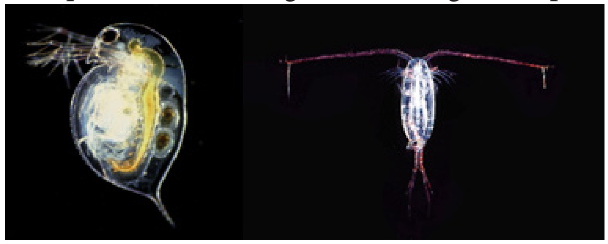

Figure 2. *Daphnia* (2A; left) and Copepod (2B; right) morphologies. Note the distinct differences in morphology that represents the type of feeding behavior exhibited by both groups.

It can be argued that the health of the entire food web hinges on the health of the zooplankton community. Any perturbation in the health of the zooplankton community can have significant impacts on both higher and lower trophic levels by causing extreme population size fluxes, limiting the transfer of energy and nutrients between trophic levels, or altering the food web structure entirely. That being said, the majority of literature detailing freshwater food webs and their dynamics explicitly detail the open water season and fail to take winter months into account.

The seasonality of both cladocera and copepods are important factors in food web and population dynamics. Carnivorous copepods feed heavily on smaller, herbivorous zooplankton and control not only population size but also the average body size of the species (Brooks and Dodson 1965). Similarly, cladocera have an influence on the populations of edible and non-edible algal species. By altering the seasonal population size and dominance of both zooplankton groups, the food web can alter in noticeable and predictable fashions.

Plankton Ecology Group (PEG) Model – Original and Revised

The 1986 PEG model (Sommer et al. 1986) is a descriptive image, based upon a series of 24 sequential statements functioning as a checklist, aimed at describing the seasonal succession of zooplankton communities in a well-studied lake (Fig 1). The model was tested against data collected from 24 temperate lakes primarily from Europe, with a few lakes from the Mediterranean and Africa. Results were successful in showing that zooplankton assemblages changed seasonally in similar ways as predicted by the PEG model. It was found that the seasonality of zooplankton dominance was influenced by factors such as fish predation, food quantity, food quality, and day length. The majority of the PEG model focused on the open-water season and largely assumed winter to be unimportant in the seasonal succession of zooplankton communities. However, following an increased understanding of seasonality, a revised PEG model was published, taking into account the importance of winter (Sommer et al. 2012).

The revised PEG model suggests that an actively overwintering population of zooplankton can alter the seasonal succession of its prey, phytoplankton. Sommer et al. (2012) suggest that overwintering zooplankton biomass may be higher than previously suspected, yet is expected to be lower than peak maxima during the open-water season (Fig 1). Reductions in biomass can be correlated with unfavorable conditions such as a decrease in food quantity and temperature (Hampton et al. 2017). Conversely, evidence suggests that overwintering zooplankton accumulate and store fatty acids and other lipids to overcome times of decreased food abundances (Mariash et al. 2017). Regardless of population sizes, the overwintering zooplankton community is not understood well enough to be deemed inconsequential.

A comprehensive understanding of the zooplankton assemblage is needed in order to begin teasing apart the structure and function of winter food webs. An important question to ask is whether zooplankton community composition within food webs change significantly over seasons or not. To comprehend whether seasonality would change zooplankton community composition over the winter months, the life history of two of the largest groups of crustacean zooplankton, the cladoceran and copepods, are further discussed.

Standard Life Cycle of Suborder Cladocera

Cladocera, model genus *Daphnia* (Fig 2A), reproduce parthenogenetically (asexually) for the majority of the year until interrupted by unfavorable conditions such as decreasing temperatures, shortening photoperiod, or decreased food abundance (Wetzel 2001) (Fig 3). Fertilized eggs, encased in a protective ephippia (Zaffagnini 1987; Fig 3) and termed resting eggs, are the common diapause form that cladoceran take during unfavorable conditions. Emergence from resting eggs coincides with the return of favorable conditions; thus, cladoceran that inactively overwinter do not play a role in the winter food web.

The majority of *Daphnia* spp. follow the PEG model (Sommer et al. 1986) in producing resting eggs; however, the seasonal population dynamics of *Daphnia* are highly variable (Wetzel 2001). Some species are shown to actively overwinter as adults, in low population densities, rather than inactively overwinter as resting eggs (Larsson and Wathne 2006; Mariash et al. 2017; Pijanowska 1990; see Table 1). Understanding which species actively versus inactively overwinter is critical due to active species' contributions to winter food webs. Additionally, actively overwintering species may play a larger role in the seasonal effects that winter imparts on the remainder of the year.

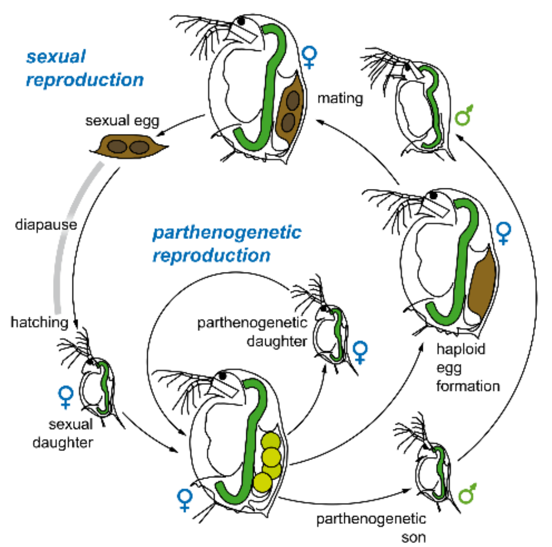

Figure 3. Standard *Daphnia* life cycle. *Daphnia* reproduce parthenogenetically during favorable conditions and resort to sexual reproduction only during times of unfavorable living conditions. Note the encasement of resting eggs within an ephippium.

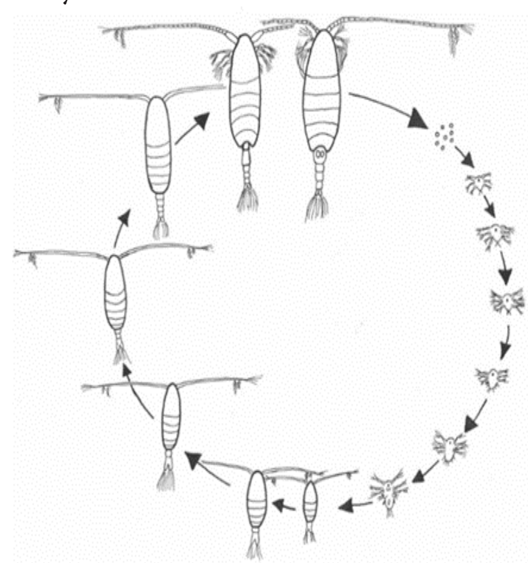

Figure 4. Standard Copepoda life cycle. Eggs grow and molt through six naupliar stages and continue to grow through another six copepodite stages with the last being the adult morph. Retrieved fromhttp://www.st.nfms.noaa.gov/copepod

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Standard Life Cycle of Subclass Copepoda

Like cladocerans, copepods (Fig 2B) can be herbivorous; however, the majority are omnivorous. Unlike cladocerans, copepods reproduce sexually throughout the year. Fertilized eggs hatch into small larvae termed nauplii, which grow in 12 successive stages into an adult copepod (Fig 4). The time required to reach adulthood from fertilized egg varies highly based on seasonal conditions and species (Wetzel 2001). Additionally, there is no a general trend in the seasonal succession of copepods like there is with the PEG model and cladocerans, but rather copepod seasonality varies by species. It is common for the continual cycle of sexual reproduction to be interrupted by a period of diapause (Wetzel 2001). Of note is that a copepod's diapause is not intimately linked with winter conditions, such as decreased temperature or photoperiod, but rather any conditions which are unfavorable to that species. To understand winter zooplankton assemblages, further investigation into which species of copepods actively overwinter as adults is needed.

Methods

Being that this meta-analysis was done independently without collaboration, the scope of the project was small and not comprehensive. Literature was compiled by conducting web searches via Google Scholar and Web of Science using key terms such as: "overwintering zooplankton, zooplankton abundances, freshwater, and zooplankton biomass." Additionally, information was collected from the book copy of *Limnology: Lake and River Ecosystems* by Wetzel (2001). From an original list of possible literature, only those concerning temperate, boreal, or subarctic lakes were considered for this analysis so as to not include lakes that did not differ in abiotic factors between summer and winter. Data was compiled from 21 literature sources published between 1959 and 2017. Sources identified 27 lakes which provided data on actively overwintering zooplankton populations. Data values were extracted from text, tables, or figures. Data collection varied in its preciseness as data provided in text and table format were understandably easier to record than those derived from figures.

Zooplankton abundances (ind L^{-1}), biomass (ug L^{-1}), and taxonomy were primary data being recorded. The methodology for reporting zooplankton data varies greatly between institutions, and thus some calculations had to be made in order to compare results. For example, zooplankton biomass recorded in mm^3 m^{-3} had to be converted to ug L^{-1} by using a mm^3 to gram conversion (Patoine et al. 2006). Additionally, other supporting abiotic variables were collected that included lake size (km^2), maximum lake depth (m), trophic state, and ice cover duration (months). Lakes included in the meta-analysis that were indicated as having zero months of ice cover were either too large to fully freeze or were located near a coast that prevented total freezing.

Data analyses consisted of producing a ratio between summer zooplankton abundance/biomass and winter zooplankton abundance/biomass termed winter/summer ratio (w/s ratio). The w/s ratio was produced using a scatter plot with the R^2 value representing the ratio value. A w/s ratio value of 1 implied identical abundance/biomass between summer and winter, while values less than 1 implied that winter abundances/biomass were less than that of summer. This ratio was then related to the four abiotic factors taken into consideration (lake size, depth, trophic state, and ice cover duration) and correlated with another R^2 value to determine causal factors. These four abiotic factors were included in this analysis because of their combined effects on pelagic zooplankton populations. Trophic state and ice cover duration can dictate the amount of algae available to zooplankton throughout the winter. Similarly, lake size and depth define the area where zooplankton can live within a lake that is safe from predators. Finally, averages for the w/s ratio, summer abundance, and winter abundance were compared between trophic state using a simple bar graph.

To make special note, organisms reported in incomparable units are exempt from data analyses. Additionally, without a proper way of displaying their positive valued w/s ratios, organisms with higher winter values than summer values were also not included in data analyses.

Results

Results indicate that both cladoceran and copepod species actively overwinter as adults in some lakes. Additionally, taxonomic data suggest that overwintering is not a trait of a single species but occurs within multiple species and genera. However, as predicted by Sommer et al. (2012), zooplankton assemblages are found to be less abundant in winter than in summer (Table 1). Associated abiotic results are displayed in Table 2. Figure 5 shows that the summer abundance explains 24% (R^2=0.2407) of winter abundance while summer biomass explains 49% (R^2=0.4924).

Lake size was shown to have very little effect on the w/s ratio based upon abundance (R^2=0.1236) (Fig 6). Winter abundance was highest in mesotrophic lakes while summer abundance increased between oligotrophic to eutrophic lakes. However, the highest average W/S ratio based on abundance was reached in oligotrophic lakes (Fig 7). Additionally, the highest average w/s ratio based on biomass was reached in mesotrophic lakes, yet the average ratio was nearly the same across trophic states (Fig 8).

Certain analyses resulted in R^2 values which were deemed insignificant (R^2<0.100) in correlation with the dependent variable. These included: w/s ratios versus lake size, maximum lake depth, and ice cover.

Based on the inherent variability between researchers' familiarity with zooplankton, published data were reported in species, genera, or higher taxonomic orders. Of the 33 reported zooplankton taxonomies, 9 were copepods ranging from species to subclass. Of the copepods reported, three species were actually identified as having higher overwintering adults than in summer. These copepods were: *Eudiaptomus graciloides* (Rautio et al. 2000), *Cyclops strenuus strenuous* (Elgmork 1959), and *Cyclops strenuus abyssorum* (Smyly 1973). The remainder of the data were cladocerans with the majority being of the genus *Daphnia*. A few species of *Daphnia* were often represented in the literature survey; however, this may not be indicative of dominance but rather sampling bias.

Table 1. Taxa with both winter and summer abundance and biomass. Values expressed as a ratio of winter to summer. Abiotic factors related to these taxa are found in Table 2, assorted by reference.

Taxonomy	Winter Abundance (ind L^{-1})	Summer Abundance (ind L^{-1})	Ratio winter/summer	Winter Biomass (ug L^{-1})	Summer Biomass (ug L^{-1})	Ratio winter/summer	Reference
Bosmina	0.5	0.7	0.71				Straile and Adrian (2000)
Bosmina	0.5	0.7	0.71				Straile and Adrian (2000)
Cladoceran				50	86.25	0.58	Jeppesen et al. (1999)
Cladoceran				60	301.5	0.20	Jeppesen et al. (1999)
Cladoceran				90	395.1	0.23	Jeppesen et al. (1999)
Copepods	13	17	0.76				Dokulil et al. (1990)
Copepods				80	138	0.58	Jeppesen et al. (1999)
Copepods				136	683.4	0.20	Jeppesen et al. (1999)
Copepods				50	219.5	0.23	Jeppesen et al. (1999)
Cyclops strenuus abyssorum	7 (ind m^{-2})	0 (ind m^{-2})	10.00				Smyly W (1973)
Cyclops strenuus strenuus	270	0	10.00				Elgmork K (1959)
D. catawba				22 (ug cm^{-2})	86 (ug cm^{-2})	0.26	Makarewicz JC, Likens GE (1979)
D. cucculata	1	16	0.06				Pijanowska (1990)
D. cucculata	5	30	0.17				Pijanowska (1990)
D. cucullata	0.7	4.3	0.15				Vijverberg and Richter (1982)
D. galeata	1	25	0.04				Carvalho and Kirika (2003)
D. galeata				34.65	374.85	0.09	Ulrich (1997); Horn (2003)
D. galeata mendotae	10	43.5	0.23				Hall DJ (1964)
D. hyalina	1.3	87.7	0.02				Vijverberg and Richter (1982)
D. hyalina	Numbers not available						Benndorf (1995); Kothe et al. (1997)
D. hyalina var lacustris	3	45	0.07				George DG, Hewitt DP (1999)
D. hyalina x galeata				40000 (ug m^{-1})	100000(ug m^{-1})	0.40	Simcic and Brancelj (2001)
D. pulicaria	0.75	24.75	0.03				Edmondson WT & Litt AH (1982)
D. pulicaria	6	25	0.24				DeStasio et al. (1995, 1996); Vavrus et al. (1996)
D. umbra	2	9	0.22				Larsson P, Wathne I. 2006
D. umbra	0.02	0.04	0.50				Mariash H, Cusson M, Rautio M (2017)
D. umbra	0.02	0.04	0.50				Mariash H, Cusson M, Rautio M (2017)
Daphnia	4	12	0.33				Dokulil et al. (1990)
Daphnia	0.6	0.75	0.80				Straile and Adrian (2000)
Daphnia	0.6	0.75	0.80				Straile and Adrian (2000)
Eudiaptomus gracilis	4.5	45	0.10				George DG, Hewitt DP (1999)
Eudiaptomus graciloides	900	50	18.00				Rautio M, Sorvari S, Korhola A. 2000
Leptodiaptomus ashlandi	3	10	0.30				Winder M, Schindler DE, Essington TE, Litt AH. 2009

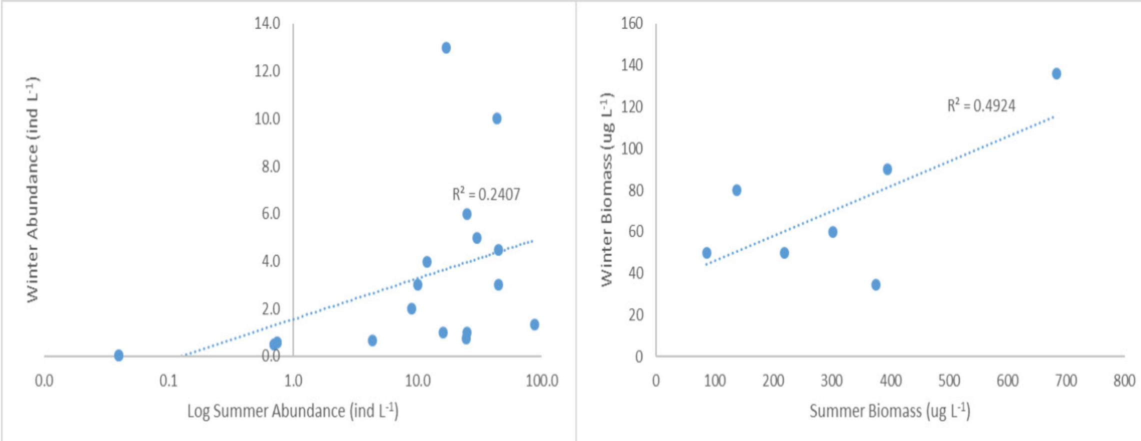

Figure 5. Winter and summer zooplankton abundances and biomasses. Values of summer abundance (left panel) are in log form.

Table 2. Abiotic factors associated with taxa in Table 1. Assorted by reference, this table provides contextual information to the lakes mentioned in Table 1.

Reference	Lake Name	Trophic State	Lake Size (km^2)	Max Lake Depth (m)	Ice Cover (months)
Benndorf (1995); Kothe et al. (1997)	Bautzen Reservoir	Hypertrophic	5.3	12	3
Carvalho and Kirika (2003)	Loch Leven	Eutrophic	13.3	25	0
DeStasio et al. (1995, 1996); Vavrus et al. (1996)	Lake Mendota	Eutrophic	39.4	25.3	4
Dokulil et al. (1990)	Mondsee	Mesotrophic	14	68	1
Dokulil et al. (1990)	Mondsee	Mesotrophic	14	68	1
Edmondson WT & Litt AH (1982)	Lake Washington	Eutrophic	88	65	0
Elgmork K (1959)	Bergstjern	Eutrophic	7.80E-03	5	N/A
George DG, Hewitt DP (1999)	Esthwaite Water	Eutrophic	1	21	0
George DG, Hewitt DP (1999)	Esthwaite Water	Eutrophic	1	21	0
Hall DJ (1964)	Baseline Lake	Oligotrophic	1.03	19.5	3
Jeppesen et al. (1999)	Damhussøen	Mesotrophic	0.48	4	0
Jeppesen et al. (1999)	Lake Hinge	Eutrophic	0.98	5	0
Jeppesen et al. (1999)	Lake Røgbølle	Mesotrophic	1.97	4	0
Jeppesen et al. (1999)	Damhussøen	Mesotrophic	0.48	4	0
Jeppesen et al. (1999)	Lake Hinge	Eutrophic	0.98	5	0
Jeppesen et al. (1999)	Lake Røgbølle	Mesotrophic	1.97	4	0
Larsson P, Wathne I. 2006	Stasjonsdammen	Oligotrophic	1.96E-03	3.3	8
Makarewicz JC, Likens GE (1979)	Mirror Lake	Oligotrophic	1.53	11	4
Mariash H, Cusson M, Rautio M (2017)	Malla South	Oligotrophic	7.85E-03	3	9
Mariash H, Cusson M, Rautio M (2017)	Saanajärvi	Oligotrophic	0.7	24	8
Pijanowska (1990)	Lake Mikolajskie	Eutrophic	4.6	27.8	3.5
Pijanowska (1990)	Lake Majcz	Mesotrophic	1.64	16.4	3.5
Rautio M, Sorvari S, Korhola A. 2000	Lake Saanajärvi	Ultraoligotrophic	0.62	24	8
Simcic and Brancelj (2001)	Lake Bled	Eutrophic	1.44	30.2	0
Smyly W (1973)	Buttermere	Oligotrophic	0.94	24	0
Straile and Adrian (2000)	Lake Constance	Oligotrophic	473	253	0
Straile and Adrian (2000)	Muggelsee	Eutrophic	7.3	8	1.5
Straile and Adrian (2000)	Lake Constance	Oligotrophic	473	253	0
Straile and Adrian (2000)	Muggelsee	Eutrophic	7.3	8	1.5
Ulrich (1997); Horn (2003)	Saidenbach Reservoir	Mesotrophic	1.46	48	4
Vijverberg and Richter (1982)	Lake Tjeukemeer	Eutrophic	21	5	1
Vijverberg and Richter (1982)	Lake Tjeukemeer	Eutrophic	21	5	1
Winder M, Schindler DE, Essington TE, Litt AH. 2009	Lake Washington	Eutrophic	88	65	0

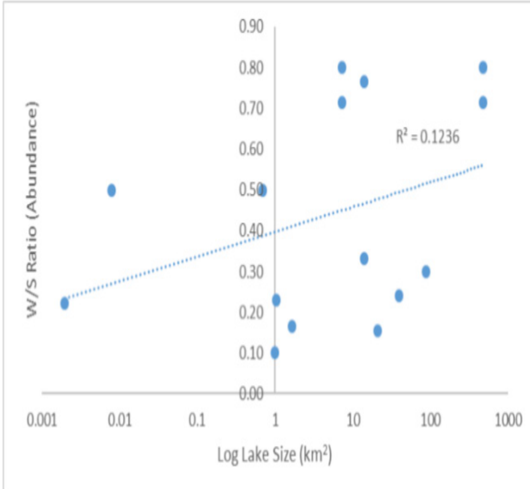

Figure6. Wintertosummerratiobasedonabundance versus the log lake size. Higher w/s ratios indicate a winter zooplankton population that is more similar to the summer zooplankton population.

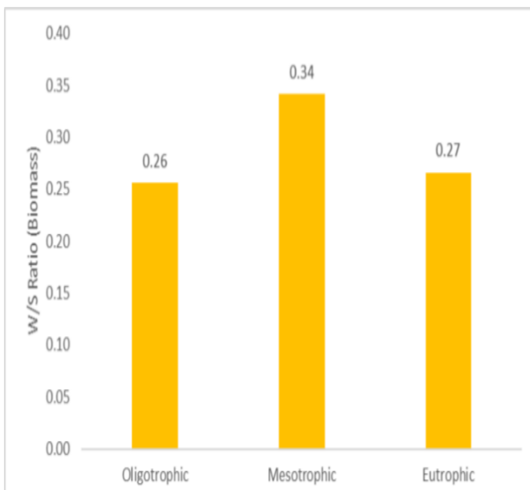

Figure 8. Mean winter to summer ratio of biomass versus the trophic state of lakes.

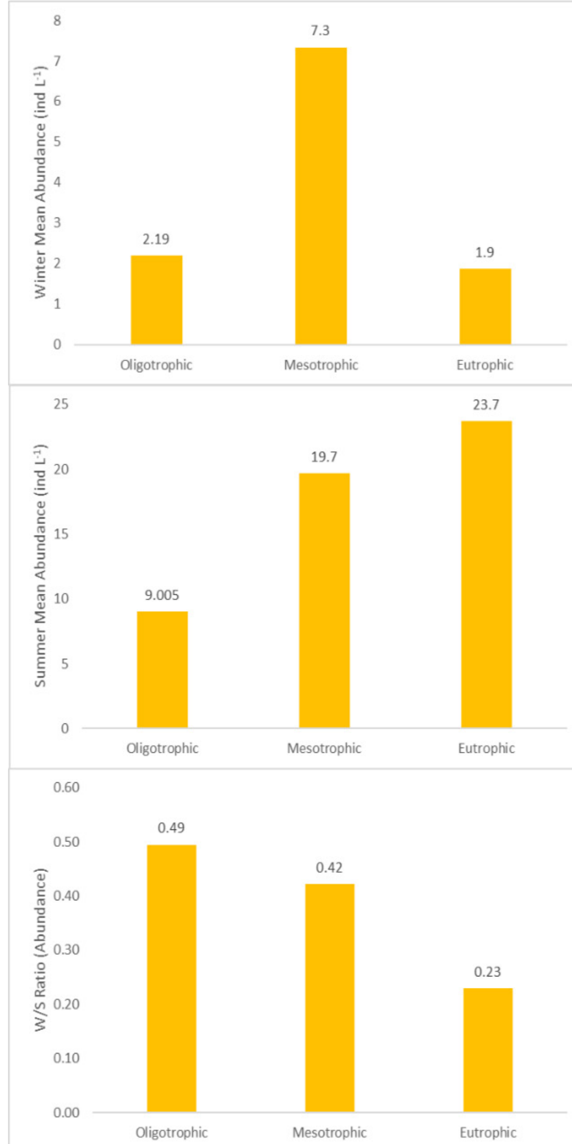

Figure 7. Winter mean abundance, summer mean abundance, and mean winter to summer ratio versus trophic state of lakes.

CONCLUSION

Evidence for this meta-analysis, collected from the literature, suggests that cladoceran and copepod zooplankton sometimes actively overwinter as adults in freshwater lakes. Results also indicate that these populations are much smaller than those during the summer months, supporting the claim made by Sommer et al. (2012). Data collected seems to indicate that lake size may have a small effect on the presence of winter zooplankton populations. Conversely, the data collected during this meta-analysis did not indicate a relationship between ice cover or depth and the size of winter populations. However, it should be emphasized that a relatively small sample size was used in this meta-analysis. The abiotic factors currently included in this meta-analysis do not show any causation for the size of overwintering zooplankton populations; however, the data present is limiting and other abiotic factors should be included in the future, such as: lake temperature, elevation, and nutrients. Research done by Hampton et al. (2017) collected data on abiotic factors both in summer and winter and correlated them similarly as what was done in the present meta-analysis.

The results of this meta-analysis are consistent with the understanding that overwintering zooplankton abundances are reduced in comparison with summer abundances due to more unfavorable conditions. Regardless, however small the zooplankton populations are in a lake during the winter months, a food web must still exist because of actively overwintering zooplankton populations. Additionally, the current results indicate that there may be copepod species that have life histories which are adapted to the winter, and are more abundant during that time than in summer (Elgmork 1959; Smyly 1973; Rautio et al. 2000).

Thus, questions arise as to whether food webs are identical throughout seasons or whether they shift to incorporate different species or other taxonomic groups altogether. Similar questions arise over the ideas of dominance when more than one species of zooplankton actively overwinters. Linking zooplankton assemblages into the larger aquatic food web is not a simple task; however, this link is vital for understanding the under-ice ecosystem of temperate lakes, because temperate lakes are ice covered for a significant portion of the year (2-9 months), and this time period cannot be neglected.

Future studies should fully investigate overwintering zooplankton and their role within an ecosystem. To do so, zooplankton densities and abundances should be correlated with densities and abundances of food prey. Additionally, it should be considered that overwintering zooplankton species may not remain dominant throughout the entire winter and may change seasonally as suggested by the PEG model (Sommer et al. 2012). Finally, the role of overwintering zooplankton on the spring and summer zooplankton community structure should be considered. Ultimately, determining what occurs during the winter will finally produce a comprehensive understanding of what really happens within a lake throughout the year.

Acknowledgments

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Biography

I recently graduated from the University of Minnesota Duluth with a B.S. in Biology. I will be attending the University of Vermont in Fall 2017 to pursue a Ph.D. in Biology. Research topics I am primarily interested in focus around the lake ecosystem level. Large scale questions I focus on include: How trophic levels interact with one another, how food webs are constructed and vary with seasonality, and how lake ecosystems will respond to climate change. Specifically, I am interested in seasonality and how food webs change as the seasons change. I will conduct the majority of my research during the winter months to compare and contrast changes that occur in food web structure, predator-prey interactions, animal behavior and more, between summer and winter months.

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