The growth, diet, and consumption of a lentic caddisfly, *Nectopsyche albida*, in Coeur d'Alene Lake, Idaho

A Thesis
Presented in Partial Fulfillment of the Requirements for the
Degree of Master of Science
with a
Major in Natural Resources
in the
College of Graduate Studies
University of Idaho

by
Stephanie E. Estell

Major Professor: Frank Wilhelm, Ph.D.
Committee Members: Ben Scofield; Janet Rachlow, Ph.D.
Department Administrator: Lisette Waits, Ph.D.

May 2019

Authorization to Submit Thesis

This thesis of Stephanie E. Estell, submitted for the degree of Master of Science with a Major in Natural Resources and titled "The growth, diet, and consumption of a lentic caddisfly, *Nectopsyche albida*, in Coeur d'Alene Lake, Idaho" has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

Major Professor: _____ Date:
Frank Wilhelm, Ph.D.

Committee Members: _____ Date:
Ben Scofield

_____ Date:
Janet Rachlow, Ph.D.

Department Administrator: _____ Date:
Lisette Waits, Ph.D.

Abstract

Understanding the role of an invasive species and its interactions with native species can be difficult. Invasive Eurasian milfoil (*Myriophyllum spicatum*) has become established in the southern end of Coeur d'Alene Lake, also known as Chatcolet Lake, Idaho, and has become a nuisance for lake managers and the public. Managers with the Coeur d'Alene Tribe have observed herbivory damage to the milfoil and to native macrophyte species, but the cause is unknown. Larvae of *Nectopsyche albida*, a native caddisfly, have been observed concurrently with herbivory. To uncover is there is a possible connection, I conducted three studies; life history development, diet characterization using stable carbon and nitrogen isotopes, and feeding rate and preference trials of *N. albida* larvae. Overall, the results reveal that caddisfly larvae are univoltine, with adult emergence and a new generation hatching in mid-summer, though the timing is temperature-dependent. The larvae progress through five instars, and they consume mainly macrophytes with no clear preference. The larvae also use macrophytes to build their cases. I conclude that the caddisflies contribute to the observed herbivory damage of macrophytes. However, because *N. albida* larvae do not appear to target any specific macrophyte species and the timing of their life cycle poorly matches that of the onset of plant growth, they are unlikely to be effective controls of macrophytes in Chatcolet Lake.

Acknowledgements

The production of this thesis would not have been possible without the collaboration of numerous individuals. The project described was partially supported by NSF award number IIA-1301792 from the NSF Idaho EPSCoR Program and by the National Science Foundation. I thank my co-advisor Ben Scofield, as not only did he provide the necessary assistance for my field work, but he also provided me with guidance, support, and respect as both a colleague and as a mentor. I also thank the entire Coeur d'Alene Tribe for allowing me to partner with them and sample their land and resources for this project. I thank Janet Rachlow for serving on my committee. I also thank Ben Harlow with the Washington State University Isotope Core Laboratory, as he analyzed my isotope samples and taught me to prepare them in his laboratory. I thank the Clearwater Fly Casters for awarding me their annual scholarship in 2018, which funded my isotope analysis and allowed me to produce my third chapter. Lastly and most of all, I thank my major professor and mentor Dr. Frank Wilhelm, without whom this thesis would not exist. He has made me a better writer, student, and scientist. Frank approaches science with careful consideration, genuine passion, and enthusiasm, and his level of effort and diligence has become that to which I aspire.

Dedication

I have received endless support from many family members and friends, and I thank each of them for their help in getting me to this point. Randi Notte has been extraordinarily kind, selfless, and supportive during our time in graduate school, and I would not have made it through without her. Thank you to Sarah Burnet for her guidance, support, and friendship through this process. Much of my success in completing this document can be traced back to them. Nicholas Clayton has every day given me the love, support, and sanity I have needed to finish this degree, and I am enormously grateful to him for standing next to me throughout this journey. Lastly, I thank and dedicate this thesis to my parents, Edward and Donna Estell. They have always been my most emphatic and loving supporters, and I would not have arrived here without them. Thank you both for your boundless love and belief in me.

Table of Contents

List of Tables

List of Figures

Chapter 1: General Introduction

Globalization has created an unprecedented culture of commerce, trade, and travel. Like never before in history, humans are leaving their homes, their countries, and even their continents to experience exotic places. In these pursuits of business and recreation, people are not only exposed to other ways of life, but also other forms of life. Organisms native to various areas of the world have become hitchhikers, unknowingly exploiting the movements of humans, resulting in range expansions, and in the worst case, invasions. When these organisms complete the journey in sufficient numbers and find a suitable environment (food, shelter, lack of predators and diseases) in which they establish flourishing populations, they become classified as invasive species. Currently it is estimated that invasive species are the second largest cause of endangerment and extinction of species (Lowe et al. 2000; Akter and Zuberi 2009). Biological invasions occur in all types of ecosystems worldwide.

Invasive species are damaging to native species for numerous reasons, and themes exist across all categories of invasive species. According to the list of '100 of the World's Most Invasive Alien Species in 2000' (Lowe et al. 2000), about 20% of the worst invasions (based on impact on local biodiversity, on humans, and how the species illustrates a biological invasion) were by aquatic species. Aquatic invasive species, just like their terrestrial counterparts, can disrupt entire ecosystems with their presence and interactions with the environment, through both biotic and abiotic means. Alterations include changing species composition, changing nutrient cycles, and reducing or preventing recreation in a water body (Pimentel et al. 2005). Nonnative fishes and nonnative fish prey have historically been added to systems to diversify fisheries in hopes of increasing production, but the species become invasive with unintended/unforeseen cascading consequences (Spencer and Ksander 1999). For example, the introduction of Lake trout in Flathead Lake, MT, USA, changed the trophic cascade and species composition of the entire lake food web (Ellis et al. 2011). Along the US coast and especially in the Great Lakes, ballast water from ships has been a route for invasive species into North America's freshwater (Ricciardi and MacIsaac 2000).

Other invasions have occurred through the escape of species specifically brought to the US to solve a specific problem. For example, Asian carp (silver [*Hypophthalmichthys*

molitrix], and bighead [*Hypophthalmichthys nobilis*]) were introduced to culture ponds to aid in removal of algae, but likely escaped to the wild during flooding (Nico et al. 2018). Asian carp are herbivores, and large populations in natural waters can decimate the natural phytoplankton communities, leaving few to no algae, which is the typical food for zooplankton and the energy source for much of traditional aquatic food webs (Lougheed et al. 1998). Without phytoplankton as food, zooplankton density decreases, leaving a lack of food for planktivorous fishes (Lougheed et al. 1998), and in turn for piscivorous fishes for which many planktivores serve as prey (Ellis et al. 2011) resulting in a classic trophic cascade (Carpenter et al. 1985) and collapse of food webs. This highlights how the addition of just one fish species can negatively affect an entire lake ecosystem. Establishment of invasive organisms at lower trophic levels can also affect ecosystems. For example, the zebra mussel which is a bivalve that originated in the Baltic but became established in North American lakes, especially the Great Lakes ecosystem, has disrupted the pelagic/benthic flow of energy. Because they are attached filter feeders, they remove algae from the pelagic zone and egest pseudofeces that drop to the benthos, diminishing the abundance of the algae and therefore the food source for other pelagic organisms, but increasing the energy available to the benthic community. This shift in available energy is known as the benthic-pelagic shunt (Hecky et al. 2004). This flow of resources results not only in changes in the availability of algae, but also reduces the amount of photosynthesis occurring in the water body. Oxygen abundance decreases when algae are removed, and the location of nutrients in the water changes. Nutrient movement also occurs due to the structure of the mussels themselves (Strayer et al. 1999). To grow, zebra mussels sequester calcium from the water column into their shells, causing calcium to become unavailable to other organisms. When the mussels die, the calcium returns to the system, but the return is concentrated in the benthos and not readily available in dissolved form until the shell is remineralized.

Myriophyllum

The genus *Myriophyllum* encompasses numerous species, and Eurasian milfoil (*M. spicatum*) and Northern milfoil (*M. sibiricum*) are included in this genus. Northern milfoil is native to the US Pacific Northwest as well as many other areas across North America (Pfingsten et al. 2018). Eurasian milfoil is thought to have entered the United States at least by the 1950s (Smith and Barko 1990) from Eurasia, but was possibly present in the US

toward the end of the 19th century (Grace and Wetzel 1978). Fragments of *M. spicatum* are thought to have spread over short distances by way of boats when boats and trailers were transferred between lakes (Nichols and Shaw 1986). Due to the need for sunlight, *M. spicatum* can only survive in the photic zone, up to a depth of approximately 7 meters in very clear lakes (Aiken et al. 1979). Reproduction occurs by seed production after flowering and by fragmentation of the plant; the latter being the more successful method (Aiken et al. 1979). Fragmentation is also what makes it so potent if a strand is left on a boat or trailer and reaches another water body. Both auto-fragmentation and fragmentation from disturbance result in new plants from nodes (Pfingsten et al. 2018). Due to its ability to fragment, fix inorganic carbon, as well as numerous other physiological factors such as fast growth rate and tolerance of deep littoral zones, *M. spicatum* is a highly successful colonizer (Grace and Wetzel 1978). Though the plant dies back in the fall and winter, the root mass in the sediment remains active and begins to re-grow shoots in spring. Growth is temperature-dependent starting at about 15 °C (Pfingsten et al. 2018). During the growing season, growth is rapid, and *Myriophyllum* biomass can quickly become a nuisance. In addition to its fast growth rate, Eurasian milfoil is able to adapt in other ways. For example, it is now known that the Eurasian and the native Northern milfoil hybridize (Thum 2017). The hybrid is not easily distinguished in the field due to combined morphological characteristics from both parent species (Sturtevant et al. 2009). The hybrid (*Myriophyllum spicatum* × *Myriophyllum sibiricum*, referred to as *Myriophyllum* or milfoil from this point forward), because it is formed by two species of *Myriophyllum*, exhibits similar reproductive and life history strategies, and is therefore treated similarly to *M. spicatum* (Sturtevant et al. 2009).

Invasive species control

Pimentel et al. (2005) estimated that in 2005, approximately $100 million dollars was spent in the United States to remove invasive aquatic species, with the cost expected to increase as more species introductions have occurred since then. To combat the numerous problems caused by invasive macrophytes, various control techniques are available. Because of the high cost of removing or reducing invasive species, preventing their establishment is the first priority of any management plan. If prevention is not a viable option, other management strategies can be used to attempt to control the abundance of an invasive species. For example, macrophyte biomass can be controlled via several physical means.

Divers can hand-pull macrophytes from the substrate (MAISRC 2015). The benefits of this strategy include a thorough removal of the plants and a low chance of the plants being fragmented. As well, the divers can target only the invasive species and leave native macrophytes intact. Habitat disturbance using divers is low. However, the time requirement for this work makes it expensive (Shaw et al. 2016). Aquatic plant harvesters can also be used to remove macrophytes. The general concept is that a harvester is driven into the water, blades attached to the frame cut the macrophytes underwater, and a conveyor belt carries the cut macrophyte pieces into a hopper, or boat where they are collected for removal from the water body (Klein 1997). Biomass is removed quickly and in large amounts using a harvester, while the personnel required is low. However, harvesters are indiscriminate and remove all plants in their path, and plants are cut at or above the substrate leaving the root system intact, thus allowing the plants to re-grow. In addition, the fragmentation or loss of plant material from the activities can be high, providing a route for new plants to establish via vegetative regeneration. Furthermore, the overall macrophyte bed is highly disturbed by the process (MAISRC 2015). Thus, this method is generally employed when the reduction of overall biomass of aquatic macrophytes is the desired endpoint.

Shade cloth is another management strategy and involves placing an opaque cloth over the substrate to block sunlight to prevent new shoots from photosynthesizing, causing them to die (Cooke 1980). Using shade cloth prevents the plants from fragmenting and reproducing due to the precision installation. However, it too is indiscriminate because the sunlight blocked by the cloth is blocked for all species, so invasive species may not be the only casualty in this process; native macrophytes and other members of the benthic community are at risk in the areas where this method is used. In addition, the installation of shade cloth usually requires the use of divers, making it expensive and limiting the size of each cloth panel because it must be managed underwater by the divers (MAISRC 2015).

The application of herbicides is one of the most commonly used methods to control invasive macrophytes (MAISRC 2015). Similar to other control methods, this strategy also has advantages and disadvantages. Chemicals have been engineered to target specific species, allowing managers to target specific species (MAISRC 2015). Both liquid and pellet forms of herbicides are available, and effects to the rest of the biota in the water column are

sufficiently few or low for many managers to justify their application. When used in water bodies, permits are required prior to application (Swistock 2008). Application of herbicides also requires some manual labor, specialized application equipment, as well as the effort to travel around the water body, either by watercraft or on foot depending how the infestation can be reached. However, once the treatment is applied there is little post-treatment work, except monitoring. The addition of chemicals to a freshwater system is not ideal, however small the effects on biota other than the target species are. With the marginal success rates of herbicide treatment on some species in some systems (Hofstra and Clayton 2001; Poovey et al. 2007; Richardson 2008), alternatives are desirable. Aquatic weed control using herbicides can also be expensive, in part due to necessary annual or even seasonal reapplication.

In some cases, use of a biocontrol exists as an option to manage invasive macrophytes (Sheldon and Creed 1995; Newman and Biesboer 2000; Carlsson and Brönmark 2006; Gassmann et al. 2006). Biocontrol, the use of other biota to control an unwanted target species, as a management practice is not a new concept and examples of this technique reach back decades (DeBach 1964). For example, much of the research of biocontrols has focused on protecting terrestrial crops from harmful insects (Meehan et al. 2012; Skevas et al. 2014). However, the reverse can be beneficial as well. Insects can be used to reduce or regulate undesirable or harmful plant species. In the case of *M. spicatum*, much of the biocontrol research has been focused on two species: an aquatic weevil native to North America and a species of aquatic moth (Johnson et al. 2000; Gross et al. 2001). In the case of the weevil, *Euhrychiopsis lecontei*, adults lay eggs on the meristem of a Eurasian milfoil plant, and once they hatch, the larvae burrow into it, damaging the plant by eating the cortex and remaining within the stem throughout the pupal stage (Mazzei et al. 1999). Weevils have been shown to damage milfoil in both laboratory and the field (Mazzei et al. 1999; Jester et al. 2000). When exposed to populations of *E. lecontei*, milfoil populations were damaged and did not recover to their previous dominance, even through fluctuations in weevil abundance (Sheldon 1997). Though milfoil weevils have been found in Coeur d'Alene Lake, Idaho, their population is not currently sufficiently dense to be considered as a suitable management tool (Creed 1998; Ward and Newman 2006). *Acentria ephemerella*, a moth with an aquatic larval stage, has been shown to congregate on the apical meristems of Eurasian milfoil, damaging the plant and therefore reducing its abundance in certain systems (Johnson et al. 2000). Timing of

lifecycle stages of both the moth and the milfoil are similar, and Johnson et al. (1998) found that herbivory of the milfoil by the moth occurred more frequently than herbivory on other macrophytes, resulting in a decline in milfoil abundance and an increase in the abundance of native macrophytes with no change in overall plant biomass. In laboratory experiments, *Acentria ephemerella* preferred *M. spicatum* over the native *Elodea* (Gross et al. 2001), which may be what caused a shift from milfoil to *Elodea* dominance in Cayuga Lake, New York. Though research on the relationship between *A. ephemerella* and *M. spicatum* is promising as a biocontrol technique, like the milfoil, the moth is originally an invasive species from Eurasia, so introducing moths into North American waterways where they are not already present could be counterproductive to the goals of conservation. Because these species are not generally established in lakes in the Pacific Northwest, their viability as a biocontrol may be limited, and the reach and pervasiveness of Eurasian milfoil continues to cause problems in freshwater ecosystems.

Reports of how quickly *M. spicatum* was spread across the country vary, but the current distribution of *M. spicatum* is cosmopolitan and widespread throughout North America, and it can be found in many freshwater aquatic systems, both lotic and lentic (Aiken et al. 1979). Forty-eight states have documented cases of *M. spicatum*, and only Hawaii and Wyoming have not officially reported any discoveries (Pfingsten et al. 2018). In northern Idaho, Lake Pend Oreille was reported to contain Eurasian milfoil in 1998, and the plant has spread widely from there (Pfingsten et al. 2018). The hybrid milfoil has also been found in the state (Sturtevant et al. 2009). In Coeur d'Alene Lake, intense plant management regimes, high levels of boat activity, high water clarity, and shallow nearshore depths create ideal habitat for *M. spicatum* throughout the lake. However, due to the coexistence of both Northern milfoil and Eurasian milfoil, the hybrid *Myriophyllum* spp. has been found and confirmed throughout Coeur d'Alene Lake (Thum 2017). Collection and genetic analysis of milfoil in 2015 and 2017 showed that the hybrid composed about 60% of milfoil samples in 2015 and increased to about 76% of milfoil samples in 2017 (Thum 2017). Though the conditions in many parts of the lake are suitable for milfoil, in some areas the plants are severely damaged, including in the Chatcolet Lake area. The damage is not limited to milfoil, but also includes the native *Elodea canadensis* and other native macrophytes. Leaves have been stripped from the stems in large patches of both plants. Damage is not observed in all

parts of the lake or all patches of the plants, so I hypothesize that herbivory of milfoil and *Elodea* is occurring in these areas where plants are damaged. Due to the abundance of the caddisfly *Nectopsyche albida* within the patches of the damaged plants, I hypothesize the *N. albida* larvae contribute, at least partially, to the observed damage via herbivory.

Caddisflies

Caddisflies are important in the transfer of energy between trophic levels in freshwater ecosystems (Wiggins 1977). Some caddisfly species can serve as indicators of water quality and ecosystem health (Wiggins 1977; Barbour et al. 1999). Based on phylogeny, caddisflies that reside in warm, lentic water bodies are genera with derived traits (Ross 1956; Wiggins 1977). The case-making styles and strategies throughout the order Trichoptera are exceptionally diverse, which is in part due to the development of caddisfly silk (analogous to that of terrestrial spiders) that allows the caddisflies to diversify their behavior (Wiggins 1977). The tube-shaped caddisfly case is a common design, particularly among genera in lentic systems (Wiggins 1977). This case design is thought to increase respiratory efficiency by funneling water into the anterior end and out the posterior end, which is supported by the structure of their abdomen; humps on the caddisfly abdomen are thought to give extra space between the body and the case to allow the flow of oxygenated water (Wiggins 1977). Given their large size and relative conspicuousness, they are a favorite food item in the diet of fish, and because most are generalist herbivores, they serve as an intermediate in the transfer of energy.

The genus *Nectopsyche* is one of eight genera in the family Leptoceridae in the order Trichoptera. Formerly known as the genus *Leptocella*, *Nectopsyche* was established by Flint in 1974 (Glover and Floyd 2004). Fifty-seven species have been described within *Nectopsyche* (Holzenthal 1996). Though the individual species are somewhat restricted in their distribution, the genus occurs from North America through Central and South America (Holzenthal 1996), and both the Nearctic and Neotropical regions are represented (Glover and Floyd 2004). The genus typically is found in lentic or slow lotic freshwaters in the New World (Oláh and Oláh Jr. 2017) in weedy, vegetated areas (Haddock 1977). As of 2004, 15 species were described in North America (Glover and Floyd 2004). Microhabitats of the larvae are thought to be determined by where they hatch from eggs, and are thus determined

by where the adult female lays eggs (Haddock 1977). Characteristics of a suitable place to lay eggs include slow water current, an abundance of vegetation, proximity to shore and water surface, and availability of sunlight (Haddock 1977; Tozer et al. 1980). Females tend to choose areas shallow enough for abundant macrophyte growth, but lay their eggs in water away from the shoreline (Tozer et al. 1980). Once the eggs hatch and the larvae mature, they incrementally move closer to shore as they approach their final instar and prepare to pupate (Tozer et al. 1980).

Nectopsyche larvae build cases around their bodies out of convenient materials ranging from particulate substrate to plant matter and is dependent on the microhabitat in which they live (Haddock 1977). Cases taper from a large opening at the anterior end to a small opening at the posterior end (Holzenthal 1996, Chapter 2 figure 2.8). Tapering at the posterior end is thought to be an adaptation to reduce drag from water current while the caddisflies swim and feed on vegetation (Haddock 1977). Case construction may also be influenced by the changes in larval size throughout successive life stages. The cases sometimes have twigs, pine needles, or pieces of other material extending out from one or both ends of the case (Glover and Floyd 2004). Like other caddisflies, larvae of *Nectopsyche* function as shredder-herbivores and collector-gatherers (Holzenthal 1996). To feed, the caddisfly first excretes a silk substance from its labial glands to anchor itself to a plant, then uses its legs to collect food and transfer it to the mouth (Haddock 1977). Analysis of gut contents has shown the presence of fine organic particulate matter and the remains of vascular plant material (Glover and Floyd 2004). Some species are free-swimming and have setae on their hind legs to facilitate movement through open water (Holzenthal 1996). All species within *Nectopsyche,* except *N. albida,* have gills on the thorax, abdomen, or both (Haddock 1977). For taxonomic purposes, the number of abdominal segments and the number of gills on each segment can be used to separate species (Haddock 1977). Taxonomically identifying larvae can be difficult, as certain features can change between instars (Wiggins 1977). However, the known characteristics at the genus level about ecology and morphology have generally been applied to the included species (Wiggins 1977).

Study site description

Coeur d'Alene (CDA) Lake is one of the largest in the state of Idaho and is located in the panhandle of the state (Figure 2.1). This lake is central to the Coeur d'Alene Tribe and is the heart of their historic territory and culture. Currently, the Tribe manages the southern third of the lake. Originally, the southern end of Coeur d'Alene Lake was segmented and composed of a series of shallow floodplain lakes including Chatcolet, Round, and Benewah lakes which were connected by the St. Joe River. The lakes are now inundated and connected throughout the year, due to the advent of lake level regulation resulting from the construction of the Post Falls dam on the Spokane River, the outflow of CDA Lake located at the northern end of the lake. Parts of the St. Joe River channel and levees remain in the southern lake, but much of it is now submerged. The remnant levees and channel remain as a loose barrier between Chatcolet and Round lakes, but overall, the former water bodies at the southern end of CDA Lake are inundated and part of the main lake.

Chapter descriptions

Chapter 2 contains the details of the life history and growth analysis. I collected quantitative samples of caddisfly larvae and vegetative biomass from Chatcolet Lake at regular intervals to examine larval development, their density, and the density and diversity of vegetative biomass. I also examined how larval characteristics overlapped with the growth of the macrophytes.

The purpose of chapter 3 was to determine the diet of the caddisflies and to examine the probability that the larvae contribute to the herbivory seen on macrophytes in Chatcolet Lake. I used analysis of stable carbon (C) and nitrogen (N) isotopes to determine ^{13}C and ^{15}N signatures of macrophytes, other potential food and caddisflies to determine the percent contribution from each to the signature of the larvae.

The purpose of Chapter 4 was to determine the feeding rate and food species preference of *N. albida* larva in laboratory feeding experiments to obtain first estimates of 'how much' plant matter is consumed. I isolated caddisflies in laboratory tanks and fed them pre-massed amounts of different macrophytes in single and choice trials.

I use Chapter 5 as a general discussion of my work, and to place my findings in a larger context. I also discuss the management implications of the results and indicate possible future studies to increase the body of knowledge regarding *Nectopsyche albida* in Coeur d'Alene Lake.

Literature Cited

Aiken, S. G., P. R. Newroth, and I. Wile. 1979. The biology of Canadian weeds. 34. *Myriophyllum spicatum* L. Can. J. Plant Sci. **59**: 201–215.

Akter, A., and M. I. Zuberi. 2009. Invasive alien species in Northern Bangladesh: Identification, inventory and impacts. Int. J. Biodivers. Conserv. **1**: 129–134.

Barbour, M. T., J. Gerritsen, B. D. Snyder, and J. B. Stribling. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: Periphyton, benthic macroinvertebrates and fish, Second. U.S. Environmental Protection Agency.

Carlsson, N. O. L., and C. Brönmark. 2006. Size-dependent effects of an invasive herbivorous snail (*Pomacea canaliculata*) on macrophytes and periphyton in Asian wetlands. Freshw. Biol. **51**: 695–704. doi:10.1111/j.1365-2427.2006.01523.x

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. Bioscience **35**: 634–639. doi:10.2307/1309989

Cooke, G. D. 1980. Covering bottom sediments as a lake restoration technique. Water Resour. Bull. **16**: 921–926. doi:10.1111/j.1752^{-1}688.1980.tb02509.x

Creed, R.P., 1998. A biogeographic perspective on Eurasian watermilfoil declines: additional evidence for the role of herbivorous weevils in promoting declines. Journal of Aquatic Plant Management **36**: 16-22.

DeBach, P. 1964. Biological control of insect pests and weeds, P. DeBach [ed.]. Reinhold Pub. Corp.

Ellis, B. K., J. A. Stanford, D. Goodman, C. P. Stafford, D. L. Gustafson, D. A. Beauchamp, D. W. Chess, J. A. Craft, M. A. Deleray, and B. S. Hansen. 2011. Long-term effects of a trophic cascade in a large lake ecosystem. Proc. Natl. Acad. Sci. **108**: 1070–1075. doi:10.1073/pnas.1013006108

Gassmann, A., M. J. W. Cock, R. Shaw, and H. C. Evans. 2006. The potential for biological control of invasive alien aquatic weeds in Europe: A review. Hydrobiologia **570**: 217–222. doi:10.1007/s10750-006-0182-4

Glover, J. B., and M. A. Floyd. 2004. Larvae of the genus *Nectopsyche* (Trichoptera:Leptoceridae) in eastern North America, including a new species from North Carolina. J. North Am. Benthol. Soc. **23**: 526–541. doi:10.1899/0887-3593(2004)023<0526:lotgnt>2.0.co;2

Grace, J. B., and R. G. Wetzel. 1978. The production biology of watermilfoil (*Myriophyllum spicatum* L.): A review. J. Aquat. Plant Manag. **16**: 1–11.

Gross, E. M., R. L. Johnson, and N. G. Hairston. 2001. Experimental evidence for changes in submersed macrophyte species composition caused by the herbivore *Acentria ephemerella* (Lepidoptera). Oecologia **127**: 105–114. doi:10.1007/s004420000568

Haddock, J. D. 1977. The biosystematics of the caddis fly genus *Nectopsyche* in North America with emphasis on the aquatic stages. Am. Midl. Nat. **98**: 382–421.

Hecky, R. E., R. E. H. Smith, D. R. Barton, S. J. Guildford, W. D. Taylor, M. N. Charlton, and T. Howell. 2004. The nearshore phosphorus shunt: A consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. **61**: 1285–1293. doi:https://doi.org/10.1139/f04-065

Hofstra, D. E., and J. S. Clayton. 2001. Evaluation of selected herbicides for the control of exotic submerged weeds in New Zealand : I . The use of Endothall , Triclopyr and Dichlobenil. J. Aquat. Plant Manag. **39**: 20–24.

Holzenthal, R. W. 1996. Catalog and bibliography of the species of *Nectopsyche* (Trichoptera:Leptoceridae). University of Minnesota.

Jester, L. L., M. A. Bozek, D. R. Helsel, and S. P. Sheldon. 2000. *Euhrychiopsis lecontei* distribution, abundance, and experimental augmentations for Eurasian watermilfoil control in Wisconsin lakes. J. Aquat. Plant Manag. **38**: 88–97.

Johnson, R. L., P. J. Van Dusen, J. A. Toner, and N. G. Hairston Jr. 2000. Eurasian watermilfoil biomass associated with insect herbivores in New York. J. Aquat. Plant Manag. **38**: 82–88.

Johnson, R. L., E. M. Gross, and N. G. Hairston Jr. 1998. Decline of the invasive submersed macrophyte *Myriophyllum spicatum* (Haloragaceae) associated with herbivory by larvae of *Acentria ephemerella* (Lepidoptera). Aquat. Ecol. **31**: 273–282. doi:10.1023/A:1009960131857

Klein, J. 1997. Sediment dredging and macrophyte harvest as lake restoration techniques. Restor. Reclam. Rev. **2**: 1–5.

Lougheed, V. L., B. Crosbie, and P. Chow-Fraser. 1998. Predictions on the effect of common carp (*Cyprinus carpio*) exclusion on water quality, zooplankton, and submergent macrophytes in a Great Lakes wetland. Can. J. Fish. Aquat. Sci **55**: 1189–1197.

Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2000. 100 of the world's worst invasive alien species.

MAISRC. 2015. Eurasian watermilfoil control options. Minnesota Aquat. Invasive Species Res. Cent.

Mazzei, K. C., R. M. Newman, A. Loos, and D. W. Ragsdale. 1999. Developmental rates of the native milfoil weevil, *Euhrychiopsis lecontei*, and damage to Eurasian watermilfoil at constant temperatures. Biol. Control **16**: 139–143. doi:10.1006/bcon.1999.0739

Meehan, T. D., B. P. Werling, D. A. Landis, and C. Gratton. 2012. Pest-suppression potential of midwestern landscapes under contrasting bioenergy scenarios. PLoS One **7**: 1–7. doi:10.1371/journal.pone.0041728

Newman, R. M., and D. D. Biesboer. 2000. A decline of Eurasian watermilfoil in Minnesota associated with the milfoil weevil *Euhrychiopsis lecontei*. J. Aquat. Plant Manag. **38**: 105–111.

Nichols, S. A., and B. H. Shaw. 1986. Ecological life histories of the three aquatic nuisance plants, *Myriophyllum spicatum, Potamogeton crispus* and *Elodea canadensis*. Hydrobiologia **131**: 3–21. doi:10.1007/BF00008319

Nico, L., P. Fuller, and J. Li. 2018. *Hypophthalmichthys nobilis* (Richardson, 1845). U.S. Geol. Surv. Nonindigenous Aquat. Species Database.

Oláh, J., and J. Oláh Jr. 2017. Fine phenomics applied to the *Nectopsyche* genus (Trichoptera): Species delineation by speciation traits. Opusc. Zool. Budapest **48**: 117–184. doi:10.18348/opzool.2017.2.117

Pfingsten, I. A., L. Berent, C. C. Jacono, and M. M. Richerson. 2018. *Myriophyllum spicatum* L.: U.S. Geological Survey, nonindigenous aquatic species database. USGS.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol. Econ. **52**: 273–288. doi:10.1016/j.ecolecon.2004.10.002

Poovey, A. G., J. G. Slade, and M. D. Netherland. 2007. Susceptibility of Eurasian watermilfoil (*Myriophyllum spicatum*) and a milfoil hybrid (*M. spicatum* × *M. sibiricum*) to Triclopyr and 2,4-D Amine. J. Aquat. Plant Manag. **45**: 111–115.

Ricciardi, A., and H. J. MacIsaac. 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. TREE **15**: 62–65.

Richardson, R. J. 2008. No Title. Weed Technol. **22**: 8–15. doi:https://doi.org/10.1614/WT-07-034.1

Ross, H. H. 1956. Evolution and classification of the mountain caddisflies, University of Illinois Press, Urbana. 213pp.

Shaw, D. W. H., Z. P. Hymanson, and T. L. Sasaki. 2016. Physical control of nonindigenous aquatic plants in Emerald Bay, Lake Tahoe, CA. Invasive Plant Sci. Manag. **9**: 138–147. doi:10.1614/ipsm-d-16-00005.1

Sheldon, S. P. 1997. Investigations on the potential use of an aquatic weevil to control Eurasian watermilfoil. Lake Reserv. Manag. **13**: 79–86. doi:10.1080/07438149709354299

Sheldon, S. P., and R. P. Creed. 1995. Use of a native insect as a biological control for an introduced weed. Ecol. Appl. **5**: 1122–1132.

Skevas, T., S. M. Swinton, T. D. Meehan, T. N. Kim, C. Gratton, and A. Egbendewe-Mondzozo. 2014. Integrating agricultural pest biocontrol into forecasts of energy biomass production. Ecol. Econ. **106**: 195–203. doi:10.1016/j.ecolecon.2014.07.027

Smith, C. S., and J. W. Barko. 1990. Ecology of Eurasian watermilfoil. J. Aquat. Plant Manag. **28**: 55–64.

Spencer, D. F., and G. G. Ksander. 1999. Seasonal changes in chemical composition of Eurasian watermilfoil (*Myriophyllum spicatum* L.) and water temperature at two sites in Northern California: Implications for herbivory. J. Aquat. Plant Manag. **37**: 61–66.

Strayer, D. L., N. F. Caraco, J. J. Cole, S. Findlay, and M. L. Pace. 1999. Transformation of freshwater ecosystems by bivalves. Bioscience **49**: 19–27.

Sturtevant, A. P., N. Hatley, G. D. Pullman, R. Sheick, D. Shorez, A. Bordine, R. Mausolf, A. Lewis, R. Sutter, and A. Mortimer. 2009. Molecular characterization of Eurasian watermilfoil, northern milfoil, and the invasive interspecific hybrid in Michigan lakes. J. Aquat. Plant Manag. **47**: 128–135.

Swistock, B. 2008. Eurasian water milfoil. Penn State Ext.

Thum, R. A. 2017. Genetic analysis of invasive Eurasian watermilfoil in Idaho waters.

Tozer, W. E., V. H. Resh, and J. O. Solem. 1980. Bionomics and adult behavior of a lentic caddisfly, *Nectopsyche albida* (Walker). Am. Midl. Nat. **106**: 133–144. doi:10.2307/2425143

Ward, D. M., and R. M. Newman. 2006. Fish predation on Eurasian watermilfoil (*Myriophyllum spicatum*) herbivores and indirect effects on macrophytes. Can. J. Fish. Aquat. Sci. **63**: 1049–1057. doi:10.1139/f06-010

Wiggins, G. B. 1977. Larvae of the North American caddisfly genera (Trichoptera), University of Toronto Press, Toronto.

Chapter 2: Life history analysis of *Nectopsyche albida* and its ecological interaction with macrophytes in Chatcolet Lake, Idaho

Abstract

Aquatic invasive species have become widespread nuisances worldwide, including the United States. Eurasian milfoil (*Myriophyllum spicatum*) has become established in Coeur d'Alene Lake, Idaho, where it has hybridized with native northern milfoil (*M. sibiricum*) to create *M.* spp. (*M. spicatum* x *M. sibiricum*). The invasive and hybrid in the southern end of the lake are currently managed by the Coeur d'Alene Tribe. A native caddisfly, *Nectopsyche albida*, has been found in milfoil beds where evidence of herbivory is also observed, indicating a possible connection. I determined the abundance and timing of growth of both species. I also collected *N. albida* larvae to examine the caddisflies' life history over two growing seasons and its occurrence with macrophytes. Macrophyte and caddisfly larval densities were higher in 2017 than in 2018. *Nectopsyche albida's* life cycle is univoltine, pupation occurred in early to mid-summer shortly before emergence, adults laid eggs, and the larvae hatched and grew to terminal head capsule size in approximately two months. Because caddisfly case length increased until pupation, it is highly probable that body size also increased until pupation. While the life cycles of *N. albida* and *Myriophyllum* do overlap, the caddisfly emerges to the adult terrestrial mating stage while milfoil growth begins. Newly hatched caddisflies did not reach a size at which they could negatively influence the abundance of milfoil until mid to late summer. Thus, the caddisflies did not prevent the initial growth of milfoil, but could have contributed to its early demise in fall.

Introduction

Changes in resource availability and distribution can occur when an invasive species enters an established system (Grace and Wetzel 1978). For example, invasive macrophytes can change entire systems once they become established (Johnson et al. 1997). After gaining a foothold in a new system, such plants tend to grow quickly displacing native species via competition (e. g., light shading, nutrient acquisition) (Madsen et al. 1991; Kuehne et al. 2016). A high abundance and biomass of plants creates a situation whereby photosynthesis

during the day can create supersaturated oxygen concentrations in the water column, and anoxia (total lack of oxygen) at night via respiration (Killgore and Hoover 2001; Katsanevakis et al. 2014). This can stress or kill other aquatic biota (Killgore and Hoover 2001; Wetzel 2001). If the macrophyte grows in dense beds of long strands, it can be lethal to humans, as swimmers that become entangled can drown (The Associated Press 2007). One example of an invasive aquatic macrophyte that causes these effects in Idaho is the Eurasian milfoil (*Myriophyllum spicatum*).

Eurasian milfoil

The genus *Myriophyllum* encompasses numerous species and Eurasian milfoil (*M. spicatum*) and Northern milfoil (*M. sibiricum*) are included in this genus. Northern milfoil is native to the US Pacific Northwest as well as many other areas across North America (Pfingsten et al. 2018). Eurasian milfoil is thought to have entered the United States at least by the 1950s (Smith and Barko 1990) from Eurasia, but was possibly present in the US toward the end of the 19th century (Grace and Wetzel 1978). Fragments of *M. spicatum* are thought to have spread over short distances by way of boats when boats and trailers were transferred between lakes (Nichols and Shaw 1986). Due to the need for sunlight, *M. spicatum* can only survive in the photic zone, up to a depth of approximately 7 meters in very clear lakes (Aiken et al. 1979). Reproduction occurs by seed production after flowering and fragmentation of the plant; the latter being the more successful method (Aiken et al. 1979). Fragmentation is what makes it so potent if a strand is left on a boat or trailer and transported to another water body. Both auto-fragmentation and fragmentation from disturbance can result in new plants from nodes (Pfingsten et al. 2018). Due to its ability to fragment, fix inorganic carbon, as well as numerous other physiological factors such as fast growth rate and tolerance of deep littoral zones, *M. spicatum* is a highly successful colonizer (Grace and Wetzel 1978). Though the plant dies back in the fall and winter, the root mass in the sediment remains active and begins to re-grow shoots in spring. Growth is temperature-dependent starting at about 15 °C (Pfingsten et al. 2018). During the growing season, growth is rapid, and milfoil biomass can quickly become a nuisance. Additional to concerns about its growth rate, Eurasian milfoil is able to adapt in other ways. For example, it is known that the Eurasian and the native Northern milfoil hybridize (Thum 2017). The resulting species (*M. spicatum* × *M. sibiricum*) is referred to as *Myriophyllum spp*. or milfoil for the remainder of

this document. The hybrid is not easily distinguishable in the field due to the presence of combinations of phenotypic characteristics from both parent species (Moody and Les 2007; Sturtevant et al. 2009). The hybrid, as it is formed by two species of *Myriophyllum*, exhibits similar reproductive and life history strategies, and is therefore managed similarly to *M. spicatum* (Sturtevant et al. 2009; Parks et al. 2016).

Caddisflies

The genus *Nectopsyche* is one of eight genera in the family Leptoceridae in the order Trichoptera. Formerly known as the genus *Leptocella*, *Nectopsyche* was established by Flint in 1974 (Glover and Floyd 2004). Fifty-seven species have been described within *Nectopsyche* (Holzenthal 1996). Though the individual species are somewhat restricted in their distribution, the genus occurs from North America through Central and South America (Holzenthal 1996), and both the Nearctic and Neotropical regions are represented (Glover and Floyd 2004). Though *Nectopsyche albida* ranges throughout much of North America including Canada and the United States, the species is indicated as not present on the Idaho species list (IDFG 2019). The genus typically is found in lentic or slow lotic freshwaters (Oláh and Oláh Jr. 2017) in weedy, vegetated areas (Haddock 1977).

Few studies have focused on *Nectopsyche albida* specifically in part because studies on insects in freshwater systems can be difficult, especially determining their ecological role (Wiggins 1977). Life history information provided in this introduction relies heavily on that in Tozer et al. (1980) for a population occurring in Delaware County, Indiana, United States. Unless otherwise cited, the following information comes from Tozer et al. (1980). *Nectopsyche albida* was previously thought to be present only in Canada and the upper Midwest and Eastern United States (Haddock 1977). However, *N. albida* is now found in Coeur d'Alene Lake, ID (Gary Lester, EcoAnanlysts, Moscow, ID personal communication), and is abundant in at least the southernmost area of the lake.

Emergence of this caddisfly species in Indiana has been recorded to occur from mid-May to September with a major peak in early-June and a secondary peak in late-August. Adult *N. albida* live only one or two days after emergence during which they mate and the female deposits egg clutches beneath the water surface. *N. albida* eggs were found in groups

of 15-25 on the shoots of a *Myriophyllum* species, with each egg inside a yolk and connected by a string-like substance. At 26°C in laboratory incubations, eggs hatched in nine days. Adult females appeared to select oviposition sites based on visual cues, such as the presence of macrophytes.

First and second instar larvae were abundant in late June and clustered in beds of *Myriophyllum*. Third instar larvae were found in late July, and fourth instar larvae dominated the population in early August. Researchers found third and fourth instar larvae during the second peak emergence in August, indicating that the caddisfly required a year for full development and that the larvae from the first hatch were still developing when the second cohort pupated and emerged. Dyar's rule models indicate that proportional size increases remain constant, and the caddisfly's five instars conformed to this rule as they each varied by 1.6 (Tozer et al. 1980; Hutchinson et al. 1997). By mid-October, fifth instar larvae were present in the population. By the time a fifth instar pupated, it nearly doubled in weight from the beginning of the fifth instar stage. However, the maximum growth rate was greatest in the third and fourth instar stages. Overwintering caddisflies, mostly fifth instars but with some fourth instars present, were found in deep water and associated with beds of *Myriophyllum*.

Case building begins immediately with the first larval instar, and it appears that the caddisflies build their cases out of whatever materials are available. Observed behavior in transition from the larval to pupal stage include a spacing of the larvae evenly around a plant before excreting silk to attach themselves to the plant and to seal their case. The entire process of sealing the case lasts about four hours. After approximately two weeks from the sealing of the case, adult caddisflies emerge and swim to the surface. Caddisflies in shallow water tended to emerge earlier in the season than those in deeper water, possibly related to differences in water temperature.

Gut content analysis has shown *N. albida* to feed on macrophytes, including species of *Myriophyllum*. To feed, the caddisflies climb over the plants and secrete a silk substance to anchor themselves to it. Some studies show feeding patterns (Hart and Resh 1980), while others (e. g., Tozer et al. 1980) have been unable to determine the timing of the caddisfly feeding.

Objectives

My main objective was to determine the life history characteristics of *N. albida* in Coeur d'Alene Lake. Specifically, I focused on growth over time and timing of life stages. I also examined if case length could be used as an indicator of caddisfly head capsule size and growth stage. Additionally, I determined if caddisfly density was related to the density, abundance and diversity of vegetation.

Methods

Study Site

Coeur d'Alene (CDA) Lake is one of the largest in the state of Idaho and is located in the panhandle of the state (Figure 2.1). This lake is central to the Coeur d'Alene Tribe and is the heart of their historic territory and culture. Currently, the Tribe manages the southern third of the lake. Originally, the southern end of Coeur d'Alene Lake was segmented and composed of a series of shallow floodplain lakes including Chatcolet Lake, Round Lake, and Benewah Lake connected by the St. Joe River. The lakes are now inundated and connected throughout the year, due to the advent of lake level regulation resulting from the construction of the Post Falls dam on the Spokane River, the outflow of CDA Lake located at the northern end of the lake. Parts of the St. Joe River channel and levees remain in the southern lake, but much of it is now submerged. The remnant levees and channel remain as a loose barrier between Chatcolet and Round lakes, but overall, the former water bodies at the southern end of Coeur d'Alene Lake are inundated and part of the main lake.

Field Collections

In 2018, profiles of temperature, dissolved oxygen, conductivity and pH were collected at one of the sampling sites at 0.25 m intervals from the surface to the bottom using a Hydrolab DSX5 multi-probe. Profile data for two additional sites in Chatcolet Lake are included in Appendices A and B.

Within the shallow area of Chatcolet Lake between the levy and Benewah Lake, I selected six sampling points within the established network of research sites used by the lake managers of the CDA tribe (Figure 2.1). To sample the six points within the Chatcolet study area, I used either a macrophyte sampler (0.66 × 0.35m) or an Ekman dredge (0.15 × 0.15m),

dependent on the amount of vegetation present during each sampling trip. The macrophyte sampler was effective in capturing long strands of macrophytes as it sampled a larger area and held the captured material in a mesh bag. The smaller Ekman dredge was effective in capturing a detritus sample when little or no vegetation was present. All material retained by each sampler was filtered through a 250µm-mesh sieve with lake water and then placed into individually labelled containers (3.5 L plastic bags with a seal, or 20 L buckets depending on season and amount of material recovered in each sample) until analysis. While taking samples I noted if vegetative material was present in the sample, and if so, the species of plants. I also noted if live caddisflies were present and with what species of plants they were associated. If the abundance of caddisflies noted in the samples was low, a macrophyte rake was used to collect additional vegetation and caddisflies from outside of the six sites, but still within the general area. I collected a minimum of 50 caddisfly larvae per sampling trip for the analysis of life history characteristics. Some macrophytes, water, and the caddisflies were transported in 20L buckets with tight-fitting lids to the University of Idaho, where lids were removed and samples stored in a walk-in refrigerator set to 4°C until analysis which occurred within 1-4 days.

Analysis

Field-collected samples were sorted manually by first removing all plant material and separating it by species into pre-massed aluminum pans. To obtain biomass per unit area by species, the plant material in all individual pans was dried at 60°C to constant mass (minimum of 24 h), allowed to cool in a desiccator and re-weighed. Percent composition of each species was calculated from the dry mass of all plant material collected in a sample.

All occupied and empty caddisfly cases were removed from each sample and counted to calculate density. Caddisflies from each sampling date were then preserved in 95% ethanol in glass vials with gas-tight lids until further analysis. To measure size, each occupied case was photographed with a Cannon Powershot 630 digital camera attached to a calibrated Leica M60 dissecting microscope at 6.3 to 10 × magnification. Individual caddisflies were then removed from cases and placed in a dish with ventral side down so that the eyes on each side of the head capsule were visible before an image was obtained at 32 or 40 × magnification. All measurements on digital images were made with ImageJ software (Hill et

al. 2005, 2011). To measure case length, the linear distance was obtained from the most anterior to most posterior point on each case (Figure 2.2) (Wiggins 1977), not including auxiliary plant material. Head length was measured from the posterior margin to the anterior end of the frontoclypeal apotome, stopping before the labrum and mandibles, while width was measured at the widest part of the head in the posterior third of the capsule (Figure 2.3; Wiggins 1977; Tozer et al. 1980). I measured a total of 1102 individuals, mostly larvae but also pupa (Appendix C). Caddisflies were then placed into a 70% ethanol solution for long-term storage.

Statistical analyses

I plotted average vegetative biomass (g/m^2) versus time and the percent composition of vegetative species found per sampling date over both sampling seasons. I also plotted average caddisfly head capsule width (mm), case length (mm), and caddisfly density ($individuals/m^2$) as a function of time for both 2017 and 2018. After plotting the average head capsule size of each group of caddisflies collected per sampling occasion, I noticed a change in average size between August and September of 2017 which was larger than the change between any subsequent dates. From September 2017 until pupation in summer of 2018, average head capsule size remained relatively constant. To test the hypothesis that there was a significant difference in head capsule dimensions between August and September, I used a Mann-Whitney test. A large difference would indicate a change in instar stage between the two groups. To determine the relationship between head capsule width and case length, I plotted the means of each parameter from all larval measurements from each sample date and fitted a nonlinear regression to reflect estimate the exponential growth pattern of the plotted data. The nonlinear regression of larval head capsule width as a function of case length was:

$$CL = A + be^{c*HW}$$

where CL is case length (mm), A, b, c are fitted coefficients, HW is head width, and e is exponent. To test the relationship between caddisflies and vegetation, I used a linear

regression comparing average total vegetative biomass and caddisfly density for sampling dates between July 2017 and October 2018.

Results

Water temperatures in Chatcolet Lake differed between sampling season. In 2017, water temperature in Chatcolet Lake peaked at just over 27°C at the end of July. In 2018, average water temperature peaked again at the end of July, but at 24.6°C (Table 2.1). Although the seasonal peak temperature was higher in 2017 than 2018 and the number of growing degree days was slightly higher in 2017 than 2018 in the early months of the years, the overall temperatures in the spring of 2017 were slightly colder than in the spring of 2018 (Scofield unpub. data). Site water depth was deepest in May 2018 during spring runoff and shallowest at the end of the season following drawdown (Table 2.1).

Trends in vegetation shifted from 2017 to 2018 including the timing of macrophyte growth and the diversity of species found at the six regular sampling sites. Biomass of plants in 2017 was higher than in 2018, with the peak biomass being about 200g/m^2 and 50g/m^2, respectively (Figure 2.4). However, the diversity of vegetation was greater in 2018 than 2017 (9 compared to 5 species, respectively) (Figure 2.5) and were identified using the guides presented in Hamel et al. (2001) and Crow and Hellquist (2006). In both years, *Elodea* and *Myriophyllum* were generally the two most abundant species. The combination of biomass of all macrophyte species apart from *Elodea* and milfoil sometimes exceeded the biomass of the two species, but rarely did one species exceed the biomass of either *Elodea* or milfoil. Thin-leaf pondweed (*Potamogeton pusillus*) was dominant early in the summer of 2018 but declined by mid-summer. In 2017, biomass decreased from July through October, and milfoil was highest in July, though I did not sample during the start of the growing season. *Myriophyllum* began its growth in July, continued through August, peaked in September, and decreased after that. Macrophytes exhibited a patchy distribution in the area sampled; in some cases there were beds of monoculture, multiple-species with extremely high biomass, and areas which were devoid of vegetation.

Caddisfly growth remained consistent between years, although timing of growth was later in 2018 compared to 2017. The average head capsule width of the sampled caddisflies

remained generally between 0.7 and 0.9mm from September 2017 to June 2018, with a notable difference in average size (0.5mm) of caddisflies sampled in August of 2017 (Figure 2.6). The average head capsule width from August to September in 2017 differed (Mann-Whitney test, U = 0.98, P< 0.001), with an increase from about 0.5mm to about 0.8mm, respectively. Head capsule growth was greatest in the period between August and September, and then leveled off (Figure 2.6).

Case length followed a pattern similar to head size, with the size increasing from August through the rest of the calendar year. This end-of-fall size was constant until spring (Figure 2.7). However, in the spring, head capsule size increased until pupation (Figure 2.8). The nonlinear regression of larval head capsule width as a function of case length was:

$$CL = 9.188 + 0.002e^{9.970*HW}$$

where the coefficients equaled A (9.188 ±1.226 (S.E.), *P*< 0.001), b (0.002± 0.006, *P* = 0.791), and c (9.970±4.123, *P* = 0.052). The coefficient of determination (R^2) was 0.90.

Similar to average biomass, average caddisfly density was higher in 2017 than in 2018 (Figure 2.9). The highest mean density of caddisfly larvae was 13 ind/m^2 in 2017, however, for most of 2018 the average density was close to zero. At most, there was one individual per square meter in 2018. The relationship of caddisfly density as a function of macrophyte biomass was significant when compared to total vegetative biomass, linear regression produced an R^2 value of 0.63 (F=27.40, d.f.=1, P<0.001) (Figure 2.10).

I observed pupation of *N. albida* in Chatcolet Lake in mid-June of 2017 and early-July of 2018. I found adult caddisflies during one sampling trip on July 3rd, 2018, on the levee separating Chatcolet Lake from the St. Joe River. In early July I found a mixture of larvae and pupa amid the macrophyte beds as well as adults on the shoreline nearest to the macrophyte beds (Figure 2.1).

The occupied larval caddisfly cases I found always had at least the indentation where a “backbone” stalk of plant material was located, and more often I found cases with the stalks

still attached. Stalks were generally missing from empty or pupal cases, but evidence remained that the stalk had once been attached. *Elodea* stems were almost universally the choice of stalk for *N. albida* larvae. For large cases that were occupied, they were easily discerned from those that were empty by appearance; occupied cases were lighter colored and had stalks attached, while empty cases were darker colored and tended to not have the extending stalk (Figure 2.2).

Discussion

Total macrophyte biomass was greater in 2017 than in 2018, in part because of the later onset of the macrophytes *E. canadensis* and *M.* spp., which could have been caused by a variety of factors. A deep draw down of CDA Lake at the end of 2017 exposed roots of macrophytes to freezing temperature throughout winter, which could have delayed a vigorous start to macrophyte growth in early spring of 2018 (Figure 2.11) (Wagner and Falter 2002; USGS 2019). Macrophyte beds in 2017 began growing from relatively well-preserved overwintering biomass, but due to a sharp decline in vegetative biomass at the end of 2017, the macrophyte beds in 2018 likely began growth for the season with fewer resources than the previous year (Scofield unpub. data). It is possible that caddisfly herbivory damaged the plant beds in 2017 enough to lessen their storage of resources in 2017, causing plants in 2018 to begin growing at a disadvantage compared to 2017. Managers have observed major fluctuations in biomass across CDA Lake that may be related to herbivory the previous year as described above. However, it is also possible that the extreme spatial variability of macrophyte density in Chatcolet skewed the values between years and is in fact not wholly representative of the total biomass in the lake.

Differing from the pattern of total biomass, macrophyte diversity was greater in 2018 than 2017. This could have been caused by a high degree of herbivory on the dominant species (*Elodea* and *Myriophyllum*) in 2017 that reduced their dominance in 2018. Environmental conditions also could have delayed the growth of *Elodea* and *Myriophyllum* in 2018, meaning other plant species made up a greater percentage of biomass than they would with thick *Elodea* and milfoil patches. Less dense *Elodea* and milfoil also allow for more resources (i. e., sunlight) to be available to the smaller species. *Potamogeton pusillus*

has been observed to grow earlier and senesce earlier than other macrophytes (Sayer et al. 2010a; b), which is consistent with the patterns observed in Chatcolet Lake in 2018. Though diversity changed between the 2017 and 2018 seasons, it is unclear which factor(s) influenced this change, or if it is part of the natural interannual variability in the plant community.

Myriophyllum growth began in July and peaked in September of 2018, when the caddisflies reached terminal head capsule growth and their fifth and final instar. At this time, the caddisflies were large enough to be seen easily with the unaided eye and presumably large enough to cause visual damage to the macrophyte beds. Until this point, the caddisflies had less of an impact on the milfoil growth as it began in June, and at that point the caddisfly larvae from the previous growing season pupated, emerged as adults, and laid their eggs. Pupation, emergence, and egg development took approximately 3-4 weeks, so larvae were not able to affect the milfoil or other macrophytes via herbivory until late-July to early-August. In August, the caddisflies molted and grew rapidly, but were at a small size (1^{st} to 2^{nd} instars) that likely prevented them from inflicting significant damage on milfoil and macrophyte beds in general (Tozer et al. 1980). Once the caddisflies reached their final instar, the milfoil had crested its peak biomass for the season and began senescing. At this time, the caddisflies were large enough to significantly damage the milfoil and potentially hasten its decline. Therefore, while caddisflies may not be able to limit the growth of invasive milfoil, they appear capable of contributing to the rapid decline of the milfoil toward the end of its growing season.

In my sampling efforts I was able to capture caddisflies representing the fourth and fifth instars, but I did not capture the first through third instars which were 0.1 to 0.4mm in size (Tozer et al. 1980). The relatively short time between observing adults and finding 4th instar larvae indicates a high growth rate. I was able to identify the caddisflies I collected as fourth and fifth instars by comparing the size of the caddisflies I collected to those of Tozer et al. (1980). The head capsule length, head capsule width, and case length of Chatcolet caddisflies matched those of the fourth and fifth instar caddisflies collected in Indiana (Tozer et al. 1980). The significant change from about 0.5mm to about 0.8mm suggests a change from the fourth to the fifth and final instar in the *N. albida* larval life stage (Tozer et al.

1980). Average head capsule width or length did not change significantly throughout the rest of the larval stage of the 2017 cohort. However, case length continued to increase throughout the year most likely indicating a continuing increase in body size. It is probable that the caddisfly's physiology, specifically their neural network, does not require a head capsule larger than 0.8mm, so instead of allocating resources to molting and a larger head capsule, they spend their energy on developing a larger soft-body that does not require molting to grow. Tozer et al. (1980) reported that larvae of *N. albida* in Indiana doubled their body mass between the fifth instar and pupation. This remains to be examined in the CDA Lake population. The shape of the case also supports this idea, as the case does not continue to grow wider after a certain time in the year, but just increases in length. A wider space is not necessary at the anterior end as the head capsule remains the same size. Based on the head and case measurements of the caddisflies, it appears that the *N. albida* larvae in CDA Lake overwinter as fifth instars, which is consistent with other research findings (Tozer et al. 1980).

Caddisfly density was lower in 2018 than in 2017, following the pattern of total plant biomass (Figures 2.4, 2.9). The positive relationship revealed through regression between caddisfly density and vegetative biomass indicates that caddisfly larva were more likely to be found in areas with macrophytes than without (Figure 2.10). Such a relationship could come about for several reasons. First, each larva will need a certain amount of food, thus the pattern may be underlain by a resource density-dependence. If the caddisflies need the macrophytes as a food source and the vegetative biomass in an area is low, the caddisflies are able to move to other areas with higher resource availability. It is not uncommon for resource-driven movement to occur for herbivorous insects (Talbot and Ward 1987; Gross et al. 2016). Predation by fish may also influence this pattern. For example, it is well known that fish can easily locate prey in sparse vegetation, but have difficulty locating prey in dense macrophyte beds. Additionally, the caddisflies require tall vegetation on which to pupate and lay their eggs, so areas with more vegetation can support larger populations of caddisflies.

Caddisfly development was also delayed in 2018 as opposed to 2017, which reflects the lower number of degree days in 2018 compared to 2017. It is possible that a higher number of degree days could be tied to increased herbivory, which would be consistent with

general observations from the lake between 2017 and 2018 (Spencer and Carruthers 2013; Scofield B. pers. comm.). Greater starting biomass in 2017 could have provided the caddisflies with a higher quality diet than they had at the beginning of 2018, despite differences in degree days, allowing them to mature faster.

I only observed one annual pupation event, either in June or July depending on the year. I also found adults only once, concurrent to when I found pupa in the lake, in July 2018. In a univoltine insect life cycle (as opposed to bivoltine, for example), the organisms produce one generation per year. In Chatcolet Lake all the caddisflies present were part of the same generation with the same life cycle timing. Because the caddisflies were all at a similar stage in their life cycle, their uniform development suggests a univoltine life cycle. This finding is contrary to what researchers have found in other locations in the past where *N. albida* was univoltine but multiple cohorts persisted simultaneously (Tozer et al. 1980).

Conclusion

The presence of the understudied caddisfly *Nectopsyche albida* in Chatcolet Lake combined with the presence of invasive Eurasian milfoil creates an interesting ecological dynamic, and an opportunity to expand the body of knowledge about both the life history of the caddisfly and its interactions with macrophytes. Often the invasive Eurasian milfoil changes the dynamics of the macrophyte community by outperforming other plant species. Macrophyte growth overall was greater in 2017 than 2018, and macrophyte diversity was lower in 2017 than 2018. *Nectopsyche albida* larvae behave differently in Chatcolet than in other parts of the country, likely due to differences in environmental factors (Tozer et al. 1980). The density of caddisflies per square meter decreased from 2017 to 2018, following the pattern of total biomass. The development of the caddisflies was delayed in 2018 relative to 2017, possibly due to differences in vegetative biomass, a lower number of growing degree days in 2018, and greater lake level drawdown prior to the 2018 growing season. Pupation was delayed almost a month from 2017 to 2018. However, regardless of the timing differences, the average larval head capsule width of the caddisflies followed the same pattern in both years. Average head capsule width reached about 0.8mm approximately 2 months after hatching from newly lain eggs. The head capsules remained that size until

pupation the subsequent year, indicating that the head capsule reaches a terminal size at the fifth and final instar. Case length contrarily continues to grow throughout the larval stage until pupation. I hypothesize a significant change in caddisfly body size throughout the larval stage and after the caddisfly reaches its final instar until pupation. Going forward, measuring the dry mass of the entire caddisfly would give insight into the change in growth occurring after the head capsule growth stagnates. While measuring the body length of the caddisflies is possible, the process would require preservation of the caddisflies in formalin, and the soft body parts are both variable in how they curl and are easily damaged. Drying and weighing individual caddisflies would provide more accurate data.

Apparent herbivory damage of macrophytes, specifically milfoil, was observed concurrently with the presence of caddisflies (see chapters 3 and 4 for evidence of herbivory). Comparison between the timing of caddisfly development and milfoil development indicate an overlap. The caddisflies are pupating, emerging, and resulting larvae are hatching as milfoil growth begins. By the time the caddisflies are sufficiently large to inflict substantial damage on the milfoil via herbivory, the macrophyte has already reached its peak biomass for the season. Therefore, though the caddisflies are unlikely to prevent the onset of milfoil, they likely damage it and contribute to an earlier reduction in biomass than would occur in their absence.

Literature Cited

Aiken, S. G., P. R. Newroth, and I. Wile. 1979. The biology of Canadian weeds.34. *Myriophyllum spicatum* L. Can. J. Plant Sci. **59**: 201–215.

Crow, G. E., and C. B. Hellquist. 2006. Aquatic and wetland plants of northeastern North America, volume II: A revised and enlarged edition of Norman C. Fassett's a manual of aquatic plants, volume II: Angiosperms: monocotyledons.

Glover, J. B., and M. A. Floyd. 2004. Larvae of the genus *Nectopsyche* (Trichoptera:Leptoceridae) in eastern North America, including a new species from North Carolina. J. North Am. Benthol. Soc. **23**: 526–541. doi:10.1899/0887-3593(2004)023<0526:lotgnt>2.0.co;2

Grace, J. B., and R. G. Wetzel. 1978. The production biology of watermilfoil (*Myriophyllum spicatum* L.): A review. J. Aquat. Plant Manag. **16**: 1–11.

Gross, E. M., C. Feldbaum, and C. Choi. 2016. High abundance of herbivorous Lepidoptera larvae (*Acentria ephemerella* Denis & Schiffermuller) on submersed macrophytes in Lake Constance (Germany). Fundam. Appl. Limnol. **155**: 1–21. doi:10.1127/archiv-hydrobiol/155/2002/1

Haddock, J. D. 1977. The biosystematics of the caddis fly genus *Nectopsyche* in North America with emphasis on the aquatic stages. Am. Midl. Nat. **98**: 382–421.

Hamel, K., J. Parsons, M. Boule, S. Feldman, I. Wertz, and L. Zempke. 2001. An aquatic plant identification manual for Washington's freshwater plants.

Hart, D. D., and V. H. Resh. 1980. Movement patterns and foraging ecology of a stream caddisfly larva. Can. J. Zool. **58**: 1174–1185. doi:https://doi.org/10.1139/z80-162

Hill, G. M., R. C. Henderson, and N. A. Mauchline. 2011. Diaspidid (Hemiptera: Coccoidea) size plasticity as an adaptive life history trait. Eur. J. Entomol. **108**: 153–159.

Hill, M. G., N. Mauchline, L. R. Cate, and P. G. Connolly. 2005. A technique for measuring growth rate and survival of armoured scale insects. New Zeal. Plant Prot. **58**: 288–293.

Holzenthal, R. W. 1996. Catalog and bibliography of the species of *Nectopsyche* (Trichoptera:Leptoceridae).

Hutchinson, J. M. C., J. M. McNamara, A. I. Houston, and F. Vollrath. 1997. Dyar's rule and the investment principle: Optimal moulting strategies if feeding rate is size-dependent

and growth is discontinuous. Philos. Trans. R. Soc. London B **352**: 113–138. doi:10.1098/rstb.1997.0007

IDFG. 2019. A caddisfly *Nectopsyche albida*. Idaho Fish Game.

Johnson, R. L., E. M. Gross, and N. G. Hairston. 1998. Decline of the invasive submersed macrophyte *Myriophyllum spicatum* (Haloragaceae) associated with herbivory by larvae of *Acentria ephemerella* (Lepidoptera). Aquat. Ecol. **31**: 273–282. doi:10.1023/A:1009960131857

Katsanevakis, S., I. Wallentinus, A. Zenetos, E. Leppäkoski, M. Ertan Çinar, B. Oztürk, M. Grabowski, D. Golani, and A. C. Cardoso. 2014. Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. Aquat. Invasions **9**: 391–423. doi:10.3391/ai.2014.9.4.01

Killgore, K. J., and J. J. Hoover. 2001. Effects of hypoxia on fish assemblages in a vegetated waterbody. J. Aquat. Plant Manag. **39**: 40–44.

Kuehne, L. M., J. D. Olden, and E. S. Rubenson. 2016. Multi-trophic impacts of an invasive aquatic plant. Freshw. Biol. doi:10.1111/fwb.12820

Madsen, J. D., J. Sutherland, J. A. Bloomfield, and L. Eichler. 1991. The decline of native vegetation under dense Eurasian watermilfoil canopies. J. Aquat. Plant Manag. **29**: 94–99.

Moody, M. L., and D. H. Les. 2007. Geographic distribution and genotypic composition of invasive hybrid watermilfoil (*Myriophyllum spicatum x M. sibiricum*) populations in North America. Biol. Invasions **9**: 559–570. doi:10.1007/s10530-006-9058-9

Nichols, S. A., and B. H. Shaw. 1986. Ecological life histories of the three aquatic nuisance plants, *Myriophyllum spicatum, Potamogeton crispus* and *Elodea canadensis*. Hydrobiologia **131**: 3–21. doi:10.1007/BF00008319

Oláh, J., and J. Oláh Jr. 2017. Fine phenomics applied to the *Nectopsyche* genus (Trichoptera): Species delineation by speciation traits. Opusc. Zool. Budapest **48**: 117–184. doi:10.18348/opzool.2017.2.117

Parks, S. R., J. N. McNair, P. Hausler, P. Tyning, and R. A. Thum. 2016. Divergent responses of cryptic invasive watermilfoil to treatment with auxinic herbicides in a large Michigan lake. Lake Reserv. Manag. **32**: 366–372. doi:https://doi.org/10.1080/10402381.2016.1212955

Pfingsten, I. A., L. Berent, C. C. Jacono, and M. M. Richerson. 2018. *Myriophyllum spicatum* L.: U.S. Geological Survey, nonindigenous aquatic species database. USGS.

Sayer, C. D., A. Burgess, K. Kari, T. A. Davidson, S. Peglar, H. Yang, and N. Rose. 2010a. Long-term dynamics of submerged macrophytes and algae in a small and shallow, eutrophic lake: implications for the stability of macrophyte-dominance. Freshw. Biol. **55**: 565–583. doi:https://doi.org/10.1111/j.1365-2427.2009.02353.x

Sayer, C. D., T. A. Davidson, and J. I. Jones. 2010b. Seasonal dynamics of macrophytes and phytoplankton in shallow lakes: A eutrophication-driven pathway from plants to plankton? Freshw. Biol. **55**: 500–513. doi:https://doi.org/10.1111/j.1365-2427.2009.02365.x

Smith, C. S., and J. W. Barko. 1990. Ecology of Eurasian watermilfoil. J. Aquat. Plant Manag. **28**: 55–64.

Spencer, D. F., and R. I. Carruthers. 2013. Predicting Eurasian watermilfoil's (*Myriophyllum spicatum*) distribution and its likely response to biological control in a spring-fed river. J. Aquat. Plant Manag. **51**: 7–14.

Sturtevant, A. P., N. Hatley, G. D. Pullman, R. Sheick, D. Shorez, A. Bordine, R. Mausolf, A. Lewis, R. Sutter, and A. Mortimer. 2009. Molecular characterization of Eurasian watermilfoil, northern milfoil, and the invasive interspecific hybrid in Michigan lakes. J. Aquat. Plant Manag. **47**: 128–135.

Talbot, J. M., and J. C. Ward. 1987. Macroinvertebrates associated with aquatic macrophytes in Lake Alexandria, New Zealand. New Zeal. J. Mar. Freshw. Res. **21**: 199–213. doi:https://doi.org/10.1080/00288330.1987.9516216

The Associated Press. 2007. Swimmer, possibly entangled, drowns in Columbia. The Seattle Times, August 27

Thum, R. A. 2017. Genetic analysis of invasive Eurasian watermilfoil in Idaho waters.

Tozer, W. E., V. H. Resh, and J. O. Solem. 1980. Bionomics and adult behavior of a lentic caddisfly, *Nectopsyche albida* (Walker). Am. Midl. Nat. **106**: 133–144. doi:10.2307/2425143

USGS. 2019. USGS surface-water daily data for the nation. United State Geol. Surv.

Wagner, T., and C. M. Falter. 2002. Response of an aquatic macrophyte community to fluctuating water levels in an oligotrophic lake. Lake Reserv. Manag. **18**: 52–65.

Wetzel, R. G. 2001. Limnology: Lake and river ecosystems, 3rd ed. Elsevier Academic Press.

Wiggins, G. B. 1977. Larvae of the North American caddisfly genera (Trichoptera). University of Toronto Press.

.

Table 2.1. Hydrolab profile data from all 2018 sampling dates. The values in brackets represent standard error. Dates are in the format of MM/DD/YYYY.

Date	Site	Average water temperature (°C)	Maximum depth (m)	Average dissolved oxygen (mg/L)
3/23/2018	n1-28	4.25 (±0.01)	1.47	13.20 (±<0.01)
4/26/2018	n1-35	8.24 (±0.02)	1.91	11.64 (±0.01)
5/8/2018	n1-35	7.67 (±0.05)	2.4	10.61 (±0.01)
5/23/2018	n1-35	11.43 (±0.35)	1.93	10.98 (±0.02)
6/5/2018	n1-35	11.61 (±0.26)	1.49	10.16 (±0.03)
6/19/2018	n1-35	15.47 (±0.25)	1.6	9.90 (±0.06)
7/17/2018	n1-35	23.01 (±0.15)	1.66	9.20 (±0.12)
7/31/2018	n1-35	24.59 (±0.07)	1.49	9.71 (±0.05)
8/13/2018	n1-35	22.91 (±0.14)	1.56	8.38 (±0.19)
8/28/2018	n1-35	18.21 (±0.03)	1.57	7.59 (±0.04)
9/11/2018	n1-35	18.12 (±0.06)	1.32	8.79 (±0.02)
9/25/2018	n1-35	14.4 (±0.01)	1.46	9.38 (±0.02)
10/9/2018	n1-35	12.01 (±0.01)	1.20	9.36 (±0.03)
10/24/2018	n1-35	10.56 (±0.01)	1.00	10.42 (±0.03)

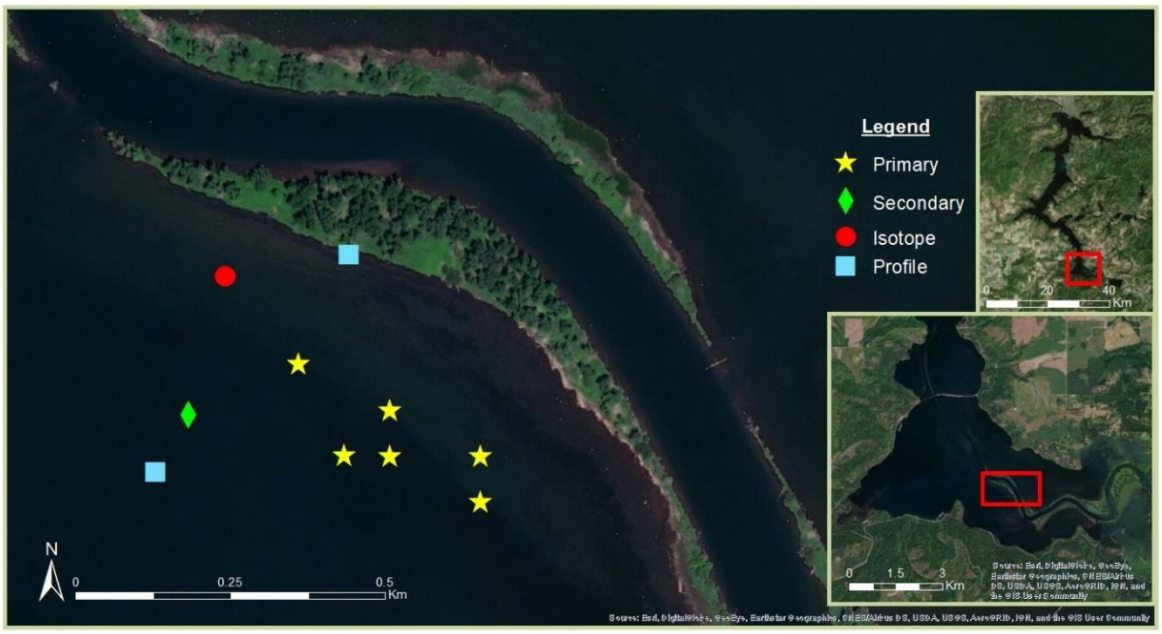

Figure 2.1. Site map of Chatcolet Lake. The yellow stars represent the six sites regularly sampled throughout 2017 and 2018, and the star at far left is where most of the 2018 Hydrolab profiles were taken. The green diamond represents a site where I collected caddisfly larvae in early 2018 when they were not present at the six regular sites. The red circle (Isotope) represents the point where I collected the samples for isotope analysis and most of the 2018 caddisflies to supplement those from the six regular sites. The blue squares represent sites where additional profile data was collected.

Figure 2.2. The top row of *Nectopsyche albida* cases are unoccupied and were found alongside the bottom row of cases, which were occupied by larva. All caddisflies shown came from the same sample. Bottom cases generally have an obvious *Elodea* stalk, and the stalk is generally missing from the top cases. The black bar represents 1 mm.

Figure 2.3. *Nectopsyche albida* larva under a calibrated Leica M60 dissecting microscope photographed at 40 × magnification. Red lines on the head capsule indicate how head capsule measurements were taken; L = length, W = width.

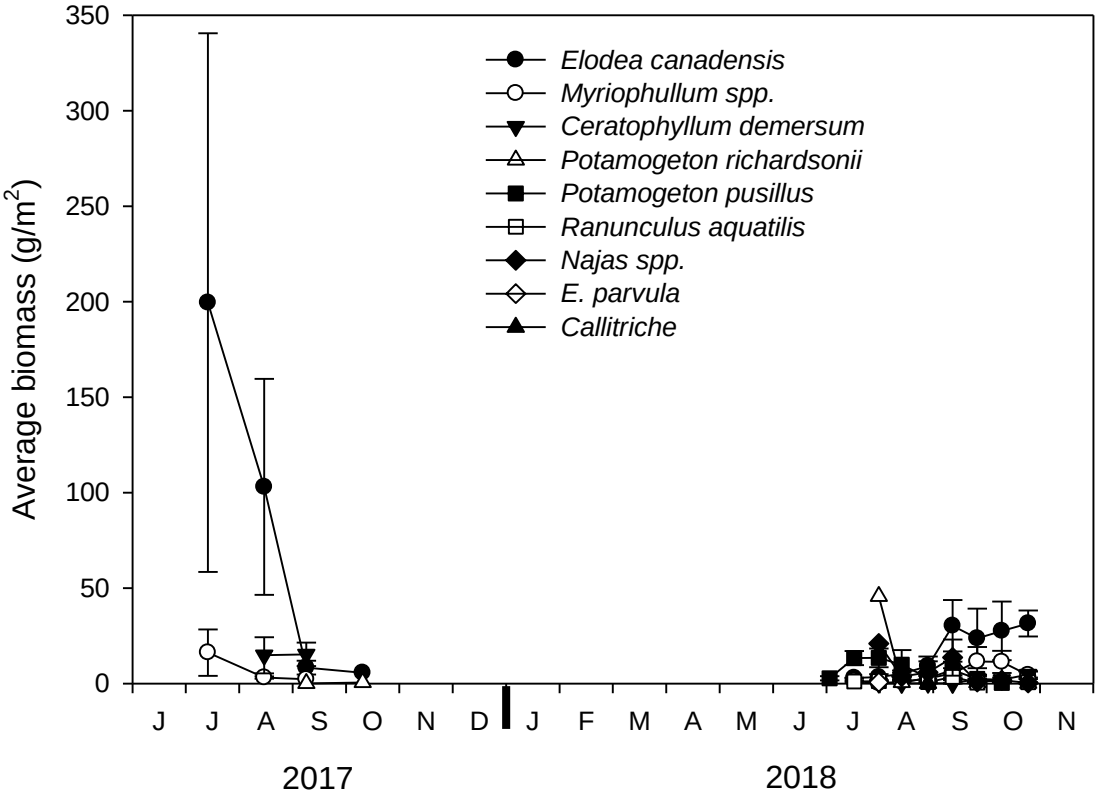

Figure 2.4. Average biomass (means±SE) of macrophyte species as a function of time at six sites in Chatcolet Lake, ID.

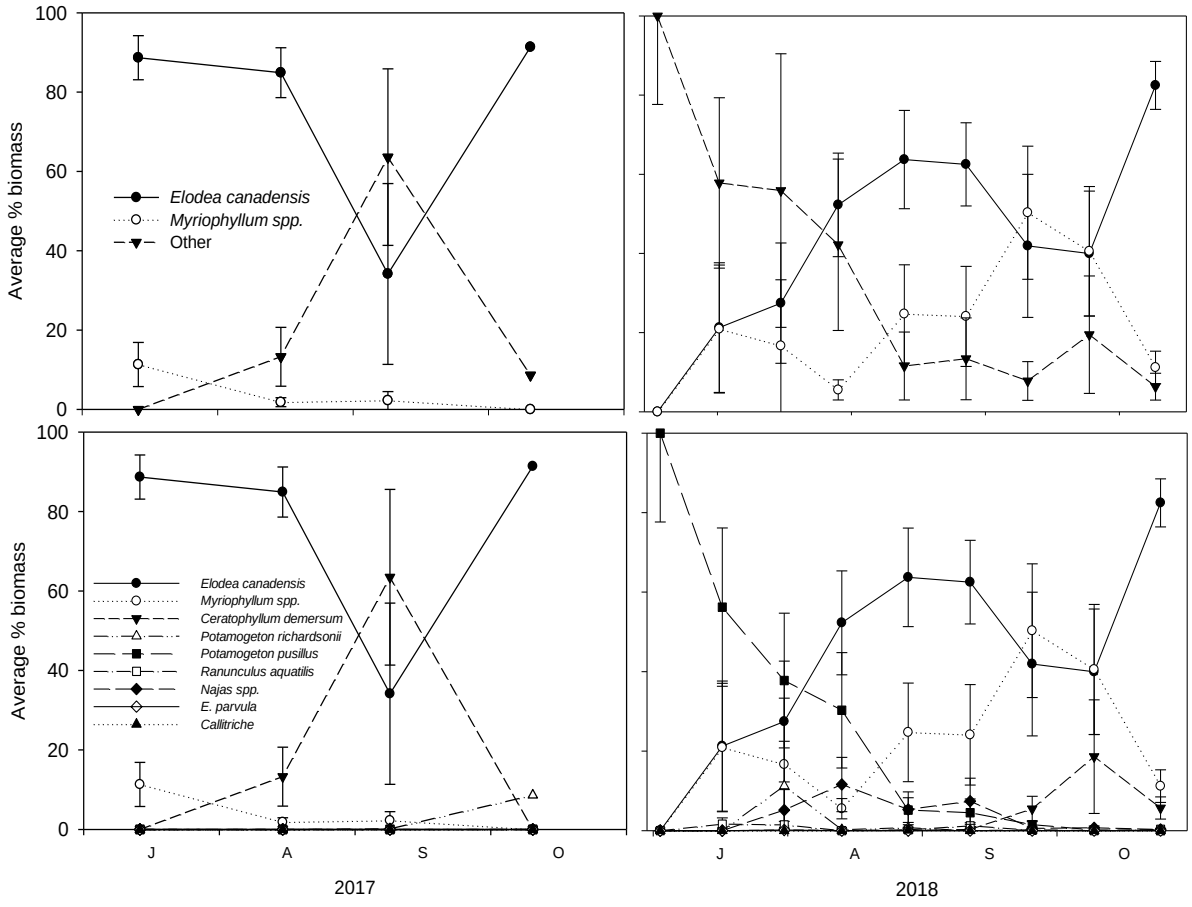

Figure 2.5. Average percent biomass (means±SE) of all macrophyte species found from all sampling occasions throughout the 2017 and 2018 field seasons. The x-axis of all plots is time, with 2017 on the left and 2018 on the right, and the y-axis is the average percent biomass of each species from each sampling date. The top two plots show *Elodea*, milfoil, and the other species of macrophytes are combined into one category, "Other". The bottom two graphs show all macrophyte species individually.

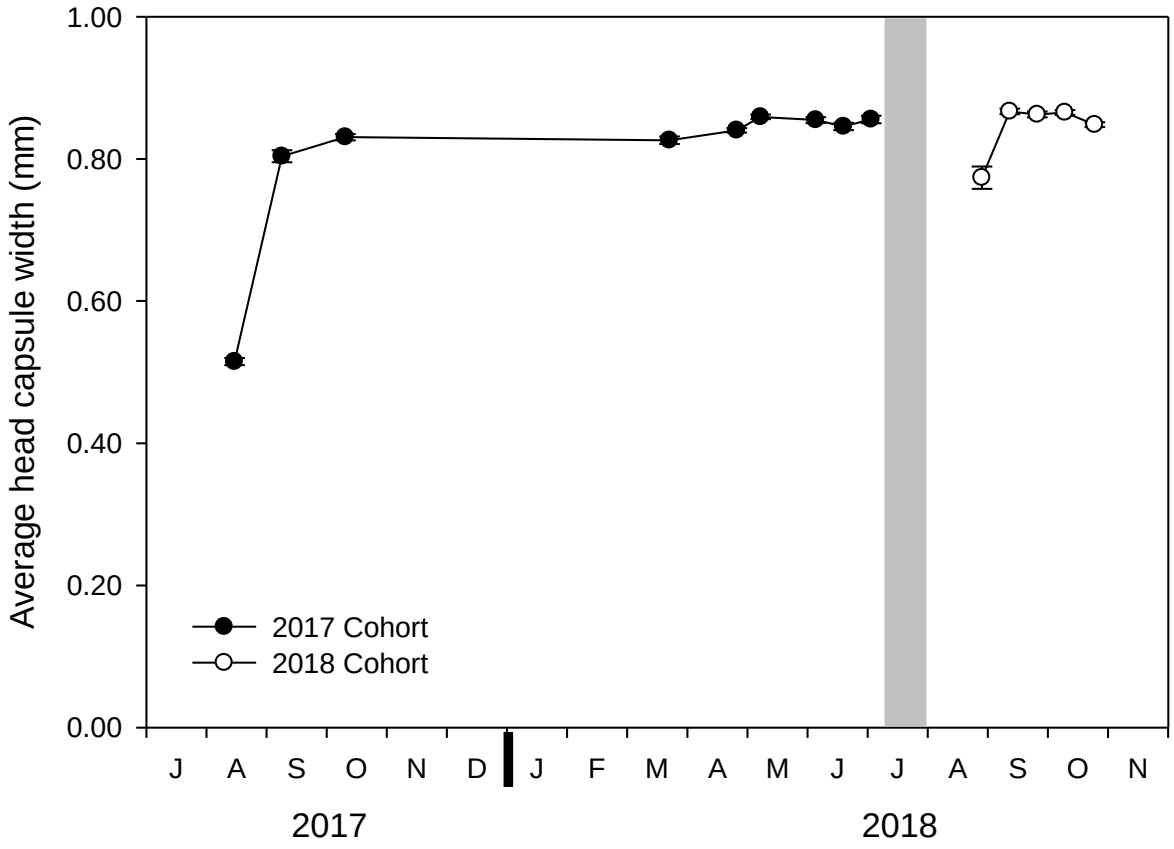

Figure 2.6. Average head capsule width (mm) (means±SE) of caddisflies collected at Chatcolet Lake, ID, as a function of time, beginning in July of 2017 through October of 2018. The 2017 cohort, represented by filled black dots, are individuals that hatched in 2017 and emerged as terrestrial adults in 2018. The 2018 cohort, represented by the open circles, are the progeny of the 2017 cohort and will emerge as adults in 2019. The grey vertical bar represents the assumed time for adult emergence and development of eggs until they hatch and larvae emerge. The sample size for 2017 was 241 individuals, and the sample size for 2018 is 850 individuals, with a total sample size of 1091 larvae.

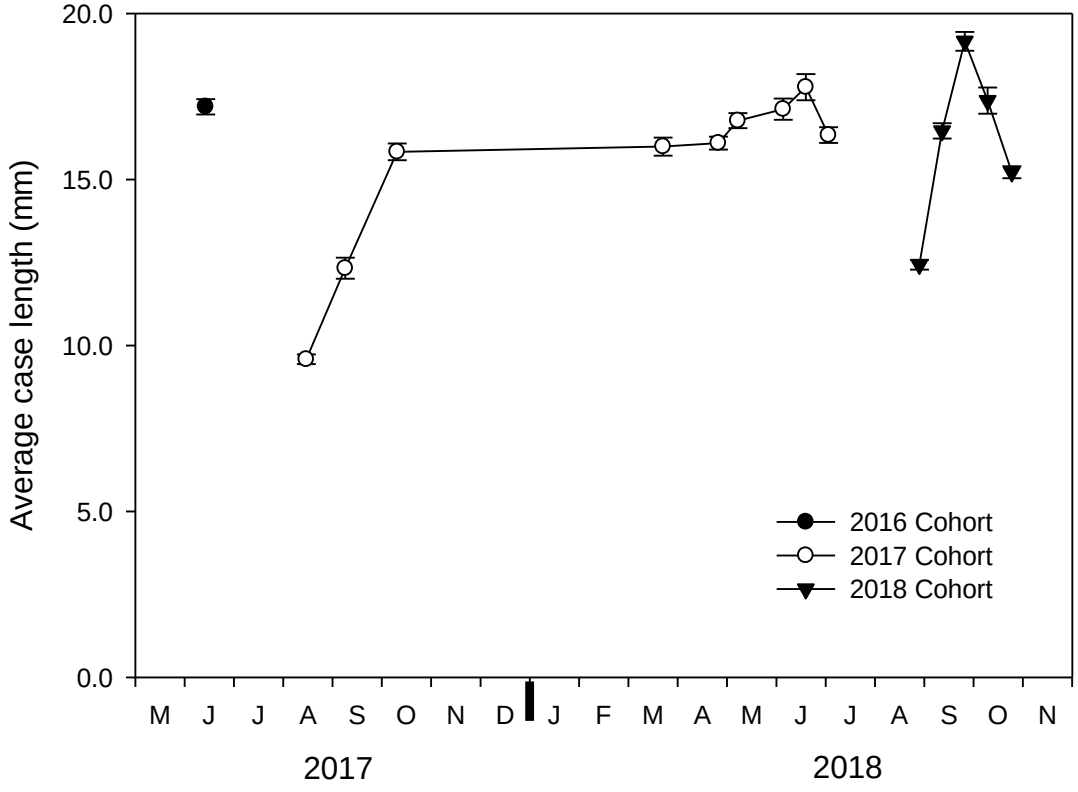

Figure 2.7. Average case length (means±SE) of *Nectopsyche albida* larvae collected at Chatcolet Lake, ID, as a function of time, beginning in June of 2017 through October of 2018. The 2016 cohort, represented by filled black dots, are individuals that hatched in 2016 and emerged as terrestrial adults in 2017. The 2017 cohort, represented by the open circles, are the progeny of the 2016 cohort and emerged as adults in 2017. The 2018 cohort, represented by the filled black inverted triangles, are the progeny of the 2017 cohort and will emerge as adults in 2019.

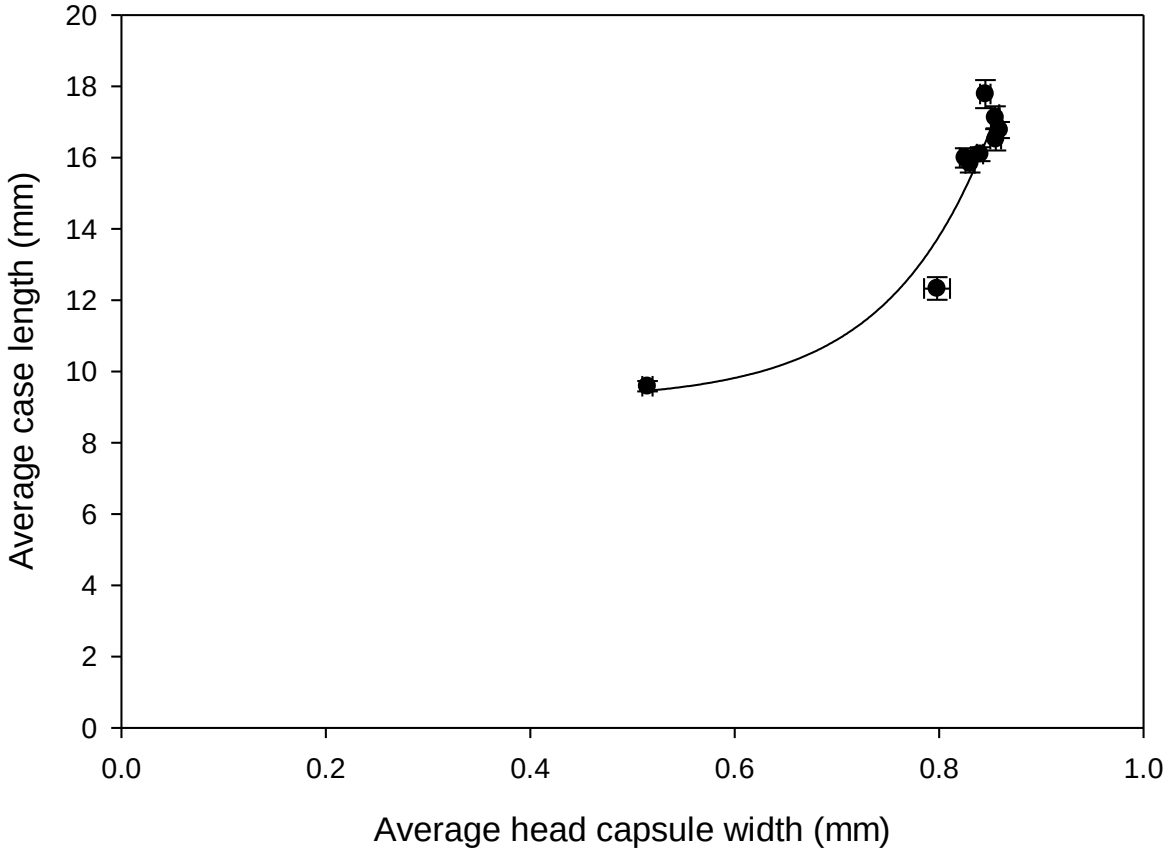

Figure 2.8. Average case length (mm) of *Nectopsyche albida* as a function of average head capsule width (mm) (means±SE) of all individuals collected from Chatcolet Lake, ID. These averages are a result of measurements of 1057 individuals. The equation for the line is $CL=A+be^{(c*HW)}$ where A = 9.188 ±1.226 (S.E.), P< 0.001, b = 0.002± 0.006, P = 0.791, c = 9.970±4.123, P = 0.052, and R2 = 0.90.

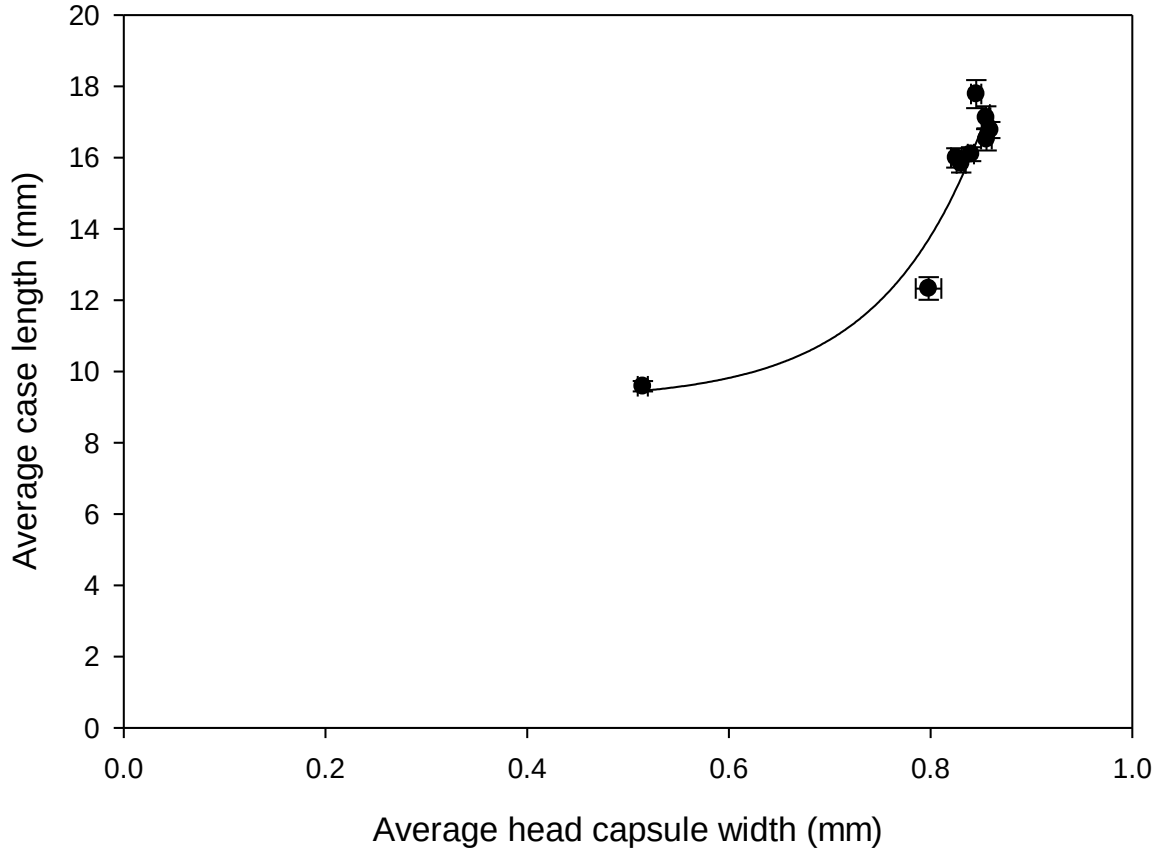

Figure 2.9. Average density (means±SE) of the caddisfly *Nectopsyche albida* (individuals/m^2) on all sampling occasions in 2017 and 2018 at six sites in Chatcolet Lake, ID.

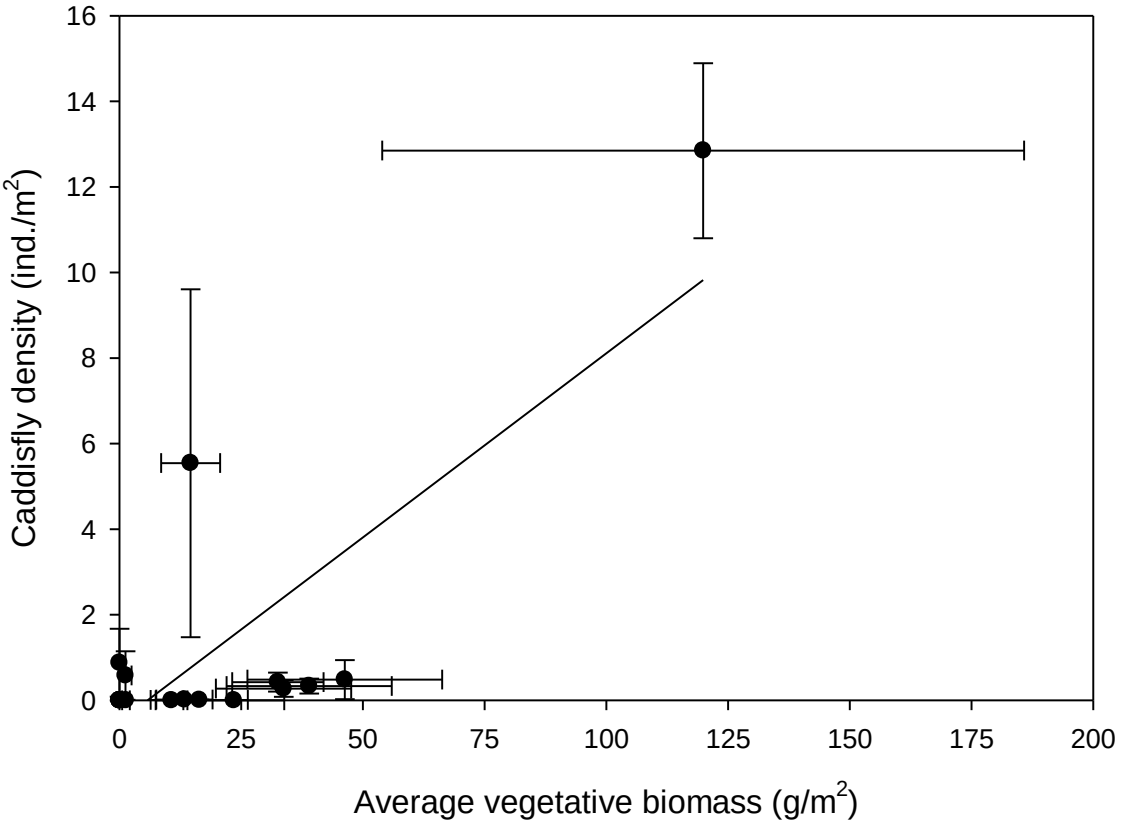

Figure 2.10. Average caddisfly density (individuals/m^2) of *Nectopsyche albida* larvae as a function of average vegetative biomass (g/m^2) (means±SE) collected from Chatcolet Lake, ID, between August 2017 and October 2018..

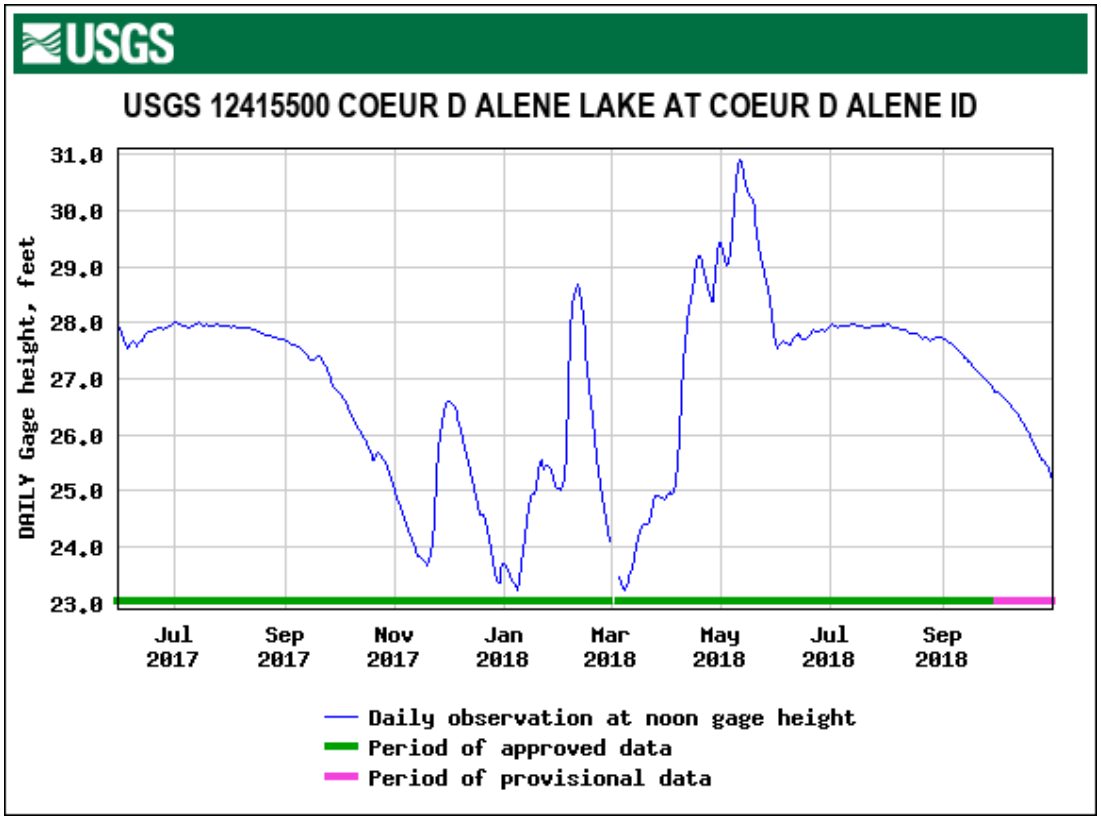

Figure 2.11. Daily lake level (ft.) for the Coeur d'Alene Lake gauge station, Idaho, taken from the United States Geological Survey website (https://waterdata.usgs.gov/id/nwis/uv?site_no=12415500). Dates range from 01-June-2017 to 31-October-2018.

Chapter 3: Food sources of *Nectopsyche albida* larvae in Chatcolet Lake, Idaho inferred from analysis of carbon and nitrogen stable isotopes

Abstract

Analysis of stable isotopes is widely used in ecology to determine the movement of nutrients through a foodweb. In freshwater, ratios of ^{13}C:^{12}C and ^{15}N:^{14}N are commonly used to distinguish food source and trophic level, respectively. In Chatcolet Lake, managers discovered extensive herbivory of macrophytes in areas where larval caddisflies (*Nectopsyche albida*) were also found. Because the diet of the caddisfly larvae *N. albida* is unknown, I used stable isotopes to determine if the larvae contribute to the damage. I collected samples of caddisflies and possible food sources in the study area for analysis of carbon and nitrogen isotopes. I used the USEPA IsoSource mixing model to help identify possible contributions of the different food sources using the isotope ratios, and therefore diet, of *N. albida*. Results indicate that the caddisflies had a generalist diet, consuming various macrophyte species without preference, and the composition of their diet shifted based on available species. Larvae also appeared to consume epiphytes, though this was likely incidental. Analysis also showed the larval cases were composed of macrophytes, meaning the larvae used macrophytes for a food source and for construction materials.

Introduction

Stable isotopes, specifically carbon and nitrogen, are widely used in ecological research to analyze food webs and the flow of energy between trophic levels (Syväranta et al. 2006; Layman et al. 2007). An important component of understanding the ecology of a species is knowing its place in a food web, both from a predator and prey perspective. While classically this has been done via direct observation, feeding/selection trials, or analysis of gut contents, the analysis of stable isotopes has revolutionized this area of ecology (Hyodo 2015) because it can indicate what is actually assimilated by a species of interest into its body tissue. While feeding trials and gut analysis show short-term behavior, isotopic signatures of tissue reveal long-term dietary habits and behavior (Rounick and Winterbourn 1986). One of

the most effective ways to study an organism's diet and place it in context in an ecosystem is through analysis of stable isotopes of carbon 13 (^{13}C) and nitrogen 15 (^{15}N) (Fry and Sherr 1989). The isotope ratio of carbon 13 to carbon 12 tracks organic matter from food resources to consumers, while the isotope ratio of nitrogen 15 to nitrogen 14 identifies trophic level differences between organisms given the preferential enrichment of ^{15}N via metabolic processes (Chappuis et al. 2017). The ^{15}N:^{14}N ratio increases approximately 3.5‰ with every trophic level, so consumers should be clearly separated from their food items (Minagawa and Wada 1984; Fry 1991; Post 2002). The location of an organism's carbon signature as compared to its possible food sources is used to infer its major dietary component. Examples of this technique have been used to determine the nutrient source from fish, to insects, to plants (Jepsen and Winemiller 2002; Black et al. 2003).

The occurrence of multiple primary producers ranging from macrophytes and their attached epiphytes to planktonic algae in freshwater ecosystems makes it difficult to easily determine the structure of food webs and specific predator-prey relationships. However, previous studies show that *Elodea canadensis* and *Myriophyllum* spp., both macrophytes, have distinct stable isotope signatures (Table 3.1), meaning that each can be clearly identified (e. g., Cremona et al. 2009; Chappuis et al. 2017). *Elodea* nitrogen signatures ranged from 1.3 to 7.96‰, and carbon signature ranged from -21.7 to -11.1‰. *Myriophyllum* nitrogen signatures ranged from 0.25 to 13.7‰, and carbon signatures ranged from -32.9 to -8.63‰ (Table 3.1). Ventura et al. (2008) also reported that epiphytes had a significantly higher carbon ratio than other primary producers, including *E. canadensis*, indicating their contribution in a consumer's diet can also be identified. Although aquatic species have signatures that differ from one another, there can also be variability within a species due to influences such as temperature, water flow, and habitat (Jacquemin et al. 2013). Hydrologic variation, an embankment for example, can also cause the isotopic signatures of plants and animals to differ even in close proximity to each other (Goecker et al. 2009). Differing patterns in the flow of water can change the nutrients in an area as water from different sources can accumulate varying ratios of nutrients (i. e., turbid water carrying more carbon from the sediment than clear water, or highly aerated water containing more dissolved nitrogen than water from a deep pool). Water with different ratios of carbon and nitrogen would change the isotopic signature of an organism. Temporary separation may not radically

change the signature of two organisms of the same species, but over time, changes in isotopic signatures are greater if organisms live with and consume different sources of water and food. Isotopic analysis is more useful in determining lasting change than temporary differences in terms of nutrient assimilation. Isotopic signatures of tissue can reveal long-term dietary habits, because the analysis reflects material that has been assimilated into the animal's tissue (Rounick and Winterbourn 1986).

In complex systems with multiple potential food sources, researchers generally employ some form of a mixing model to mathematically determine the contribution of each food source to the diet of the organism under consideration (Phillips and Gregg 2001). Models such as IsoSource (USEPA 2017) produced by scientists at the United States Environmental Protection Agency (USEPA) can be used to distinguish the extent that a source contributes to an organism's tissue (Phillips and Gregg 2001).

Before conducting isotopic analysis of an organism, however, it is important to understand its general ecology and life history. Species-specific research has not been conducted on many species of caddisflies and *Nectopsyche albida* is no exception. Members of the genus are typically found in various freshwater habitats, including lakes and other slow flowing water bodies, with a tendency to be found in weedy, vegetated areas (Haddock 1977; Oláh and Oláh Jr. 2017). *Nectopsyche* larvae build cases out of material ranging from particulate substrate to plant matter depending on what is available where they occur (Haddock 1977). The cases sometimes have twigs, pine needles, or pieces of other material extending out from one or both ends of the case (Chapter 2, figure 2.8) (Glover and Floyd 2004). About 24% of all Trichoptera genera are considered shredder-detritivores, and about 26% of genera which occur in warm, lotic habitats are identified as shredders (Jacobsen 1993). Like other caddisflies, larvae of *Nectopsyche* have been shown to function as shredder-herbivores and collector-gatherers, and have been found to be generalist consumers (Holzenthal 1996; Harms and Grodowitz 2009). The caddisfly first excretes a silk substance from its labial glands to anchor itself to a plant, then uses its legs to collect food and transfer it to the mouth (Haddock 1977). Analysis of gut contents has shown the presence of fine organic particulate matter and the remains of vascular plant material (Glover and Floyd 2004). With all the information gathered about the genus *Nectopsyche* and the species *N.*

albida, little is known about its trophic ecology. Therefore, I elected to use analysis of carbon and nitrogen stable isotope ratios to determine potential food sources of *N. albida* in Chatcolet Lake, ID. Additionally, samples collected at different times of the year were used to examine any temporal trends.

Methods and Materials

Study Site

Coeur d'Alene (CDA) Lake is one of the largest lakes in the state of Idaho and is located in the panhandle of the state. This lake is central to the Coeur d'Alene Tribe and is the heart of their historic territory. Currently, the Tribe manages the southern third of the lake. Originally, the southern end of Coeur d'Alene Lake was segmented and composed of a series of shallow floodplain lakes including Chatcolet Lake, Round Lake, and Benewah Lake connected by the St. Joe River. The lakes are now inundated and connected throughout the year, due to the advent of lake level regulation resulting from the installation of the Post Falls dam on the Spokane River, the outflow of CDA Lake located at the northern end of the lake. Parts of the St. Joe River channel and levees remain in the southern lake, but much of it is now submerged. The remnant levees and channel remain as a loose barrier between Chatcolet and Round lakes, but overall, the former water bodies at the southern end of Coeur d'Alene Lake are inundated and part of the main lake. (Figure 3.1).

Field collection of samples for analysis of stable isotopes

Once in October 2017, and at different times in 2018 (Table 3.2), I collected vegetative biomass and caddisfly larvae from a site within the Chatcolet Lake study area. Samples were generally taken from the same point within the lake, or within a short distance from that point (Figure 3.1). I collected samples of i) all macrophytes (*Elodea canadensis*, *Myriophyllum spp*, *Ceratophyllum demersum* [coontail], *Potamogeton richardsonii* [Richardson's pondweed], *Ranunculus aquatilis* [buttercup], *Potamogeton amplifolius* [big-leaf pondweed], *Najas* spp.), ii) 10-15 *N. albida* larvae, iii) samples of detritus, iv) cases of *N. albida*, and v) macrophytes from which I removed epiphytes/fungus. Not all plant species were collected on each date due to seasonal succession.

Preparation of samples for analysis of stable isotopes

I separated all plants by species, removed caddisflies from their cases, and removed epiphytes from macrophytes into pre-massed aluminum pans which were placed in a drying oven at 60°C until they reached constant mass (minimum of 72 hours). Epiphytes were removed from macrophytes by shaking samples of macrophytes in a Nalgene bottle filled with distilled water for 1 minute after which macrophyte material was removed and the epiphyte solution frozen (-26°C) until analysis (Cremona et al. 2009). On two occasions I also combined and dried the caddisfly cases for analysis. I homogenized cases to obtain a representative "average" case signature. Although this somewhat limits interpretation in this case, I was limited by funds available for analysis. After drying the samples, they were stored in glass vials with gas-tight lids until preparation for analysis.

To prepare the dried samples, I used an alcohol-rinsed mortar and pestle to grind the plants to a fine powder. I prepared more biomass than necessary to create an inclusive sample that integrated some of the spatial variation in the plants. I analyzed three replicates from the homogenized powder. I did not homogenize caddisflies, as their soft tissue was of sufficient mass to analyze individuals after drying. Using either the powders or parts of dried caddisflies, I placed 0.5 mg for animal tissue, and 2.5 mg to 3.5 mg for plant tissue of the sample into individual pre-tared 4×6 mm tin capsules (Costech Analytical, Valencia, CA) for analysis in an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA). I submitted all isotope samples to the Isotope Core Laboratory at Washington State University, Pullman, WA, for $^{15/14}$N and $^{13/12}$C analysis.

Analysis

The results of the C and N ratios were returned in both ratios and percentages, and the ratios were plotted by sampling date, with each point representing the average value for that item. For the complete data set of all carbon and nitrogen values, see Appendix D. Some species from spring 2018 did not have replicates, and therefore represent only one sample instead of an average (*Myriophyllum*, *Elodea*, epiphytes, chironomids, and fungus). I chose to use the $^{13/12}$C and $^{15/14}$N ratios instead of the C and N percentages to better compare my results to that of other studies, as well as to more accurately represent the signature of each sample.

To evaluate the food sources of *N. albida*, I used the IsoSource program (USEPA 2017) using a 1% source increment (Phillips and Gregg 2003). Smaller increments could be used; however, the computing power would be too great to determine differences with an extremely large dataset (Phillips and Gregg 2003). The tolerance value used to analyze the source contribution represents the difference in signatures typically to 0.1‰, but up to 0.5‰ (Phillips and Gregg 2003). Differences greater than 0.5‰ would allow too much room for inaccuracy as to what is a realistic source of nutrients, because an increase in tolerance means two distinct signatures could become indistinguishable from each other (Phillips and Gregg 2003).

The accuracy of the IsoSource mixing model is affected by factors such as sample size and the differences in signature, both of which can create difficult circumstances to precisely identify the food sources of a given organism (Phillips and Gregg 2001). Because isotopic signatures can be highly variable among freshwater bodies, and even within a single ecosystem, it is important to study the isotopic signatures of each specific study area. I used the averages of the isotope values from the Washington State Isotope Core Laboratory and compared the caddisfly signature to the carbon and nitrogen signatures of all possible food sources on each individual sampling occasion. To determine the composition of the caddisfly cases, I ran IsoSource again for the two October dates, but with the average case signature as the standard to be compared to the other samples collected (including the *N. albida* larvae, as the caddisflies use silk to bind together the materials used to build the case) as the possible sources.

Results

Stable isotope ratios of carbon and nitrogen of all samples (species or groupings) on each sampling occasion were distinct but changed temporally. Carbon ratios followed a slight pattern of increase but remained mostly consistent over time. The most divergent carbon signature in all groups was a sample of filamentous algae, which in the spring samples had a much more negative carbon signature than other species, though the epiphyte samples also had much more negative carbon values than other species (Figure 3.2). Generally, the nitrogen ratios rose throughout the growing season, and there were no obvious anomalies.

Figure 3.2 shows all average signatures plotted based on each sampling occasion. For more specific figures separated by sampling occasion, see Appendix E.

In October of 2017, *Ranunculus* had the highest stable nitrogen isotope ratio near 3.25‰, detritus had the lowest nitrogen ratio (~1.25‰). It also had the lowest stable carbon isotope ratio (~-21‰), while *Elodea* had the highest carbon ratio (-18‰). The nitrogen isotope ratio of *N. albida* larvae was 2.5‰ while the carbon ratio was -19‰. *Myriophyllum* had a nitrogen value almost matching the caddisflies at ~2.5‰ but had a lower carbon ratio of about -19.7‰.

Few species were available during a single sample date in the first half of 2018, so the spring values represent a composite of multiple sampling occasions between 26-April-2018 to June 5th, 2018 (Appendix E, figure E.2). Fungus collected from the exposed roots of macrophytes from the previous-season had the highest nitrogen value of ~3.5‰ and a relatively high carbon ratio of -18‰. *Elodea* had the highest carbon ratio at about -17‰, and a nitrogen ratio just above 0‰. Filamentous algae had a nitrogen ratio of just below 2.0‰, on par with other species, but an extremely low carbon ratio of about -32‰ which was the lowest carbon ratio of any sample collected during this study. The caddisfly nitrogen ratio was just above 2.0‰, while the carbon ratio was about -21‰. *Myriophyllum* had almost the exact same signature, falling only slightly lower in the nitrogen ratio. Epiphytes and chironomids both had a carbon ratio near -21‰, but the chironomids had a higher ratio of nitrogen (2.1‰ and 1.75‰, respectively).

On August 28th, 2018, carbon ratios were somewhat higher than previous samples and nitrogen ratios were generally lower. *Ceratophyllum* had a low carbon ratio (-19‰) and the highest nitrogen value (~1.8‰). *Myriophyllum* had the highest carbon ratio at 14‰, while its nitrogen ratio was similar to that of *Ceratophyllum* at about 1.8‰. *Nectopsyche albida* had the lowest carbon ratio at -18‰ and a nitrogen ratio of about -2.5‰. *Najas* had the lowest nitrogen ratio (-4.0‰). *Elodea*, *Ranunculus*, *P. richardsonii*, and *P. pusillus* had signatures between the other species.

At the end of September (September 25th, 2018), *Myriophyllum* had the highest nitrogen ratio of ~2.4‰ and also the highest carbon ratio of ~-14.7‰. Epiphytes had the lowest carbon ratio of about -18.8‰ and a nitrogen ratio of just over 2‰. *Elodea* had a

carbon value of -15.6‰ and the lowest nitrogen ratio (~0.2‰). The carbon signature of the caddisflies was again -18‰ and their nitrogen signature was 0.5‰. *Potamogeton richardsonii* and *Ranunculus* had carbon values of -15‰ and -14.9‰ and nitrogen values of 1.6‰ and 2.1‰, respectively.

Most of the species' signatures clustered on October 9th, 2018, however, epiphytes were somewhat of a deviation with the lowest carbon ratio (~-28‰) and the highest nitrogen ratio (~4.6‰). *Myriophyllum* again had the highest carbon value at about -15.5‰ and had the second highest nitrogen value of 3.0‰. *Elodea* had a carbon value of ~-16.5‰ and again had the lowest nitrogen ratio (0.4‰). The caddisfly larvae had a carbon ratio of about -19‰ and a nitrogen ratio of about 1.2‰. The cases of the caddisfly larvae had a signature between those of *Myriophyllum* and *Elodea*, and slightly higher than the caddisflies (C: ~16‰, N: 1.3‰). *Potamogeton richardsonii* and *Ceratophyllum* had similar signatures to each other, with carbon signatures of -17‰ and about -18‰ and nitrogen ratios of about 2‰, respectively. The species' signatures from a year previous to this collection (Figure 3.2) were similar, but did not match exactly, and the 2017 signatures generally had more variation than those in 2018.

The last sampling occasion on October 24th, 2018 revealed a pattern of signatures similar to that of early October. Again, the epiphytes had the lowest carbon ratio and the highest nitrogen ratio (-24‰ and 3.8‰). *Ceratophyllum* had a carbon signature of -16.5‰ and the lowest nitrogen ratio in this round at -0.5‰. *Elodea* had the highest carbon ratio of the group at -15‰, and a nitrogen ratio of about -0.1‰. The caddisflies had a carbon signature of ~-18‰ and a nitrogen signature of ~1.7‰. The larval cases again had a slightly higher carbon ratio of -17.5‰ and a slightly higher nitrogen value than the caddisflies at 1.8‰. *Potamogeton richardsonii* fell in the middle of the other signatures, with carbon and nitrogen values of ~-16‰ and ~1.6‰, respectively.

IsoSource determined possible combinations of food item contribution for four of the six sampling dates, using the *N. albida* signature as the source to which the food item signatures were converged (Table 3.3) *Myriophyllum* was a dietary component of the *N. albida* in three of the four analyses (about 8.3%, 23%, and 23%) but never contributed the majority of the caddisfly signature. *Elodea* contributed to the diet in all four, ranging from

3.3% to 78%. Twice *Elodea* comprised the majority of the larval signature, once at 78% and again with 44%. Fungus contributed nearly half (48%) of the larval signature in one group, the majority for that group. Epiphytes contributed the majority in the last analysis (~36%), though by a smaller margin than the fungus, as the next largest contributor was *Ceratophyllum* at 20% and then *Elodea* at 19.3% of the *N. albida* signature.

On October 9th, 2018 the composition of the cases was *E. canadensis* 51%, *Myriophyllum* just under 48%, *P. richardsonii* 0.9%, *Ceratophyllum* 0.5%, *N. albida* 0.1%, and epiphytes 0.0%. (Note this analysis required a source increment of 1% and a tolerance of 0.45 to successfully compute a solution). On October 24th, 2018 the composition of cases was determined to consist of *P. richardsonii* 22%, *N. albida* 21%, *Myriophyllum* 20%, epiphytes 17%, *E. canadensis* 11%, and *Ceratophyllum* 9.0%. This analysis ran with a source increment of 1% and a tolerance of 0.1.

Discussion

Although the results from IsoSource were variable over time, there were two consistencies; *Elodea canadensis* was included in the caddisflies' diet on every sampling occasion, and on dates on which epiphytes were sampled, they also contributed to the diet (Figures 3.3; 3.5-3.7). Though always included in the caddisfly diet, epiphytes did not make up as much of their diet as the combined percentages of macrophytes, as the volume of the thin layer of epiphytic biomass was considerably less than the biomass of the macrophytes. The range of carbon and nitrogen signatures strongly suggests that *N. albida* assimilates nutrients from different sources. However, macrophytes seem to majorly contribute based on the average isotopic signature examined in 2017 and 2018. Given the change in the ratios of both *N. albida* and the food sources over time, no macrophyte species was consistently the dominant contributor to the caddisfly diet, indicating a lack of species preference, and a generalist diet. Temporal changes in caddisfly and macrophyte signatures are likely due to the natural, seasonal changes in macrophyte diversity in the lake. These changes are consistent with field observations of damage to macrophytes presumably via herbivory, as damage could be found on various macrophyte species throughout the year. Variation within species on the same date could be explained by differences in the epiphytic community and

its variability among macrophytes. Epiphytes have been shown to be important members of freshwater communities and of invertebrate diets (Bärlocher 1985; Newman 1991). Some macrophyte species, such as *Elodea canadensis*, exude allelochemicals to discourage epiphytic growth, particularly algae and cyanobacteria (Erhard and Gross 2006; Lürling et al. 2006). The presence of these chemicals could create a highly variable epiphytic community among the macrophytes in Chatcolet Lake, especially because *Elodea* often comprises much of the macrophyte biomass in the community (Chapter 2, figure 2.2). The allelochemicals are thought to leach into the water column, therefore affecting the epiphytic growth on other macrophyte species as well (Erhard and Gross 2006). High variation in the stable isotope ratios could also originate from the inclusion of contamination such as detritus. The sample size also was limited, which could have contributed to high variability. The combination of larval signatures and observed macrophyte damage indicates that the hypothesis of herbivory is supported, and that the *N. albida* larvae at least partially contribute to the observed damage. Given that macrophytes were identified as the main contributor to the isotope ratios in the body tissue of the caddisflies, it is reasonable to conclude that the contribution of epiphytes in the diet was incidental. Epiphytes are present on most macrophyte surfaces which would result in ingestion along with macrophyte tissue. Overall, previous research labeling the larvae *N. albida* as a generalist herbivore and shredder was supported.

The macrophyte species with isotopic signatures surrounding the caddisflies differed between sample dates, but on the last three sampling occasions (September 25, October 9, and October 24, 2018), epiphytes had an important influence on at least the carbon signature of the larvae. Due to the similarity in caddisfly carbon signature between 28-August and 25-September of 2018, it is likely that if I had collected epiphytes in August, the caddisfly would have been between the epiphytes and the rest of the species in terms of carbon ratio. Apart from the August date, the caddisfly larvae signature fell between the signatures of the potential food sources. It is likely that the main caddisfly diet is represented in the collected samples, though there may be other minor contributors. As *N. albida* are generalists, they tend to feed on a variety of sources, indicated by the combinations of multiple contributors in each IsoSource analysis. While it is possible that the samples I collected all contribute to the diet of the larvae, it is also possible that some of the plants I collected are not part of the caddisflies' diet given their similarity in isotope ratios. IsoSource assumes all included

sources are possible contributors, so while the caddisflies fall between many sources, their signature could be influenced by multiple plants with similar signatures in the analysis, even if they only consumed one.

Two groups of isotope samples did not allow for analysis with IsoSource. The August 2018 samples did not include signatures completely surrounding the caddisflies, preventing the software from determining the composition of caddisflies' signatures given the analyzed potential food sources. Without a signature on each side of the source (the caddisfly in this case), the composition of the source signature cannot be fully resolved. The other problematic sample date was in September 2018, which did included sources with signatures surrounding the caddisflies. However, the tolerance level necessary to produce a reasonable solution of food sources was 0.75, exceeding the reasonable tolerance limit of the model. It is possible that some signatures were too similar to each other on this date to produce realistic relationships at a small difference interval. Future analyses should focus on collecting an exhaustive suite of macrophytes to ensure that the food source can be elucidated via a mixing model.

Overall, the IsoSource results show a variable caddisfly diet, spread mostly between macrophytes, indicating that herbaceous plants are probably their main food source. Fungus contributed a surprising amount to the caddisfly signature when it was present and analyzed in 2018, possibly because in the early spring, most macrophytes had not begun growing for the season and the residual plants from 2017 were highly degraded. A study by Arsuffi and Suberkropp (1989) showed that macroinvertebrates, particularly Trichopteran shredders, tend to consume more biomass when it has been colonized by fungus, possibly because the fungus makes the food item more palatable. This could also explain the high consumption of macrophytes by *N. albida* if there are epiphytes, possibly including fungus, present on the surface of most of the macrophytes. Because there was not a consistent lead contributor to the caddisfly signature, the *N. albida* larvae in Chatcolet Lake seem to follow the standard of being generalist consumers.

Following the general pattern of consumption, the signatures of the caddisfly cases between the first and second sample dates in October 2018 varied widely, probably due to changes in the condition of the macrophytes throughout the month. Caddisflies make their

cases from proximate materials, so *Myriophyllum* and *Elodea* may have been usable toward the end of September and into October, but their condition at the collection site may have decreased over time. A decline in their vitality may have led the larvae to use other macrophytes in their case construction that were of better quality. It is possible that the caddisflies have a preference as to which macrophytes they use to build their cases, but it is likely that they use whatever is nearby, and probably what is healthiest at the time. Given the typically increasing case size over the larval life stage (Chapter 2, figure 2.6), the case composition likely changes with the seasonal succession of macrophytes in the lake. Such a wide difference could also be due to sample size, as few cases were averaged to calculate the signature compared to the number of caddisflies and cases in the lake, and the larvae came from the same macrophyte patch. If other cases were collected from macrophyte beds with different species diversity and densities, the signatures may have differed. If the caddisfly larvae mature in a monoculture bed, their case is likely to consist of mostly of that single plant, and similarly if the caddisfly moves frequently through diverse macrophyte beds, their case would probably have a more diverse signature. The wide difference in *N. albida* input to the case contribution exists possibly because the use of some macrophyte species in construction requires a greater input of silk from the larvae to maintain case integrity. Sediment could also be considered in the future as a possible resource for the *N. albida* in case construction.

Conclusion

Trophic relationships in aquatic ecosystems are important facets of ecology for managers to understand as they consider management strategies. Stable isotope analysis, specifically ^{13}C and ^{15}N, is a useful tool to understand the trophic relationships in a system. Such an analysis allows researchers to uncover the relationship between a study species and its possible food sources. In the case of Chatcolet Lake, stable isotope analysis of carbon and nitrogen with the use of a mixing model (IsoSource) revealed the diet of the caddisfly larvae *Nectopsyche albida* to consist predominantly of macrophytes, while epiphytes were of secondary importance. The signatures of the caddisflies and all their possible food sources collected for this study remained individually distinct by species or grouping over time,

though the ratios of carbon and nitrogen shifted temporally. Overall, these data support the hypothesis that the caddisfly larvae are generalist herbivores and shredders. Subsequent research should focus on collections of a higher number of samples to better understand the natural variation within plant species, and to reduce the influence of an individual sample at extreme ends of the distribution. Because stable isotope analysis is generally most useful in uncovering long-term dietary trends, future analyses may benefit by focusing on the larval tissue turnover time. An integrated signature of a caddisfly larva may not be representative of the food sources in its nearby environment on a given day, as there is an inherent lag time between food source consumption and isotope assimilation. Gratton and Forbes (2006) found this lag time occurring in beetle tissue turnover after providing the insects with a C3-based diet, then switching them to a diet of C4, and measuring the time between a change in isotopic signature. Caddisfly larvae move between macrophyte patches of varying diversity throughout the lake, meaning a larva collected at a given location could have arrived that day and therefore would not have a signature reflecting the macrophyte patch diversity where it was captured. This movement also affects case analysis, as each individual case represents where a caddisfly has spent its life and combining cases to obtain an average signature obscures individual differences in composition. Future studies should concentrate on individual cases to more accurately assign specific signatures. Laboratory experiments could be conducted to determine the rate of tissue turnover and level of incorporation of different food sources. Comparing signatures of caddisflies with controlled diets to signatures of larvae from the field could further verify the contribution of each dietary component to the *N. albida* larvae in Chatcolet Lake.

Literature Cited

Arsuffi, A. T. L., and K. Suberkropp. 1989. Selective feeding by shredders on leaf-colonizing stream fungi: Comparison of macroinvertebrate taxa. Oecologia **79**: 30–37.

Bärlocher, F. 1985. The role of fungi in the nutrition of stream invertebrates. Bot. J. Linn. Sociey **91**: 83–94. doi:https://doi.org/10.1111/j.1095-8339.1985.tb01137.x

Black, A. R., G. W. Barlow, and A. T. Scholz. 2003. Carbon and nitrogen stable isotope assessment of the Lake Roosevelt aquatic food web. Northwest Sci. **77**: 1–11.

Burke, S. M., A. D. Persaud, and P. J. Dillon. 2015. A case against acidifying freshwater macrophytes prior to C and N stable isotope analysis. Aquat. Ecol. **49**: 251–261. doi:10.1007/s10452-015-9519-2

Chappuis, E., V. Seriñá, E. Martí, E. Ballesteros, and E. Gacia. 2017. Decrypting stable-isotope (δ13C and δ15N) variability in aquatic plants. Freshw. Biol. **62**: 1807–1818. doi:10.1111/fwb.12996

Cremona, F., S. Hamelin, D. Planas, and M. Lucotte. 2009. Sources of organic matter and methylmercury in littoral macroinvertebrates: A stable isotope approach. Biogeochemistry **94**: 81–94. doi:10.1007/s10533-009-9309-9

Erhard, D., and E. M. Gross. 2006. Allelopathic activity of *Elodea canadensis* and *Elodea nuttallii* against epiphytes and phytoplankton. Aquat. Bot. **85**: 203–211. doi:https://doi.org/10.1016/j.aquabot.2006.04.002

Fry, B. 1991. Stable isotope diagrams of freshwater food webs. Ecology **72**: 2293–2297. doi:10.2307/1941580

Fry B., and Sherr E.B. 1989. δ13C measurements as indicators of carbon flow in marine and freshwater ecosystems, p. 196–229. *In* Rundel P.W., Ehleringer J.R., and Nagy K.A. [eds.], Stable isotopes in ecological research. Springer.

Glover, J. B., and M. A. Floyd. 2004. Larvae of the genus *Nectopsyche* (Trichoptera:Leptoceridae) in eastern North America, including a new species from North Carolina. J. North Am. Benthol. Soc. **23**: 526–541. doi:10.1899/0887-3593(2004)023<0526:lotgnt>2.0.co;2

Goecker, M. E., J. F. Valentine, and S. A. Sklenar. 2006. Effects of exotic submerged aquatic vegetation on waterfowl in the Mobile-Tensaw Delta. Gulf Mex. Sci. **24**: 68–80.

Goecker, M. E., J. F. Valentine, S. A. Sklenar, and G. I. Chaplin. 2009. Influence from hydrological modification on energy and nutrient transference in a deltaic food web. Estuaries and Coasts **32**: 173–187. doi:10.1007/s12237-008-9105-0

Gratton, C., and A. E. Forbes. 2006. Changes in δ13C stable isotopes in multiple tissues of insect predators fed isotopically distinct prey. Oecologia **147**: 615–624. doi:10.1007/s00442-005-0322-y

Haddock, J. D. 1977. The biosystematics of the caddis fly genus *Nectopsyche* in North America with emphasis on the aquatic stages. Am. Midl. Nat. **98**: 382–421.

Harms, N. E., and M. J. Grodowitz. 2009. Insect herbivores of aquatic and wetland plants in the United States: A checklist from literature. J. Aquat. Plant Manag. **47**: 73–96.

Herwig, B. R., D. A. Soluk, J. M. Dettmers, and D. H. Wahl. 2004. Trophic structure and energy flow in backwater lakes of two large floodplain rivers assessed using stable isotopes. Can. J. Fish. Aquat. Sci. **61**: 12–22. doi:10.1139/f03-139

Holzenthal, R. W. 1996. Catalog and bibliography of the species of *Nectopsyche* (Trichoptera:Leptoceridae).

Hyodo, F. 2015. Use of stable carbon and nitrogen isotopes in insect trophic ecology. Entomol. Sci. **18**: 295–312. doi:10.1111/ens.12128

Jacobsen, D. 1993. Trichopteran larvae as consumers of submerged angiosperms in running waters. Oikos **67**: 379–383.

Jacquemin, S. J., C. Miller, and M. Pyron. 2013. Identifying local scale food web variation using stable C and N isotopes in a central Indiana reservoir and downstream river. Proc. Indiana Acad. Sci. **122**: 62–68.

Jepsen, D. B., and K. O. Winemiller. 2002. Structure of tropical river food webs revealed by stable isotope ratios. Oikos **96**: 46–55.

Kovalenko, K. E., and E. D. Dibble. 2014. Invasive macrophyte effects on littoral trophic structure and carbon sources. Hydrobiologia **721**: 23–34. doi:10.1007/s10750-013-1633-3

Layman, C. A., D. A. Arrington, C. G. Montana, and D. M. Post. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology **88**: 42–48.

Lürling, M., G. Van Geest, and M. Scheffer. 2006. Importance of nutrient competition and allelopathic effects in suppression of the green alga *Scenedesmus obliquus* by the

macrophytes *Chara*, *Elodea* and *Myriophyllum*. Hydrobiologia **556**: 209–220. doi:10.1007/s10750-005-1168-3

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}N$ and animal age. Geochim. Cosmochim. Acta **48**: 1135–1140. doi:10.1016/0016-7037(84)90204-7

Newman, R. M. 1991. Herbivory and detritivory on freshwater macrophytes by invertebrates: A review. J. North Am. Benthol. Soc. **10**: 89–114.

Nystrom, P., C. Bronmark, and W. Graneli. 1999. Influence of an exotic and a native crayfish species on a littoral benthic community. Oikos **85**: 545–553. doi:10.2307/3546704

Oláh, J., and J. Oláh Jr. 2017. Fine phenomics applied to the *Nectopsyche* genus (Trichoptera): Species delineation by speciation traits. Opusc. Zool. Budapest **48**: 117–184. doi:10.18348/opzool.2017.2.117

Phillips, D. L., and J. W. Gregg. 2001. Uncertainty in source partitioning using stable isotopes. Oecologia **127**: 171–179. doi:10.1007/s004420000578

Phillips, D. L., and J. W. Gregg. 2003. Source partitioning using stable isotopes: Coping with too many sources. Oecologia **136**: 261–269.

Post, D. M. 2002. Using stable isotopes To estimate trophic position: Models, methods, and assumptions. Ecology **83**: 703–718. doi:Doi 10.2307/3071875

Rounick, J. S., and M. J. Winterbourn. 1986. Stable carbon isotopes and carbon flow in ecosystems. Bioscience **36**: 171–177. doi:10.2307/1310304

Syväranta, J., H. Hämäläinen, and R. I. Jones. 2006. Within-lake variability in carbon and nitrogen stable isotope signatures. Freshw. Biol. **51**: 1090–1102. doi:10.1111/j.1365-2427.2006.01557.x

Toetz, D. 1997. Does Eurasian watermilfoil, *Myriophyllum spicatum*, contribute to the diet of animals in a turbid reservoir? J. Freshw. Ecol. **12**: 545–551. doi:10.1080/02705060.1997.9663569

USEPA. 2017. Stable isotope mixing models for estimating source proportions.

Ventura, M., L. Liboriussen, T. Lauridsen, M. Søndergaard, M. Søndergaard, and E. Jeppesen. 2008. Effects of increased temperature and nutrient enrichment on the stoichiometry of primary producers and consumers in temperate shallow lakes. Freshw. Biol. **53**: 1434–1452. doi:10.1111/j.1365-2427.2008.01975.x

Verburg, P., C. W. Hickey, and N. Phillips. 2014. Mercury biomagnification in three geothermally-influenced lakes differing in chemistry and algal biomass. Sci. Total Environ. **493**: 342–354. doi:10.1016/j.scitotenv.2014.05.097

Table 3.1. Stable isotope values of ^{15}N and ^{13}C from various papers. Dashes indicate a lack of information for that isotope.

	Isotope (‰)		
Species	$\delta^{15}N$	$\delta^{13}C$	Source
Elodea	1.3, 3.2, 4.5	-20.8, -21.7, -19.7	Burke et al. 2015
	-	-20.1	Chappuis et al. 2017
	~2	~-19	
	7.7 ± 0.3	-14.7 ± 0.1	Cremona et al. 2009
	~6	~-20.8	Nystrom et al. 1999
	7.96	-11.1	Verburg et al. 2014
Myriophyllum	-	-32.9 to -13.8	Chappuis et al. 2017
	~4	~-17	
	7.4 ± 0.4	-20.7 ± 0.5	Cremona et al. 2009
	6.23 ± 0.08	-17.69 ± 0.17	Goecker et al. 2006
	4.69 ± 0.14, 5.93 ± 0.11	−19.38 ± 0.01, −19.83 ± 0.08	Goecker et al. 2009
	~13.7	~-23.4	Herwig et al. 2004
	0.25, 2.13	-8.63, -11.50	Kovalenko and Dibble 2014
	-	-11.3, -8.2, -12.6, -11.2	Toetz 1997

Table 3.2. All sampling occasions listed with all samples taken on that occasion for stable ^{13}Carbon and ^{15}Nitrogen isotope analysis. Spring 2018 encompasses all samples taken from 26-April, 8-May, 23-May, 5-June, and 19-June.

Date	Samples
10-Oct-17	*Nectopsyche albida*
	Myriophyllum spp.
	Elodea canadensis
	Ceratophyllum demersum
	Detritus
26-Apr-18	Filamentous algae
	Chironomids
	Fugus
	Epiphytes
8-May-18	*Nectopsyche albida*
	Potamogeton amplifolius
23-May-18	*Nectopsyche albida*
	Nectopsyche albida
	Filamentous algae
5-Jun-18	*Nectopsyche albida*
	Myriophyllum spp.
19-Jun-18	*Elodea canadensis*
28-Aug-18	*Nectopsyche albida*
	Myriophyllum spp.
	Elodea canadensis
	Ceratophyllum demersum
	Potamogeton richardsonii
	Ranunculus aquatilis
	Potamogeton pusillis
	Najas spp.

Table 3.2 cont.

Date	Samples
25-Sep-18	*Nectopsyche albida*
	Myriophyllum spp.
	Elodea canadensis
	Potamogeton richardsonii
	Ranunculus aquatilis
	Epiphytes
9-Oct-18	*Nectopsyche albida*
	Myriophyllum spp.
	Elodea canadensis
	Ceratophyllum demersum
	Potamogeton richardsonii
	Epiphytes
	Nectopsyche albida case
24-Oct-18	*Nectopsyche albida*
	Myriophyllum spp.
	Elodea canadensis
	Ceratophyllum demersum
	Potamogeton richardsonii
	Epiphytes
	Nectopsyche albida case

Table 3.3. Results of contributions of potential food sources to the diet of *Nectopsyche albida* in Chatcolet Lake, as determined by the mixing model IsoSource. Percentages are mean values of contribution from the indicated food item to the source signature, the *N. albida* larvae, while values brackets represent standard error. The source increment for each analysis was 1%, and the tolerance value was 0.15 for 10-October-2017 and 9-October-2018, and 0.1 for Spring 2018 and 24-October-2018.

Species	Percentage contribution on each date			
	10 October 2017	Spring 2018	9 October 2018	24 October 2018
Myriophyllum spp.	22.8% (±0.01)	22.9% (±<0.01)	0% (±0)	8.3% (±<0.01)
Elodea canadensis	44.2% (±<0.01)	3.3% (±<0.01)	78.3% (±<0.01)	19.3% (±<0.01)
Epiphytes	-	11.7% (±<0.01)	21% (±0)	35.6% (±<0.01)
Ceratophyllum demersum	32.6% (±<0.01)	-	0.3% (±<0.01)	20% (±<0.01)
Potamogeton richardsonii	-	-	0.3% (±<0.01)	16.8% (±<0.01)
Potamogeton amplifolius	-	1% (±<0.01)	-	-
Filamentous algae	-	13.1% (±<0.01)	-	-
Fungus	-	48.1% (±<0.01)	-	-
Detritus	0.4% (±<0.01)	-	-	-

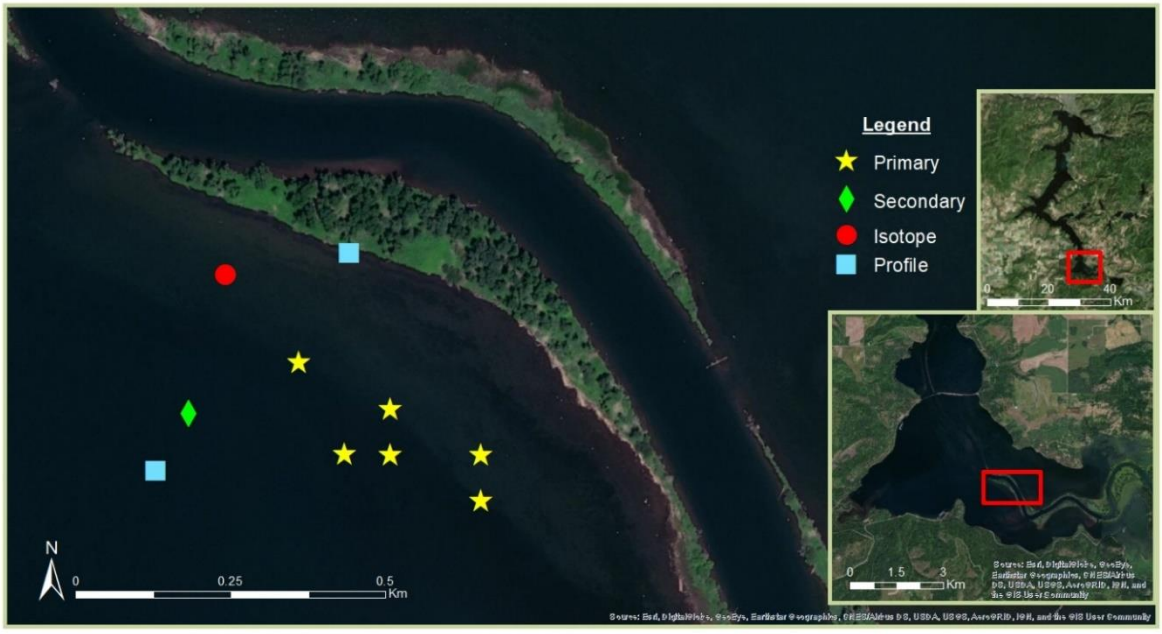

Figure 3.1. Site map of Chatcolet Lake. The yellow stars represent the six sites regularly sampled throughout 2017 and 2018, and the star at far left is where most of the 2018 Hydrolab profiles were taken. The green diamond represents a site where I collected caddisfly larvae in early 2018 when they were not present at the six regular sites. The red circle (Isotope) represents the point where I collected the samples for isotope analysis and most of the 2018 caddisflies to supplement those from the six regular sites. The blue squares represent sites where additional profile data was collected.

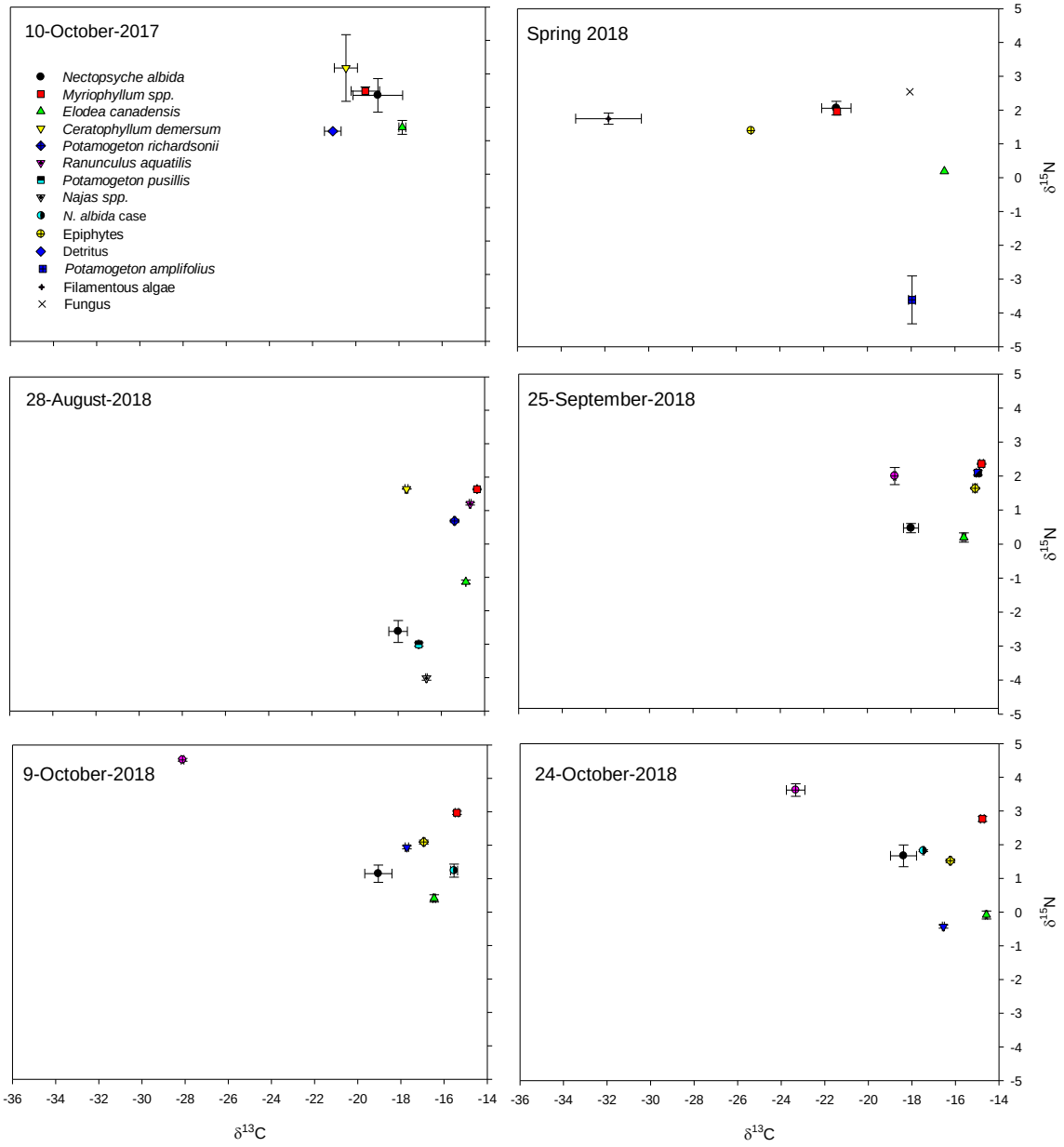

Figure 3.2. Isotope data (means±SE) from samples collected between 10-Oct2017 and 24 Oct 2018 from Chatcolet Lake. The nitrogen ratio is ^{15}N:^{14}N, and the carbon ratio is ^{13}C:^{12}C. Figures are sequential left to right.

Chapter 4: The selection and consumption of native and invasive macrophytes by *Nectopsyche albida* larvae in Chatcolet Lake, Idaho

Abstract

Feeding trials are a commonly used tool in ecological research to provide insight into what food sources organisms consume and prefer, and the rate of consumption. In Chatcolet Lake, Idaho, the caddisfly *Nectopsyche albida* occurs among a variety of macrophytes including an invasive milfoil hybrid, *Myriophyllum* spp. (*Myriophyllum spicatum* × *Myriophyllum sibiricum*), *Elodea canadensis, Ceratophyllum demersum,* and others which appear to suffer damage from herbivory, suggesting a possible relationship between the caddisfly larvae and the macrophytes. To determine if and how much the caddisfly larvae contributed to the damage, three feeding experiments were undertaken between August and October 2018. Individual *Nectopsyche albida* larvae were given isolated *Myriophyllum* spp. and native *Elodea canadensis,* as well as both species combined in varying ratios. Consumption occurred in all three experiments but was highly variable. The caddisfly cases also grew in two of the three experiments, indicating that the larvae consumed the macrophytes both for assimilation of nutrients and to construct their cases. Further experiments with a higher number of replicates and with more potential food sources should be the focus of future research to allow researchers to estimate the lake-wide effect of caddisfly herbivory on macrophyte beds.

Introduction

Observing and quantifying consumption through feeding trials is an approach frequently used in ecology. When studying aspects of an ecosystem, determining a study organism's diet and feeding rate is important for both the elucidation of their life history and determining their role in the environment. When studying an invasive species, feeding trials can provide important information to better understand how organisms interact with the invasive. Invasive species can be extremely disruptive to an ecosystem because a lack of a control (usually a characteristic of an invasive species) which can allow it to rapidly expand its population resulting in unanticipated consequences (Doody et al. 2009). In some cases,

organisms can serve as natural controls, or biocontrols, of other organisms (Mazzei et al. 1999; Newman and Biesboer 2000). Feeding trials can help to understand if certain species can serve as controls for others by providing isolated, specific combinations of food or prey items with which an organism can interact (Van Klinken and Heard 2000). Before feeding experiments are conducted, however, selection of study organisms and their suspected food source must occur. Realistic choices should be made about which food items to include for a given organism based on their previously established ecology.

Some generalist species can be effective in reducing invasive species. For example, Symondson et al. (2002) reported that in about 75% of feeding experiments, generalist predators were able to reduce pests. This success is in part due to the nondiscriminatory nature of generalist species which results in a reduction of all available food items, including the invasive. However, abundance of all food items decreases in this scenario, which is not always a desired outcome. Other species are adapted to feed specifically on one organism (e. g., Creed and Sheldon 1995; Sheldon and Creed 1995; Tamayo and Grue 2004). Despite the success of generalists, species that are specialized to a certain food source tend to be more effective in reducing a target species than a generalist predator (Riechert and Lockley 1984; DeBach and Rosen 1991; Polis and Holt 1992; Snyder and Wise 1999).

Determining how organisms feed on their chosen food source can be another focus of feeding experiments. In the case of aquatic insects, scrapers and shredders affect plants differently, so identifying which type of herbivore is in a system is important to determine how to use their presence for management (Graça et al. 1993). According to Holzenthal (1996) larvae of *Nectopsyche* function as shredder-herbivores and collector-gatherers similar to other caddisflies. The caddisfly first exudes a silk substance from its labial glands to anchor itself to a plant, then uses its legs to collect food and transfer it to the mouth (Haddock 1977). Analysis of gut contents has shown the presence of fine organic particulate matter and the remains of vascular plant material (Glover and Floyd 2004). Gut content analysis has shown that *N. albida* feed on macrophytes, including species of *Myriophyllum* (Tozer et al. 1980). This diet is also true for CDA Lake as borne out by analysis of stable carbon and nitrogen isotopes (Chapter 3). However, their rate of consumption of macrophytes in CDA Lake is unknown.

Nectopsyche albida larvae and the milfoil hybrid *Myriophyllum* spp. (*Myriophyllum spicatum* × *Myriophyllum sibiricum*) occur together in Chatcolet Lake, Idaho, along with numerous other species of macrophytes (Thum 2017). Damage to *Myriophyllum* and other plant species, specifically the native *Elodea canadensis*, resembling herbivory has been observed on plants on which *N. albida* larvae were present. Given that caddisfly density is related to density of vegetative biomass (Chapter 2, figure 2.10) and stable isotope analysis (Chapter 3) indicated assimilation of these macrophytes, I undertook controlled feeding and selection experiments to determine rates of consumption and preference of *N. albida* larvae for *Myriophyllum* spp. and *Elodea canadensis*. This would provide an indication of which macrophytes the species is most likely to target in the lake and allow me to calculate the amount of damage that would be inflicted on the macrophytes in general, an important management consideration.

Methods and Materials

Study Site

Coeur d'Alene (CDA) Lake is one of the largest in the state of Idaho and is located in the panhandle of the state. This lake is central to the Coeur d'Alene Tribe and is the heart of their historic territory. Currently, the Tribe manages the southern third of the lake. Originally, the southern end of Coeur d'Alene Lake was segmented and composed of a series of shallow floodplain lakes including Chatcolet Lake, Round Lake, and Benewah Lake connected by the St. Joe River. The lakes are now inundated and connected throughout the year, due to the advent of lake level regulation resulting from the installation of the Post Falls dam on the Spokane River, the outflow of CDA Lake located at the northern end of the lake. Parts of the St. Joe River channel and levees remain in the southern lake, but much of it is now submerged. The remnant levees and channel remain as a loose barrier between Chatcolet and Round lakes, but overall, the former water bodies at the southern end of Coeur d'Alene Lake are inundated and part of the main lake (Figure 4.1).

Field Collections

For each experiment, I used a 30.5 cm -wide rake to collect fresh vegetation from Chatcolet Lake and the St. Joe River (immediately adjacent and flowing into Chatcolet Lake). I collected the greenest and most robust *Elodea canadensis* and *Myriophyllum* spp. I could find in the area and estimated that I required approximately 40 grams of biomass for the experiments, split evenly between *Myriophyllum* and *Elodea*. At the same time, I also collected at least 25 caddisfly larvae for each experiment from the area where the plants were gathered. Native lake water was collected in 20 L (5 gal) buckets.

Macrophyte consumption and selection experiments

Field-collected macrophytes and caddisfly larvae separated by species. All samples were processed in shallow water to prevent their desiccation. Caddisfly larvae for the feeding experiments were isolated and maintained in aerated 80 µm-filtered lake water until needed (approximately 24 h) to allow them to void their guts, encourage feeding during the experiment, and to better standardize their appetite.

To prepare each experiment, I determined the wet mass of individual sprigs of each plant species included in each experiment. Each sprig was blotted on a paper towel until surface water was no longer evident, after which I obtained the mass to the nearest 0.1 mg, similar to the method used by Grutters et al. (2016). I then adjusted the plant material to the target mass of 1.0 g for each chamber. I then repeated the massing and blotting three times, dunking plant sprigs in lake water between blotting, before placing them in their respective 18.4L × 12.2W × 9.8H cm chambers containing 800 mL of 80 µm-filtered lake water and a single air stone set to release a slow series of bubbles continuously to maintain oxygen concentrations at night. All experiments were run at a temperature of 20°C for a period of 7.5 days (August 31-September 8, 2018) and 7 days (September 12-19; October 5-12, 2018).

For the single species consumption experiments, five chambers contained only 1 g of *Myriophyllum*, each of which was paired with a control chamber that only contained the macrophyte and no larva, totaling to ten chambers. This set up was duplicated, but with *Elodea* instead of *Myriophyllum* as the included macrophyte species. Preference experiments, set up in triplicate with a total of nine chambers, contained 1 g of total biomass in the ratios of *Myriophyllum* to *Elodea* of 75:25, 50:50, 25:75. Experiments were started by placing one

pre-measured (case length, see Chapter 2 for measurements) *N. albida* larva in each experimental chamber.

At the conclusion of each experiment I measured the caddisfly case lengths again to calculate any size differences. I also used the blotting technique again to obtain the wet mass (in triplicate) of any plant biomass remaining in the chambers. In some instances, the plants became so degraded over the course of the experimental period that I could not obtain all three replicate post-experiment masses.

Analysis of results

Control chambers containing only macrophytes served to indicate changes in mass of the plant sprigs. The change in mass of controls for each respective experiment were averaged and subtracted from the mean mass of the five or three replicates of the single species or selection experiments, respectively. For the single species experiments, I conducted Mann-Whitney tests to examine if the mean consumption of biomass differed between *Myriophyllum* and *Elodea* in each of the three experiments.

To examine if the mean consumption of each species in the selection experiments differed, I used two-way ANOVAs with mean consumption of *Myriophyllum* and *Elodea* as the response variable, and experiment and ratios as treatments. These analyses were used to indicate if mean consumption differed due to experiment (temporally) or ratio of macrophyte species present in a given treatment. Any significant ANOVA was followed by a Tukey Post-Hoc test to detect means that differed.

Results

The results of the single plant species experiments varied, but in two of the three experiments caddisflies consumed more *Myriophyllum* than *Elodea* (Figure 4.2). In the August experiment, the change in mass of *Myriophyllum* could not be attributed to herbivory given a larger loss of mass in the controls. However, the *N. albida* larvae consumed an average of about 20.1±8.9 mg/ind./day of *Elodea* (Mean ±SE; Figure 4.2). However, the consumption did not differ between the two species (Mann-Whitney test, $U = 10.0$, $p = 0.690$). This is the only single plant species experiment in the mass of plants in the controls exceeded consumption by the caddisflies, and the only experiment in which there was no net

consumption of *Myriophyllum*. The experiment run in mid-September resulted in an average consumption of *Elodea* of 20.1±3.9 mg/ind./day which was similar to the August experiment. However, unlike the first experiment, the consumption of *Myriophyllum* was 27.0±8.3 mg/ind./day. Consumption of biomass did not differ between the species (Mann-Whitney test, $U = 5.00$, $p = 0.151$). The results of the experiment in October were similar to those of the second experiment; caddisflies consumed an average of 14±2.9 mg/ind./day of *Elodea* and 18±3.5 mg/ind./day of *Myriophyllum* (Figure 4.2). Again, consumption did not differ between the species (Mann-Whitney test, $U = 8.00$, $p = 0.421$).

Results of the preference feeding experiments also were varied (Table 4.1); in some cases there was preference for *Myriophyllum*, while in others there was preference for *Elodea*. For consumption rates, positive values indicate where more consumption than plant growth occurred, and negative values indicate where plant growth occurred and overshadowed consumption by the larvae. In the 75:25 and 25:75 (ratios of *Myriophyllum* : *Elodea*) trials of the three experiments, *Myriophyllum* biomass increased between -7.1±2.8 to -45.7±15.4 mg/ind./day. In the 75:25 trials, *Elodea* gained mass in the third experiment (-4.6±2.4) but was consumed up to 6.2±2.2. Consumption of *Myriophyllum* in the 50:50 treatment ranged from 4.3±7.5 to 12.7±4.5 mg/ind./day, while *Elodea* gained biomass in one experiment (-3.3±3.6) and was consumed up to 10.5±1.3 mg/ind./day. *Myriophyllum* gained biomass in one of the 25:75 treatments (-0.9±1.2) but was consumed up to 9.2±1.0 mg/ind./day. *Elodea* was consumed in all three 25:75 treatments, ranging from 0.7±5.4 to 30.1±11.7 mg/ind./day (Table 4.1).

Results of the two-way ANOVAs from the preference experiments showed that date of experiment did not influence mean consumption for *Myriophyllum* ($F= 2.93$, $d.f.= 2$, $p= 0.16$). However, the ratio at which plants were presented did influence the mean consumption rates ($F= 9.07$, $d.f.= 2$, $p= 0.03$). Tukey Post-Hoc testing revealed that only the 75:25 and 25:75 ratio treatments differed ($p= 0.048$). Date of experiment did not have a significant influence on mean consumption of *Elodea* ($F= 1.05$, $d.f.= 2$, $p= 0.43$), nor did the ratio of plant species ($F= 0.80$, $d.f.= 2$, $p= 0.51$).

At most, the average density of the larvae in samples taken from Chatcolet Lake was 13 ind./m^2 (Chapter 2, figure 2.9). The highest mean consumption of *Myriophyllum* was

0.013 g/ind./day, and the highest mean consumption of *Elodea* was 0.030g/ind./day from the feeding experiments. From these consumption rates and the highest average number of caddisflies per square meter from the field (13 ind./m^2), the larvae would consume about 0.026 g/day of *Myriophyllum* biomass and about 0.059 g/day of *Elodea* biomass (Dry mass assuming it is approximately 15% of wet mass). The highest average dry biomass of *Myriophyllum* from field samples was 16.25 g/m^2, and the highest average dry biomass of *Elodea* was 200 g/m^2.

Changes in case length followed a pattern of decreased growth throughout the three experiments (Table 4.2) and is consistent with the pattern seen in the lake (Chapter 1). Average case length increased the most during the first experiment in the individual species chambers containing *Myriophyllum* (0.83mm to 3.20 mm). Case length increased less during the second experiment, ranging from 0.90 to 1.17 mm. In the third experiment, the average case length decrease ranged from -2.70 to -7.33 mm over the course of the experiment (Table 4.2). Patterns do not appear to exist in the same treatments between experiments.

Discussion

In all three experiments, the average biomass of some plants increased indicating that plant growth exceeded the consumption by *N. albida* larvae. This highlights some of the difficulties of this type of experiment by using live plants for which biomass of live specimen must be obtained before and after the experiment. In addition, the experiments are further constrained because sufficient biomass must be provided so the larvae will not run out of food, while at the same time the fraction consumed must be a measurable difference. For the trials in which the consumption of plants was measurable, it is unlikely that the plants also did not grow, meaning the caddisfly larvae consumed more biomass than the plants accrued during growth over the course of the experiment. Growth did not necessarily occur for all plant sections, however, as some of the plant sprigs may not have included nodes from which growth would occur.

Although I recognize that laboratory conditions are highly artificial and are difficult to extrapolate to the natural environment, the consumption rates I report provide initial consumption rates and selection of *Myriophyllum* and *Elodea* by *N. albida*. The entirety of

the lake encompasses many more food options from which the larvae can choose than the one or two macrophyte species I offered in the laboratory. Forcing an organism to choose one or between two food items is not generally realistic or representative of nature, including in the case of food item diversity in Chatcolet Lake (Jacobsen 1993). Conditions such as light were also dissimilar, and may have changed the behavior of the insects in the laboratory compared to the field (Lactin and Johnson 1995). Differences in available space also changes how insects group together, and therefore how they feed and interact with each other. Competition for the same desirable food source in the field changes the rate at which caddisflies feed (Matczak and Mackay 1990), and because my experimental chambers held one caddisfly each, this phenomenon was not captured. Based on the overall patterns of the feeding experiment results, my observations of fecal matter in the bottom of the chambers, and the general increase in case size, the caddisflies did consume the macrophytes.

Results of the ANOVAs show that experiment date did not influence mean consumption, but the ratio of species did for *Myriophyllum*. The difference in mean consumption rates between the 25% and 75% *Myriophyllum* treatments comes from a much higher growth in biomass in the 75% tanks than the 25% tanks. Because the growth in the 75% *Myriophyllum* majority tanks was so high, the actual amount of consumption was obscured. It is possible that if the *Myriophyllum* had grown less over the course of the experiments, the mean consumption rate may have been more similar to that of the other treatments. *Myriophyllum* probably grew more when it was 75% of the biomass in a tank because the stalks included in these treatments were longer, meaning more of the plant could sprout new growths. The mean consumption of *Elodea* did not differ based on date or ratio, indicating that the caddisfly larvae consumed *Elodea* at the same rate regardless of time or ratio of species present, and consumption of *Elodea* remained constant despite the presence of *Myriophyllum*.

The high variation in these experiments could be related to several factors such as time (season) of collection, variation in individual caddisflies, and individual variation in macrophytes. Because the samples were collected over time from Chatcolet Lake, not all macrophytes used in the experiments were at the same life stage. Though I collected and selected the greenest, most robust plants I could find for each experiment, the plants were in

noticeably poorer overall condition for the third experiment compared to the first, while they appeared healthiest for the second experiment. *Myriophyllum* appeared to worsen most over time, though *Elodea* became more prone to fragmenting as the plants underwent transformations for winter. By the time I collected plants for the third trial, *Elodea* had begun to grow winter buds, which were thicker with more densely spaced leaves compared to summer growth, possibly affecting its palatability. Macrophytes also tend to become degraded over time, making them a less robust food source. Some variation could also have been the result of different epiphytes on the plants temporally. I noticed a thicker layer of epiphytes in fall, which may be related to the poorer condition of the macrophytes then. The size of the caddisfly larvae also increased over the course of the three experiments, which could have contributed to the variation. Towards the end of the growing season the metabolism of larvae slows as the lake water cools. Thus, although all experiments were run at the same temperature in the laboratory, individuals may have been at different physiological stages which could have influenced their preference and consumption rates. Obtaining an accurate wet mass of the plants also contributed to the variability. I chose to use the blotting method as opposed to using a salad spinner, for example, to remove the water from the plants for pre- and post-experiment masses. The spinning method would have been too destructive to the plants and spinning the plants possibly could have removed desirable epiphytes, and the plants themselves could have disintegrated. Despite exercising care in handling the plants, it was difficult to keep them intact with the blotting method, especially in the third experiment as they were very fragile then. Additionally, *Elodea* stems are much thinner and denser than those of *Myriophyllum*, meaning they held less water which could have easily affected the mass. However, because of the differences in stems, I had to use smaller pieces of *Myriophyllum* than for *Elodea* to arrive at the same blotted dry mass. It is possible that this biased caddisflies to consume more *Elodea* than *Myriophyllum*, as there were more leaves on the longer *Elodea* stems than I was able to include on the shorter *Myriophyllum* stems.

Extrapolating consumption rates with field-based densities of caddisflies give estimates of possible macrophyte consumption in Chatcolet Lake. The dry biomass of the field samples included both stems and leaves of both plants, but the herbivory observed in both the feeding experiments and the field was damage to only the leaves. Without

measuring the difference in biomass between stems and leaves, it is unclear if the larvae would cause the damage seen in the field. However, personal observations indicated that the stems of the macrophytes constituted more of the total biomass of the plant than the leaves. It is possible that with the larval density and the amount of time they have in the field to consume the macrophyte leaves, much of the observed damage could be attributed to the larvae. Though it is unclear how well the artificial nature of the experiments reflects actual consumption in the field, these values serve as a baseline for future studies and gives managers a rough expectation of macrophyte consumption by *N. albida* larvae.

Increases in case lengths during the first and second experiments indicate that the caddisflies assimilated the macrophyte mass lost in those experimental tanks. Decreased growth in the second experiment compared to the first follows the seasonal pattern observed in the field (Chapter 2) because the second group of caddisflies were already subject to cooling in the lake at the time of the experiment. The lower growth may have been related to changes in the physiology of individuals in preparation for winter. However, the decrease in case length in the third experiment is curious and difficult to explain. It is possible that the macrophytes in the third experiment were too degraded to provide enough quality sustenance to the larvae and they consumed their own cases as a supplement. This raises an interesting point; in Chapter 2 head capsule width ceased to increase after August, while case length continued to increase. While I suggested that this increase may be to accommodate a larger body, perhaps it is because the case serves as a self-contained energy reserve that is consumed during the period (fall to early spring) when macrophytes are absent from the lake. Another possible cause of case shortening could be the presence of a parasite. Parasites are known to cause damage to the protective shells of other organisms (e. g., Wells and Wells 1962). The damage to only the third group of caddisflies could be explained if there is a seasonally active parasite present in the population which lessens the integrity of the caddisfly case. This deserves further investigation.

With the level of variation in the experiments it is difficult to make any claim to larval food preferences. While the caddisflies did consume *Myriophyllum*, they also consumed *Elodea*, indicating that the caddisflies are content to consume either species. Too much overlap occurred in the consumption values to definitively say that *N. albida* larvae

might target *Myriophyllum*, despite the weak indication of greater *Myriophyllum* consumption in the isolated species experiments. *Nectopsyche albida* are thought to be generalists and based on the data from these three feeding experiments and field observations, it appears that the larvae exhibit a generalist pattern of macrophyte consumption in Chatcolet Lake.

Conclusions and Future Work

Nectopsyche albida larva are classified as generalist herbivores (Harms and Grodowitz 2009) which is supported by the results of these feeding experiments. Given macrophytes from their natural habitat in a laboratory setting, the caddisflies consumed both *Myriophyllum spp*. and *Elodea canadensis*, though at different rates. Coupling these experiments with field observations and the stable isotope results (Chapter 3), it is clear that the caddisflies consume macrophytes, however, given the high variability in the selection experiments, it is unclear if they prefer the invasive *Myriophyllum* over native *Elodea*. This will require further study. I also would suggest adding other macrophytes such as Richardson's pondweed which can be the sole macrophyte in Chatcolet Lake early in the season and thus could be a potential food source. Future experiments should also consider chamber size to ensure that the behavior of caddisflies is not unduly influenced by chamber size. In addition, it would be insightful to examine consumption at different temperatures to reflect the annual cycle in the lake and provide seasonally realistic consumption rates. Because feeding rate probably changes based on larval life cycle stage, conducting feeding trials at all stages of larval development would also give insight into how the caddisflies feed and what they feed on temporally. If the caddisflies were grown from eggs, their feeding rate and preference could be determined for their entire aquatic stage. Such insight would provide accurate information and indicate the role of *N. albida* larvae in the Chatcolet Lake ecosystems.

Literature Cited

Creed, R. P., and S. P. Sheldon. 1995. Weevils and watermilfoil: Did a North American herbivore cause the decline of an exotic plant? Ecol. Appl. **5**: 1113–1121.

DeBach, P., and D. Rosen. 1991. Biological control by natural enemies, 2nd ed. Cambridge Univ. Press.

Doody, J. S., B. Green, D. Rhind, C. M. Castellano, R. Sims, and T. Robinson. 2009. Population-level declines in Australian predators caused by an invasive species. Anim. Conserv. **12**: 46–53. doi:10.1111/j.1469-1795.2008.00219.x

Glover, J. B., and M. A. Floyd. 2004. Larvae of the genus *Nectopsyche* (Trichoptera:Leptoceridae) in eastern North America, including a new species from North Carolina. J. North Am. Benthol. Soc. **23**: 526–541. doi:10.1899/0887-3593(2004)023<0526:lotgnt>2.0.co;2

Graça, M. A. S., L. Maltby, and P. Calow. 1993. Importance of fungi in the diet of *Gammarus pulex* and *Asellus aquaticus* I: feeding strategies. Oecologia **93**: 139–144. doi:10.1007/BF00321203

Grutters, B. M. C., E. M. Gross, and E. S. Bakker. 2016. Insect herbivory on native and exotic aquatic plants: Phosphorus and nitrogen drive insect growth and nutrient release. Hydrobiologia **778**: 209–220. doi:10.1007/s10750-015-2448-1

Haddock, J. D. 1977. The biosystematics of the caddis fly genus *Nectopsyche* in North America with emphasis on the aquatic stages. Am. Midl. Nat. **98**: 382–421.

Harms, N. E., and M. J. Grodowitz. 2009. Insect herbivores of aquatic and wetland plants in the United States: a checklist from literature. J. Aquat. Plant Manag. **47**: 73–96.

Holzenthal, R. W. 1996. Catalog and bibliography of the species of *Nectopsyche* (Trichoptera:Leptoceridae).

Jacobsen, D. 1993. Trichopteran larvae as consumers of submerged angiosperms in running waters. Oikos **67**: 379–383.

Van Klinken, R. D., and T. A. Heard. 2000. Estimating fundamental host range: A host-specificity study of a potential biocontrol agent for *Prosopis* species (Leguminosae). Biocontrol Sci. Technol. **10**: 331–342. doi:10.1080/09583150050044600

Lactin, D. J., and D. L. Johnson. 1995. Temperature-dependent feeding rates of *Melanoplus sanguinipes* nymphs (Orthoptera: Acrididae) in laboratory trials. Environ. Entomol. **24**: 1291–1296. doi:10.1093/ee/24.5.1291

Matczak, T. Z., and R. J. Mackay. 1990. Territoriality in filter-feeding caddisfly larvae: Laboratory experiments. J. North Am. Benthol. Soc. **9**: 26–34.

Mazzei, K. C., R. M. Newman, A. Loos, and D. W. Ragsdale. 1999. Developmental rates of the native milfoil weevil, *Euhrychiopsis lecontei*, and damage to Eurasian watermilfoil at constant temperatures. Biol. Control **16**: 139–143. doi:10.1006/bcon.1999.0739

Newman, R. M., and D. D. Biesboer. 2000. A decline of Eurasian watermilfoil in Minnesota associated with the milfoil weevil *Euhrychiopsis lecontei*. J. Aquat. Plant Manag. **38**: 105–111.

Polis, G. A., and R. D. Holt. 1992. Intraguild predation: The dynamics of complex trophic interactions. Trends Ecol. Evol. **7**: 151–154.

Riechert, S. E., and T. Lockley. 1984. Spiders as biological control agents. Annu. Rev. Entomol. **29**: 299–320.

Sheldon, S. P., and R. P. Creed. 1995. Use of a native insect as a biological control for an introduced weed. Ecol. Appl. **5**: 1122–1132.

Snyder, W. E., and D. H. Wise. 1999. Predator interference and the establishment of generalist predator populations for biocontrol. Biol. Control **15**: 283–292. doi:10.1006/bcon.1999.0723

Symondson, W. O. C., K. D. Sunderland, and M. H. Greenstone. 2002. Can generalist predators be effective biocontrol agents? Annu. Rev. Entomol. **47**: 561–594. doi:10.1146/annurev.ento.47.091201.145240

Tamayo, M., and C. E. Grue. 2004. Developmental performance of the milfoil weevil (Coleoptera: Curculionidae) on watermilfoils in Washington state. Environ. Entomol. **33**: 872–880. doi:10.1603/0046-225X-33.4.872

Thum, R. A. 2017. Genetic analysis of invasive Eurasian watermilfoil in Idaho waters.

Tozer, W. E., V. H. Resh, and J. O. Solem. 1980. Bionomics and adult behavior of a lentic caddisfly, *Nectopsyche albida* (Walker). Am. Midl. Nat. **106**: 133–144. doi:10.2307/2425143

Wells, H. W., and M. J. Wells. 1962. The polychaete *Ceratonereis tridentata* as a pest of the scallop *Aequipecten gibbus*. Biol. Bull. **122**: 149–159. doi:10.2307/1539328

Table 4.1. Results of laboratory preference experiments of *Nectopsyche albida* given a choice of *Myriophyllum* spp. and *Elodea canadensis* at different ratios. Values listed are the mean consumption rates (mg/ind./day) of *Myriophyllum spp.* and *Elodea canadensis* by individual *Nectopsyche albida* larvae. Standard error values are listed directly below in brackets. Three replicate tanks for each treatment with three controls were included in all experiments. Shading indicates tanks where that plant increased in average biomass. Experiments were conducted at the University of Idaho, Moscow, ID. Materials for experiments were collected from Chatcolet Lake, ID.

Experiment	Date[1]	*Myriophyllum* spp. : *Elodea canadensis* (milligrams/individual/day)					
		75:25		50:50		25:75	
1	August	-45.7 (±15.4)[2]	6.2 (±2.2)	5.0 (±16.9)	-3.3 (±3.6)	-0.9 (±1.2)	4.8 (±4.4)
2	September	-15.7 (±16.8)	2.2 (±6.1)	4.3 (±7.5)	7.0 (±4.2)	6.8 (±4.1)	30.1 (±11.7)
3	October	-7.1 (±2.8)	-4.6 (±2.4)	12.7 (±4.5)	10.5 (±1.3)	9.2 (±1.0)	0.7 (±5.4)

[1] For exact dates, see Methods section

[2] Values in brackets represent standard error

Table 4.2. Average difference in case length from the beginning of the experiment to the end. The treatment column indicates if the caddisflies were part of the isolated species experiments or the preference experiments. All ratios are from the preference experiments, and they indicate the ratio of included plant biomass (*Myriophyllum spp.* : *Elodea canadensis*). Values in brackets represent standard error.

Experiment	Treatment	Average case difference (mm)
	Myriophyllum spp.	3.20 (±0.34)
	Elodea canadensis	1.70 (±0.62)
1	75:25	0.83 (±1.01)
	50:50	1.67 (±0.88)
	25:75	2.50 (±0.29)
	Myriophyllum spp.	1.10 (±0.62)
	Elodea canadensis	0.90 (±0.19)
2	75:25	1.17 (±0.17)
	50:50	1.00 (±0.05)
	25:75	1.00 (±0.00)
	Myriophyllum spp.	-2.70 (±1.94)
	Elodea canadensis	-4.10 (±1.32)
3	75:25	-7.17 (±0.60)
	50:50	-7.33 (±0.44)
	25:75	-4.33 (±2.19)

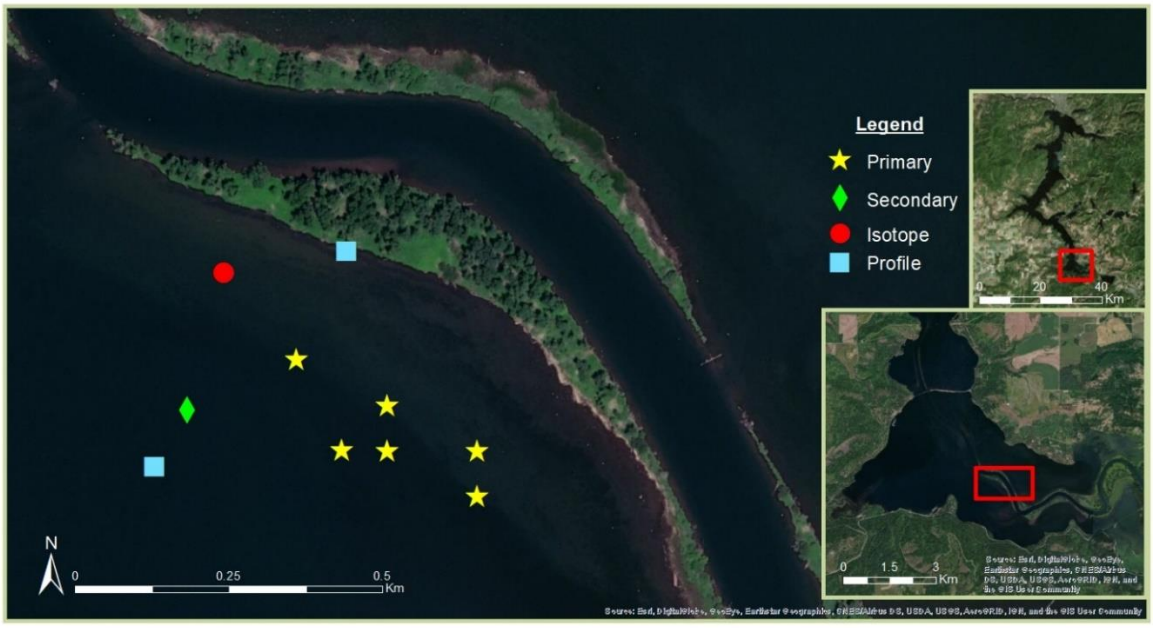

Figure 4.1. Site map of Chatcolet Lake. The yellow stars (Primary) represent the six sites regularly sampled throughout 2017 and 2018. The green diamond (Secondary) represents a site where I collected caddisfly larva in early 2018 when they were not present at the six regular sites. The red circle (Isotope) represents the point where I collected most of the 2018 caddisflies to supplement those from the six regular sites. The blue squares (Profile) represent sites where additional profile data was collected.

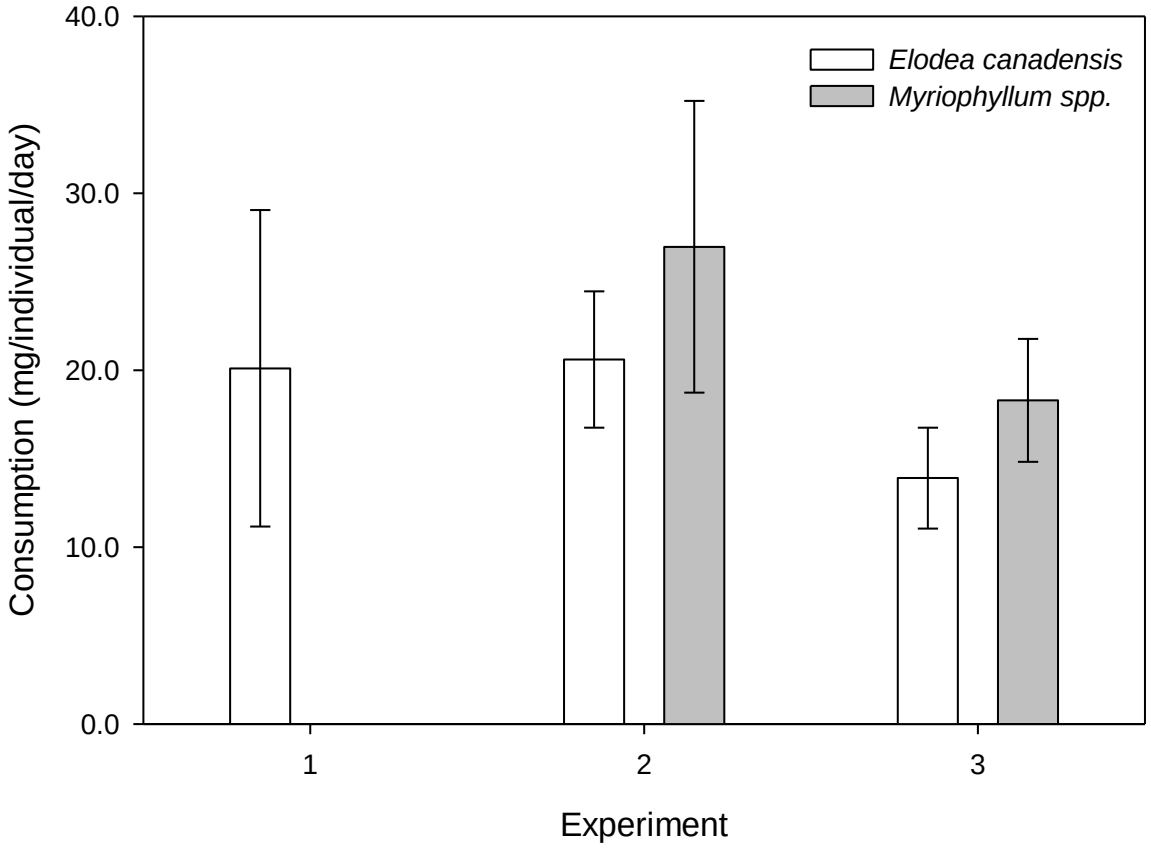

Figure 4.2. Results of the individual species feeding experiments. The experiment number is on the x-axis, with experiment one at the end of August, experiment two in September, and experiment three in October (for exact dates, see Methods section). The light bars represent consumption of *Elodea canadensis*, and the dark bars represent consumption of *Myriophyllum* spp., with all error bars representing standard error values.

Chapter 5: Conclusion

In the midst of normal sampling efforts, managers of Chatcolet Lake noticed damage to macrophyte communities that resembled herbivory. They also noticed large populations of larvae of the caddisfly, *Nectopsyche albida*, in tandem with the damage. Naturally the possibility of a connection between the two formed and raised more questions about the role of the caddisflies in this ecosystem, particularly due the herbivory observed on the invasive Eurasian watermilfoil, *Myriophyllum spp*. The possibility of the caddisflies as a natural biocontrol of the milfoil was enticing, as measures of milfoil and macrophyte control were already occurring in the lake. To answer these questions and to discover details of the relationship between the larvae and the macrophytes, I undertook this thesis to specifically provide more information about the macrophyte community and distribution in Chatcolet Lake, the growth pattern of larvae of *N. albida*, to learn the diet of the larvae in this system, and if the larvae caused or contributed to the damage of macrophytes seen in the lake.

Based on the combined results of the life history analysis, stable isotope analysis, and feeding experiments, I found that *N. albida* larvae do consume macrophytes in Chatcolet Lake. Though the timing of the growth of the larvae does not exactly match that of the macrophytes, they use the macrophyte biomass both throughout their larval stage, as pupa, and as adults. The larvae consume proximate vegetation for both feeding, as they are generalist herbivores, and for construction of their case. The density and diversity of macrophytes changes temporally during the year, changing what is available to the caddisflies to use as food items and building materials. Some plant species grow early in spring and senesce in the summer, while others start growing in the summer and senesce in the fall. Caddisflies are adaptable with their diet and with how much they consume, both of which are dependent on time of year. Larvae approaching pupation in early to mid-summer do not consume the same amount of macrophytes for feeding and case building as the next generation that appears later in the year. Most of the observed macrophyte damage occurred in late summer, when the larvae reached the largest 5^{th} instar larval stage and were preparing to overwinter. Therefore, the consumption rates change, as does their diet and the composition of their cases.

Life history analysis of the caddisfly larvae revealed that in Chatcolet Lake, *N. albida* was univoltine producing only one cohort per year. The caddisflies laid eggs on macrophytes in early to mid-summer, and the eggs took between 1-2 weeks to hatch. The larvae then developed through five instar stages. Caddisflies in Chatcolet Lake reached their terminal instar and head capsule size about two months after adults were found. The 5^{th} instar larvae overwintered and although their head capsules did not increase after September, the case length and presumably body size increased until early to mid-summer when they attached their case to macrophyte stems and pupated. Adults emerged approximately two weeks later, laid eggs, and produced a new generation. As part of collecting caddisflies for the analysis of life history characteristics, I also estimated caddisfly density. In 2017, the density of caddisflies was high (13 individuals m^{-2}), while in 2018 the density at the same location was at most 1 ind. m^{-2}. However, adjacent to the main sampling sites, I found macrophyte patches with caddisfly densities similar to those observed in 2017. This shows that interannual variability at a site can be high and suggests that future sampling efforts to track the density of larvae needs to encompass a larger spatial extent than I used. It is also interesting that I found that caddisfly larvae where vegetation was also present suggesting a close relationship between caddisflies and macrophytes.

Examination of vegetative biomass from the six main sites within Chatcolet Lake also revealed high interannual variability between 2017 and 2018 with higher total macrophyte density in 2017 compared to 2018. Inconsistent macrophyte biomass has been commonly observed in this area between sampling seasons. Variable vegetative biomass in other systems is also common, especially where herbivores are present or where macrophytes are competing with phytoplankton for sunlight (Lodge et al. 1998; Hidding et al. 2016; Valley 2016). Interestingly, the species diversity of macrophytes was lower in 2017 than in 2018. Given the degree of herbivory observed in 2017 when the density of caddisfly larvae was high, it could be possible that the removal of leaves by the larvae prevented the macrophytes from building sufficient energy reserves in their root systems to successfully overwinter, or start growth as usual in 2018, contributing to the lower overall biomass, and its delayed appearance. This plausibility should be examined further to determine to what extent the larvae do negatively affect the phenology of macrophytes, as this could be exploited by lake managers. However, the high variability in density of both caddisfly larvae and vegetation

requires further examination to determine the factors or processes that contribute to it, and if it can be exploited and formulated into a management strategy to control macrophytes.

Based on my research, I would conclude that larvae of *N. albida* are not suited to control the onset of milfoil growth because of the misalignment of their life cycles. Milfoil growth generally begins in July, while the caddisflies are pupating, emerging as adults, and laying eggs, and therefore not consuming any macrophytes. The caddisflies hatch from the eggs as extremely small larvae that cannot consume and control macrophytes which are in their exponential growth phase at that time. However, as the larvae increase in size, their consumption for assimilation as body tissue and to increase their cases removes macrophyte biomass at increasing rates. Once they reach late (4^{th} and 5^{th}) instars, the caddisflies are able to consume noticeable macrophyte biomass, including milfoil. By the time the caddisflies reach this point in their development, however, milfoil is at its peak growth for the season and subsequently begins to senesce. Caddisflies therefore are not able to limit the onset of milfoil in early summer. However, it is possible that through their consumption of milfoil in the second half of the season, the caddisflies contribute to milfoil demise earlier than would naturally occur without their consumption. This phenomenon also requires further examination, especially given the potential linkage to preventing the macrophytes to produce sufficient energy reserves to overwinter successfully as mentioned above.

The stable isotope analysis of carbon and nitrogen signatures of caddisflies and their possible food sources confirmed that macrophytes were assimilated into body tissue and cases. The contribution of epiphytes to 20-35% of the diet was interesting and was ascribed to incidental ingested with macrophyte leaves. It is well known, that many invertebrates consume conditioned leaves preferentially because the material is easier to assimilate, or in some cases, the ‘peanut butter’ (ephipytic community) is the energy focus, and the leaf is incidental as the ‘cracker’ (Kostalos and Seymour 1976; Bärlocher 1985; Hall Meyer 1998). I used the IsoSource mixing model to calculate the percent contribution of each food source to the diet of the larvae, which revealed that the importance of any individual macrophyte species varied over time. This was consistent with the patterns of density and diversity of macrophyte species observed in the lake and supports the classification of *N. albida* as a generalist herbivore and shredder. Analysis of their case composition via the mixing model

revealed that they were made mainly of macrophytes, with some input from the larvae themselves. This was not unexpected because the cases are cemented together with silk that the larvae produced. The inclusion of various other macrophytes besides *Myriophyllum* in the diet further suggests that the larvae would not be an ideal and effective biocontrol of *Myriophyllum*. Alternatively, if managers are interested in the overall reduction of macrophyte biomass, the rate of consumption of the caddisflies further informs the role they could contribute in such a strategy.

The high variability in the feeding experiments makes it difficult to provide unequivocal rates and preferences of the larvae. However, although the experiments were carried out in highly artificial laboratory settings, they do provide an initial insight into the mass of macrophytes consumed by the larvae that can provide boundaries for 'back-of-the-envelope-calculations' to inform future research either in the field or the laboratory (Newman 1991; Lodge et al. 1998; Hidding et al. 2016). The higher consumption of *Myriophyllum* in one and *Elodea* in the other two experiments could be suggestive of a seasonal pattern that requires further examination. In the preference tanks, the consumption rates varied seemingly regardless of ratio between the three experiments, confirming the conclusion that the larvae are generalist feeders. When I compared the caddisfly case lengths between the three experiments, average case length increased in two of the three experiments, but decreased in one. The latter could only occur if the caddisflies consumed part of their case. As explained in chapter 4, this could indicate that the macrophytes incorporated into the case may serve as an energy reserve when food in the environment is poor. Again, this will require further examination. Future research should also consider the proximate composition and nutrition value of each of the macrophytes to determine if the larvae select macrophytes based on this characteristic. Including more food items in experiments ranging the entire year would provide a more complete picture of feeding rate and preference.

The results of all three components of this larger study strongly indicate that the caddisflies contribute to the herbivory damage seen on macrophytes in Chatcolet Lake. However, the caddisflies would not be effective as a biocontrol of the invasive Eurasian milfoil. The larvae are generalist consumers, they have a patchy distribution that does not cover the extent of the macrophyte beds, and their life cycle does not align with the onset of

milfoil growth. However, they still contribute to the overall control of macrophytes. Managers should continue to use other control methods in areas of high concern, such as around boat launches, but macrophyte patches in areas where caddisfly populations tend to occur in high densities and with consistency might be considered as less of a concern. However, macrophytes are necessary for the continued existence of the caddisfly, resulting in a conundrum. Areas from which macrophytes are removed or where their density is greatly reduced can no longer serve as a location for pupation and egg laying, so the caddisflies move to where they can function through their life cycle. This means they will be present in high abundance only in areas with established macrophyte growth. Areas where macrophytes are continually removed will likely not experience high densities of caddisflies in subsequent years. The caddisflies are most effective where they can establish populations and continue to find reliable food and habitat- aka consistent macrophyte beds. Allowing nature to reach an equilibrium may be the best strategy to use the natural presence and life history development of the caddisfly, *Nectopsyche albida,* as part of the management strategy for macrophytes including the invasive milfoil, *Myriophyllum spp*.

Studies of caddisfly size across a wider area might also be informative of small habitat differences in Chatcolet Lake and the rest of Coeur d'Alene Lake in general. Different influences from other areas (i. e., differences in temperature and depth) might change the timing of development of *N. albida*. Tozer et al. (1980) found that *N. albida* emerged at various points throughout the summer in a midwestern lake, and while this pattern was not observed at my study site, it is possible that the overall pattern on a larger scale may reflect what has been reported elsewhere.

A large data gap from the life history of this study lies in the caddisfly development between pupation and fifth instar. I was not able to track the length of pupation and adulthood, and I also did not observe mating or egg deposition by adults. I also failed to locate or capture early instars because they were too small, and I did not have suitable experience to identify them. Rearing adults in the laboratory would allow observation of emergence, egg laying, and capture of small *N. albida* instars. Obtaining dry body mass of the larvae along with head capsule measurements would provide more accurate growth data as the hardened head capsule stops growing at the fifth instar, but the soft body likely

continues to grow until pupation. Collecting the early instars and measuring the time of pupation, adulthood, and egg development would complete the story of the caddisfly life cycle and further add to the life history development of *Nectopsyche albida* in the Pacific Inland Northwest.

Literature Cited

Bärlocher, F. 1985. The role of fungi in the nutrition of stream invertebrates. Bot. J. Linn. Sociey **91**: 83–94. doi:https://doi.org/10.1111/j.1095-8339.1985.tb01137.x

Hall Jr., R. O., and J. L. Meyer. 1998. The trophic significance of bacteria in a detritus-based stream food web. Ecology **79**: 1995–2012. doi:https://doi.org/10.1890/0012-9658(1998)079[1995:TTSOBI]2.0.CO;2

Hidding, B., E. S. Bakker, M. J. M. Hootsmans, and S. Hilt. 2016. Synergy between shading and herbivory triggers macrophyte loss and regime shifts in aquatic systems. Oikos **125**: 1489–1495. doi:https://doi.org/10.1111/oik.03104

Kostalos, M., and R. L. Seymour. 1976. Role of microbial enriched detritus in the nutrition of *Gammarus minus* (Amphipoda). Oikos **27**: 512–516. doi:10.2307/3543471

Lodge, D. M., G. Cronin, E. van Donk, and A. J. Froelich. 1998. Impact of herbivory on plant standing crop: Comparisons among biomes, between vascular and nonvascular plants, and among freshwater herbivore taxa, 131st ed. Springer.

Newman, R. M. 1991. Herbivory and detritivory on freshwater macrophytes by invertebrates: A review. J. North Am. Benthol. Soc. **10**: 89–114.

Tozer, W. E., V. H. Resh, and J. O. Solem. 1980. Bionomics and adult behavior of a lentic caddisfly, *Nectopsyche albida* (Walker). Am. Midl. Nat. **106**: 133–144. doi:10.2307/2425143

Valley, R. D. 2016. Spatial and temporal variation of aquatic plant abundance: Quantifying change. J. Aquat. Plant Manag. **54**: 95–101.

Appendix A. 2018 Hydrolab profile data from Chatcolet Lake, ID

Table A.1. 2018 Hydrolab profile data from Chatcolet Lake, ID, site 15con1WQ. Dates range from 23-March-2018 to 24-October-2018 and should be read as "MM/DD/YYYY". The data collected are profiles taken at various depths throughout the water column, indicated by the column "Depth (m)". Other metrics listed are from left to right: temperature, pH, specific conductivity, dissolved oxygen, dissolved oxygen, photosynthetically active radiation, and chlorophyll *a*.

Date	Depth m	Temperature °C	pH	Sp.Cond. µS/cm	DO %	DO mg/L	PAR. $\mu Es^{-1}m^{-2}$	Chla v
3/23/2018	0.52	4.01	6.87	44	0.00	0.00	1810.00	0.0035
3/23/2018	0.55	4.00	6.87	44	0.00	0.00	1293.00	0.0035
3/23/2018	1.01	3.97	6.79	44	0.00	0.00	942.67	0.0035
3/23/2018	1.54	3.95	6.77	44	0.00	0.00	355.67	0.0035
3/23/2018	2.08	3.94	6.43	44	0.00	0.00	98.67	0.0035
3/23/2018	2.52	3.95	6.51	44	0.00	0.00	68.67	0.0035
3/23/2018	3.03	3.89	6.63	44	0.00	0.00	19.33	0.0035
3/23/2018	3.55	3.92	6.70	44	0.00	0.00	4.00	0.0035
3/23/2018	3.56	3.92	6.70	44	0.00	0.00	4.00	0.0035
3/23/2018	4.04	3.87	6.73	44	0.00	0.00	3.00	0.0035
3/23/2018	4.51	3.85	6.76	44	0.00	0.00	3.00	0.0035
3/23/2018	5.05	3.84	6.77	44	0.00	0.00	1.00	0.0035
3/23/2018	5.57	3.82	6.78	44	0.00	0.00	1.00	0.0035
4/26/2018	0.63	10.93	7.47	37	112.20	11.56	2240.33	0.0094
4/26/2018	0.97	9.92	7.46	37	112.80	11.89	1800.33	0.0096
4/26/2018	1.53	9.50	7.44	37	109.37	11.65	1190.33	0.0090
4/26/2018	1.98	9.07	7.41	37	106.47	11.45	930.33	0.0081
4/26/2018	2.51	8.41	7.40	37	103.90	11.36	662.67	0.0082
4/26/2018	2.99	8.33	7.38	37	102.83	11.26	534.67	0.0084
4/26/2018	3.50	8.33	7.36	37	103.17	11.30	420.00	0.0094
4/26/2018	4.00	8.25	7.36	37	103.70	11.38	322.00	0.0107
4/26/2018	4.47	8.21	7.33	37	105.00	11.54	253.00	0.0118
4/26/2018	5.01	8.20	7.36	37	104.90	11.53	187.67	0.0118
4/26/2018	5.50	8.20	7.34	37	104.97	11.53	143.67	0.0122
4/26/2018	6.00	7.99	7.35	37	106.17	11.72	117.33	0.0137

Table A.1. cont.

Date	Depth m	Temperature °C	pH	Sp.Cond. µS/cm	DO %	DO mg/L	PAR. $\mu Es^{-1}m^{-2}$	Chla v
4/26/2018	6.29	7.95	7.35	37	108.00	11.94	98.00	0.0314
5/8/2018	0.59	9.36	6.99	30	98.90	10.55	2374.00	0.0087
5/8/2018	0.71	9.36	6.99	31	98.60	10.52	2069.00	0.0087
5/8/2018	1.01	8.84	6.95	30	98.27	10.61	1814.00	0.0089
5/8/2018	1.48	8.36	6.97	29	97.50	10.65	1222.67	0.0099
5/8/2018	2.04	8.34	6.93	29.67	97.23	10.63	631.67	0.0103
5/8/2018	2.51	7.88	6.93	29	97.07	10.73	340.00	0.0127
5/8/2018	3.03	7.67	6.91	29	96.63	10.74	169.67	0.0134
5/8/2018	3.51	7.52	6.89	29	95.93	10.70	82.00	0.0152
5/8/2018	4.00	7.49	6.89	29	95.70	10.69	44.67	0.0159
5/8/2018	4.50	7.15	6.87	28	95.10	10.70	28.00	0.0177
5/8/2018	4.98	7.11	6.85	28	94.93	10.70	16.33	0.0181
5/8/2018	5.47	7.09	6.84	28	94.90	10.70	9.33	0.0191
5/8/2018	6.01	7.06	6.80	28	94.57	10.67	8.00	0.0186
5/8/2018	6.51	7.04	6.81	28	94.57	10.68	10.00	0.0187
5/8/2018	7.01	7.04	6.78	28	94.07	10.62	6.67	0.0197
5/23/2018	0.39	12.61	7.29	30	111.97	10.95	376.67	0.0100
5/23/2018	1.10	11.98	7.22	30	111.10	11.02	192.33	0.0103
5/23/2018	1.50	11.17	7.21	30	108.83	11.00	199.67	0.0102
5/23/2018	2.00	10.76	7.19	29	107.93	11.01	152.33	0.0104
5/23/2018	2.49	10.69	7.18	29	108.30	11.07	118.00	0.0101
5/23/2018	3.06	10.35	7.16	29	108.60	11.19	94.67	0.0097
5/23/2018	3.53	10.19	7.16	29	108.07	11.17	79.67	0.0094
5/23/2018	3.99	10.01	7.14	29	108.20	11.23	67.67	0.0094
5/23/2018	4.51	9.82	7.14	29	107.87	11.25	53.00	0.0166
5/23/2018	4.96	9.76	7.13	28.67	107.57	11.24	46.00	0.0112
5/23/2018	5.52	9.73	7.12	29	107.37	11.22	41.00	0.0115
5/23/2018	6.02	9.69	7.12	29	107.13	11.21	45.33	0.0125
5/23/2018	6.53	9.66	7.11	29	106.57	11.16	38.33	0.0186
6/5/2018	0.52	12.61	7.20	32	109.40	10.73	2622.00	0.0086
6/5/2018	0.55	12.61	7.19	32	109.20	10.71	2373.00	0.0086

Table A.1. cont.

Date	Depth m	Temperature °C	pH	Sp.Cond. µS/cm	DO %	DO mg/L	PAR. $\mu Es^{-1}m^{-2}$	Chla v
6/5/2018	1.04	12.76	7.19	32	109.60	10.71	1432.00	0.0087
6/5/2018	1.06	12.74	7.19	32	109.70	10.72	1478.00	0.0087
6/5/2018	1.56	12.75	7.20	32	109.30	10.69	1176.33	0.0091
6/5/2018	2.01	12.58	7.22	32	109.23	10.72	833.33	0.0091
6/5/2018	2.49	12.22	7.20	32	109.00	10.79	804.00	0.0100
6/5/2018	2.94	12.20	7.19	32	107.90	10.68	588.00	0.0119
6/5/2018	2.96	12.19	7.19	32	107.80	10.67	581.00	0.0119
6/5/2018	3.45	12.00	7.18	32	106.77	10.62	285.67	0.0114
6/5/2018	3.99	11.94	7.16	32	106.80	10.63	344.00	0.0114
6/5/2018	4.57	11.83	7.17	32	106.07	10.59	255.33	0.0112
6/5/2018	5.04	11.76	7.14	32	105.33	10.53	215.33	0.0112
6/5/2018	5.51	11.56	7.15	32	105.27	10.57	179.00	0.0105
6/5/2018	6.01	11.54	7.19	32	108.57	10.91	142.33	0.0214
6/19/2018	0.42	16.59	7.24	38	111.17	10.07	NA	NA
6/19/2018	1.06	16.09	7.19	38	112.17	10.27	NA	NA
6/19/2018	1.43	15.43	7.10	38	112.10	10.40	NA	NA
6/19/2018	1.47	15.43	7.09	38	111.90	10.39	NA	NA
6/19/2018	2.01	14.96	7.08	38	113.73	10.66	NA	NA
6/19/2018	3.05	14.51	7.05	39	109.90	10.40	NA	NA
6/19/2018	3.06	14.52	7.05	39	110.10	10.42	NA	NA
6/19/2018	3.59	14.36	7.01	39	108.37	10.29	NA	NA
6/19/2018	4.49	14.03	6.84	39	107.70	10.30	NA	NA
6/19/2018	5.01	13.83	6.96	39	107.20	10.31	NA	NA
6/19/2018	5.56	13.76	6.89	39	105.93	10.20	NA	NA
6/19/2018	5.97	13.46	6.85	39	80.57	7.81	NA	NA
6/19/2018	6.25	12.29	6.70	41	46.20	4.60	NA	NA
6/19/2018	6.28	12.29	6.70	41	46.05	4.59	NA	NA
7/17/2018	0.19	25.70	7.67	48	125.63	9.48	NA	NA
7/17/2018	0.60	23.83	7.70	47.33	127.20	9.94	NA	NA
7/17/2018	1.00	23.31	7.69	47	126.97	10.02	NA	NA
7/17/2018	1.59	22.74	7.50	47	123.97	9.89	NA	NA

Table A.1. cont.

Date	Depth m	Temperature °C	pH	Sp.Cond. µS/cm	DO %	DO mg/L	PAR. $\mu Es^{-1}m^{-2}$	Chla v
7/17/2018	1.97	22.42	7.30	49	101.13	8.12	NA	NA
7/17/2018	2.49	21.67	7.14	49	100.20	8.16	NA	NA
7/17/2018	3.03	21.29	7.26	45	109.40	8.98	NA	NA
7/17/2018	3.06	21.28	7.27	45	110.30	9.05	NA	NA
7/17/2018	3.58	20.76	7.41	44	124.33	10.31	NA	NA
7/17/2018	4.03	20.25	7.42	44	122.50	10.26	NA	NA
7/17/2018	4.49	19.45	7.12	44	102.37	8.71	NA	NA
7/17/2018	4.99	17.69	6.89	43	91.50	8.07	NA	NA
7/17/2018	5.46	16.57	6.64	42	62.70	5.66	NA	NA
7/17/2018	5.97	16.02	6.42	44	27.40	2.50	NA	NA
7/17/2018	6.38	15.65	6.30	47	14.73	1.36	NA	NA
7/31/2018	0.50	25.55	8.99	52.67	135.70	10.27	717.00	0.0234
7/31/2018	1.03	25.14	8.95	52	134.87	10.29	346.00	0.0244
7/31/2018	1.47	24.64	8.82	53	133.70	10.29	220.33	0.0485
7/31/2018	2.02	23.92	8.77	49	120.37	9.39	115.33	0.0340
7/31/2018	2.45	23.46	8.69	48.33	120.13	9.45	77.00	0.0250
7/31/2018	2.97	23.02	8.53	48	115.97	9.21	58.00	0.0377
7/31/2018	3.54	22.51	7.87	47	100.70	8.07	48.00	0.0482
7/31/2018	4.03	22.14	7.51	47	90.63	7.32	32.33	0.0458
7/31/2018	4.48	21.70	7.32	47	79.93	6.51	21.00	0.0335
7/31/2018	5.03	19.98	7.08	46	48.30	4.06	17.00	0.0284
7/31/2018	5.48	19.06	6.74	46	24.60	2.11	15.67	0.0321
7/31/2018	5.97	18.25	6.61	46	15.27	1.34	18.00	0.0385
7/31/2018	6.44	17.51	6.54	52	0.00	0.00	12.00	0.0423
7/31/2018	6.45	17.51	6.55	51	0.00	0.00	12.00	0.0424
8/13/2018	0.52	23.75	8.83	53	120.10	9.44	1398.50	0.0452
8/13/2018	0.55	23.76	8.83	53	120.00	9.43	1346.00	0.0457
8/13/2018	0.99	23.79	8.89	53	120.60	9.47	903.33	0.0582
8/13/2018	1.50	23.53	8.92	53	122.80	9.69	541.33	0.0722
8/13/2018	1.96	23.27	8.86	52	116.17	9.22	335.33	0.2341
8/13/2018	2.51	22.95	8.67	51	113.70	9.07	178.00	0.0852

Table A.1. cont.

Date	Depth m	Temperature °C	pH	Sp.Cond. µS/cm	DO %	DO mg/L	PAR. $\mu Es^{-1}m^{-2}$	Chla v
8/13/2018	3.09	22.74	8.52	50	101.17	8.11	95.00	0.0644
8/13/2018	3.52	22.64	8.15	50	90.10	7.23	76.67	0.0527
8/13/2018	4.03	21.96	7.36	48	67.10	5.46	50.33	0.0429
8/13/2018	4.56	21.64	7.14	48	55.93	4.58	35.67	0.0350
8/13/2018	4.99	21.32	6.98	48	44.50	3.66	21.00	0.0305
8/13/2018	5.46	20.17	6.75	48	13.77	1.16	18.00	0.0292
8/13/2018	6.01	19.48	6.65	47	1.50	0.12	9.00	0.0273
8/13/2018	6.51	18.94	6.46	50	0.00	0.00	5.00	0.0923
8/28/2018	0.28	20.15	7.73	43	94.43	7.96	1242.33	0.0291
8/28/2018	0.50	19.83	8.02	43	100.13	8.49	1344.33	0.0455
8/28/2018	0.99	19.66	8.23	43	102.13	8.70	682.33	0.0591
8/28/2018	1.47	19.29	8.29	43	102.47	8.79	494.33	0.0737
8/28/2018	1.97	19.15	8.01	43	95.10	8.18	271.00	0.0783
8/28/2018	2.47	18.97	7.76	43	87.37	7.54	157.00	0.0949
8/28/2018	2.99	18.90	7.61	43	84.97	7.34	88.67	0.0753
8/28/2018	3.53	18.66	7.39	43.67	74.03	6.43	48.33	0.0558
8/28/2018	4.05	18.59	7.36	44	73.40	6.38	31.00	0.0495
8/28/2018	4.09	18.60	7.36	44	73.30	6.38	31.00	0.0493
8/28/2018	4.48	18.57	7.33	43.67	72.90	6.34	20.00	0.0432
8/28/2018	4.98	18.56	7.32	44	72.50	6.31	12.00	0.0490
8/28/2018	5.54	18.55	7.32	44	73.70	6.41	6.00	0.0445
8/28/2018	6.00	18.54	7.32	43.33	74.00	6.44	4.00	0.0480
8/28/2018	6.28	18.48	7.31	43.33	74.33	6.48	3.67	0.0517
9/11/2018	0.33	18.50	8.00	45	100.60	8.71	465.00	0.0451
9/11/2018	0.37	18.50	8.01	45	100.60	8.70	274.00	0.0453
9/11/2018	1.02	18.50	7.99	45	99.93	8.65	191.67	0.0444
9/11/2018	1.55	18.50	7.99	45	100.00	8.66	117.00	0.0482
9/11/2018	2.08	18.50	7.99	45	100.50	8.70	58.00	0.0505
9/11/2018	2.55	18.48	7.94	45	98.67	8.55	47.67	0.0632
9/11/2018	3.04	18.47	7.91	45	98.53	8.53	34.00	0.0604
9/11/2018	3.55	18.38	7.75	45	86.10	7.47	23.00	0.0666

Table A.1. cont.

Date	Depth m	Temperature °C	pH	Sp.Cond. µS/cm	DO %	DO mg/L	PAR. $\mu Es^{-1}m^{-2}$	Chla v
9/11/2018	3.56	18.40	7.75	45	86.40	7.49	22.00	0.0666
9/11/2018	4.04	18.30	7.59	45	82.30	7.15	13.00	0.0672
9/11/2018	4.19	18.29	7.59	45	82.40	7.16	13.00	0.0651
9/11/2018	4.56	18.25	7.51	45	81.93	7.12	9.00	0.0499
9/11/2018	5.00	18.23	7.49	45	83.40	7.26	6.00	0.0491
9/11/2018	5.52	18.18	7.49	45	82.13	7.15	4.00	0.0639
9/11/2018	5.85	18.14	7.24	44	64.60	5.63	3.00	0.1008
9/11/2018	5.86	18.14	7.24	45	64.50	5.62	3.00	0.1015
9/25/2018	0.59	16.07	7.79	46	97.67	9.00	1664.33	0.0161
9/25/2018	1.02	15.80	7.81	46	98.60	9.13	1164.67	0.0380
9/25/2018	1.52	15.65	8.12	46	104.47	9.71	734.33	0.1423
9/25/2018	2.08	15.50	8.00	46	100.03	9.32	379.67	0.1181
9/25/2018	2.55	15.40	7.91	46	98.60	9.21	222.00	0.0736
9/25/2018	3.07	15.32	7.83	46	96.83	9.06	140.33	0.0593
9/25/2018	3.53	15.26	7.79	46	96.50	9.04	91.00	0.0632
9/25/2018	4.06	15.17	7.73	46	94.47	8.87	57.00	0.0469
9/25/2018	4.53	15.12	7.66	46	92.17	8.66	39.67	0.0488
9/25/2018	5.00	15.10	7.63	46.67	91.90	8.64	27.00	0.0564
9/25/2018	5.51	15.08	7.63	47	92.47	8.70	17.00	0.0547
9/25/2018	6.01	14.82	7.76	47	97.93	9.26	11.00	0.0716
9/25/2018	6.28	14.81	7.79	47	97.93	9.26	9.00	0.0823
10/9/2018	0.42	12.47	7.68	43	97.30	9.53	787.33	0.0281
10/9/2018	0.53	12.47	7.70	43	96.77	9.48	648.00	0.1244
10/9/2018	0.90	12.47	7.72	43	96.40	9.44	446.67	0.0445
10/9/2018	1.38	12.47	7.77	43	97.00	9.50	261.00	0.0495
10/9/2018	1.47	12.47	7.76	43	97.00	9.50	262.50	0.0460
10/9/2018	2.05	12.46	7.75	43	96.97	9.50	213.67	0.0554
10/9/2018	2.48	12.46	7.75	43	96.87	9.49	143.33	0.0560
10/9/2018	2.97	12.46	7.75	43	96.10	9.42	168.33	0.0561
10/9/2018	3.54	12.46	7.77	43	96.30	9.43	102.67	0.0599
10/9/2018	4.08	12.45	7.75	43	96.00	9.40	72.33	0.0564

Table A.1. cont.

Date	Depth m	Temperature °C	pH	Sp.Cond. µS/cm	DO %	DO mg/L	PAR. $\mu Es^{-1}m^{-2}$	Chla v
10/9/2018	4.57	12.43	7.73	43	94.80	9.29	60.33	0.0551
10/9/2018	5.03	12.41	7.69	43	93.70	9.19	43.00	0.0400
10/9/2018	5.06	12.39	7.69	44	93.70	9.19	40.00	0.0414
10/9/2018	5.53	12.20	7.63	44	90.57	8.92	27.33	0.0325
10/9/2018	5.80	12.15	7.48	44	88.40	8.72	20.00	0.0247
10/9/2018	5.98	12.15	7.49	44	88.30	8.72	21.00	0.0245
10/9/2018	6.10	12.14	7.42	44.33	86.53	8.54	23.00	0.0437
10/24/2018	0.48	10.54	7.63	43.67	99.23	10.25	1212.00	0.0180
10/24/2018	1.00	10.40	7.67	43.33	99.17	10.28	406.00	0.0334
10/24/2018	1.49	10.27	7.70	43.67	99.63	10.36	359.00	0.0614
10/24/2018	1.97	10.27	7.73	44	99.30	10.32	602.00	0.0548
10/24/2018	2.53	10.20	7.73	43.67	98.00	10.21	355.67	0.0669
10/24/2018	3.05	10.18	7.72	43	97.23	10.13	137.33	0.0658
10/24/2018	3.53	10.08	7.65	43.33	93.07	9.72	85.33	0.0350
10/24/2018	4.05	9.94	7.60	43	88.90	9.32	61.00	0.0280
10/24/2018	4.06	9.94	7.60	43	88.90	9.32	63.00	0.0236
10/24/2018	4.57	9.89	7.58	43	88.50	9.28	52.67	0.0136
10/24/2018	5.03	9.87	7.56	43	88.17	9.26	42.33	0.0227
10/24/2018	5.49	9.87	7.46	43	82.43	8.65	37.00	0.0229
10/24/2018	5.82	9.87	7.41	43	78.67	8.25	28.67	0.0260

Appendix B. HOBO logger data from Chatcolet Lake, ID

Table B.1. HOBO logger data from Chatcolet Lake, Idaho, on the levee of the St. Joe River just north of the study area. The included data are daily temperature averages from 01-January-2017 to 31-October-2018, and are measured in °C.

Cumulative Julian Date	Average Daily Temperature	Standard Error
1	-2.051	0.163
2	-2.912	0.141
3	-2.935	0.181
4	-7.004	0.460
5	-7.794	0.579
6	-5.861	0.352
7	-7.457	0.360
8	-2.147	0.160
9	-0.709	0.035
10	-0.702	0.030
11	-2.062	0.093
12	-2.956	0.119
13	-4.371	0.111
14	-5.297	0.122
15	-5.120	0.186
16	-5.123	0.178
17	-3.435	0.230
18	0.072	0.181
19	0.942	0.227
20	2.140	1.293
21	0.026	0.432
22	1.539	0.665
23	0.379	0.215
24	0.121	0.204
25	-0.576	0.172
26	-0.354	0.864
27	-3.563	1.294
28	-1.444	1.084
29	0.308	1.411
30	1.513	0.921
31	-1.260	0.393
32	-6.753	1.620

Table B.1. cont.

Cumulative Julian Date	Average Daily Temperature	Standard Error
33	-10.282	2.247
34	-5.518	0.681
35	-0.971	0.165
36	0.826	0.190
37	2.740	0.624
38	-1.588	0.557
39	-1.200	0.267
40	3.528	0.617
41	4.795	0.871
42	1.732	1.149
43	0.814	1.541
44	0.532	1.488
45	1.901	1.843
46	0.543	0.467
47	3.214	0.219
48	2.523	0.325
49	2.539	0.076
50	3.299	0.110
51	3.202	0.077
52	3.357	0.015
53	3.363	0.034
54	2.997	0.035
55	2.707	0.072
56	2.739	0.049
57	2.571	0.058
58	2.254	0.037
59	1.924	0.108
60	2.401	0.183
61	3.254	0.242
62	4.172	0.222
63	3.675	0.153
64	2.168	0.124
65	2.055	0.308
66	0.804	0.189
67	2.886	0.255
68	2.913	0.403

Table B.1. cont.

Cumulative Julian Date	Average Daily Temperature	Standard Error
69	7.450	0.716
70	4.807	0.385
71	5.898	0.470
72	5.330	0.105
73	5.153	0.048
74	5.017	0.058
75	3.682	0.118
76	3.618	0.076
77	4.439	0.046
78	4.839	0.074
79	4.624	0.033
80	4.850	0.019
81	5.081	0.052
82	5.532	0.049
83	5.680	0.020
84	5.490	0.019
85	5.267	0.031
86	5.602	0.046
87	5.623	0.023
88	5.657	0.020
89	5.610	0.034
90	5.670	0.064
91	6.050	0.035
92	6.101	0.054
93	6.013	0.079
94	5.850	0.098
95	5.996	0.099
96	6.142	0.043
97	6.739	0.128
98	6.347	0.047
99	5.835	0.105
100	5.637	0.105
101	5.895	0.100
102	6.761	0.072
103	6.839	0.076
104	7.058	0.080

Table B.1. cont.

Cumulative Julian Date	Average Daily Temperature	Standard Error
105	7.181	0.128
106	7.398	0.107
107	7.665	0.028
108	7.803	0.082
109	7.997	0.130
110	7.692	0.074
111	8.343	0.207
112	8.300	0.205
113	8.413	0.122
114	8.759	0.108
115	9.076	0.146
116	7.904	0.097
117	7.268	0.108
118	7.505	0.103
119	8.314	0.266
120	8.107	0.083
121	7.948	0.076
122	8.524	0.138
123	8.716	0.161
124	9.924	0.295
125	10.236	0.183
126	9.867	0.112
127	9.267	0.180
128	8.625	0.132
129	9.301	0.098
130	10.074	0.175
131	10.520	0.085
132	10.604	0.078
133	9.198	0.087
134	8.261	0.090
135	8.320	0.200
136	8.523	0.087
137	8.256	0.100
138	8.844	0.097
139	8.936	0.210
140	10.050	0.258

Table B.1. cont.

Cumulative Julian Date	Average Daily Temperature	Standard Error
141	11.288	0.261
142	12.103	0.186
143	13.479	0.409
144	12.372	0.175
145	11.235	0.140
146	10.881	0.266
147	11.694	0.334
148	12.498	0.205
149	13.048	0.306
150	13.467	0.245
151	13.534	0.171
152	12.027	0.100
153	12.324	0.266
154	12.199	0.249
155	12.203	0.108
156	13.047	0.262
157	13.153	0.264
158	14.498	0.352
159	14.150	0.131
160	13.979	0.292
161	13.706	0.155
162	13.862	0.287
163	14.418	0.161
164	13.900	0.165
165	14.056	0.293
166	14.071	0.110
167	14.054	0.070
168	13.818	0.220
169	14.013	0.113
170	15.146	0.356
171	17.944	0.337
172	17.182	0.168
173	16.569	0.188
174	17.495	0.190
175	18.745	0.226
176	20.381	0.260

Table B.1. cont.

Cumulative Julian Date	Average Daily Temperature	Standard Error
177	20.713	0.137
178	20.787	0.148
179	20.404	0.203
180	20.735	0.195
181	21.500	0.174
182	22.300	0.148
183	23.424	0.150
184	23.589	0.187
185	23.051	0.205
186	23.666	0.166
187	24.470	0.168
188	25.597	0.234
189	25.386	0.123
190	25.309	0.234
191	24.760	0.103
192	23.953	0.185
193	24.415	0.248
194	24.740	0.256
195	24.791	0.196
196	24.956	0.130
197	23.443	0.166
198	23.090	0.202
199	23.353	0.197
200	23.916	0.196
201	23.663	0.116
202	23.296	0.208
203	23.617	0.181
204	24.476	0.317
205	24.591	0.190
206	24.438	0.187
207	24.425	0.165
208	24.641	0.218
209	24.481	0.178
210	24.975	0.208
211	25.479	0.239
212	25.085	0.174

Table B.1. cont.

Cumulative Julian Date	Average Daily Temperature	Standard Error
213	24.903	0.175
214	25.102	0.177
215	25.309	0.143
216	25.517	0.200
217	25.314	0.126
218	25.256	0.159
219	25.152	0.126
220	24.775	0.113
221	24.490	0.097
222	24.179	0.104
223	24.215	0.116
224	24.005	0.067
225	22.581	0.112
226	22.308	0.228
227	22.374	0.190
228	22.491	0.204
229	22.822	0.186
230	22.715	0.179
231	22.416	0.185
232	21.861	0.176
233	21.715	0.203
234	22.132	0.195
235	22.267	0.206
236	22.365	0.100
237	21.922	0.228
238	21.652	0.171
239	21.573	0.203
240	21.318	0.136
241	21.770	0.141
242	22.502	0.161
243	22.181	0.120
244	22.107	0.203
245	22.084	0.161
246	22.167	0.140
247	21.791	0.115
248	21.028	0.074

Table B.1. cont.

Cumulative Julian Date	Average Daily Temperature	Standard Error
249	20.795	0.167
250	20.953	0.130
251	21.029	0.102
252	21.342	0.128
253	21.000	0.095
254	20.643	0.161
255	20.699	0.221
256	19.893	0.097
257	18.513	0.134
258	18.254	0.164
259	17.561	0.260
260	17.011	0.130
261	16.812	0.066
262	16.021	0.114
263	15.736	0.066
264	15.495	0.049
265	15.615	0.182
266	15.063	0.112
267	15.445	0.176
268	15.467	0.084
269	15.654	0.206
270	16.367	0.210
271	16.764	0.196
272	16.897	0.225
273	15.097	0.193
274	13.498	0.161
275	13.329	0.170
276	13.346	0.341
277	13.631	0.348
278	13.380	0.238
279	13.025	0.295
280	11.342	0.133
281	11.605	0.279
282	10.857	0.427
283	10.832	0.199
284	11.243	0.320

Table B.1. cont.

Cumulative Julian Date	Average Daily Temperature	Standard Error
285	9.582	0.155
286	8.508	0.104
287	9.216	0.396
288	10.149	0.486
289	10.034	0.560
290	9.176	0.361
291	8.656	0.230
292	9.776	0.202
293	8.212	0.150
294	6.903	0.368
295	9.259	0.291
296	8.756	0.656
297	9.361	0.724
298	9.597	0.583
299	11.045	0.687
300	8.882	0.596
301	9.005	0.605
302	8.910	0.433
303	6.618	0.479
304	5.769	0.507
305	7.276	0.353
306	7.101	0.226
307	5.738	0.231
308	4.414	0.208
309	4.250	0.226
310	2.920	0.124
311	3.335	0.395
312	3.494	0.285
313	4.614	0.305
314	4.509	0.324
315	5.827	0.388
316	5.179	0.624
317	2.967	0.378
318	3.857	0.458
319	3.971	0.535
320	3.937	0.311

Table B.1. cont.

Cumulative Julian Date	Average Daily Temperature	Standard Error
321	3.112	0.261
322	3.086	0.566
323	2.005	0.408
324	4.048	0.181
325	4.160	0.384
326	9.201	0.313
327	9.951	0.575
328	4.540	0.342
329	4.492	0.623
330	6.117	0.160
331	4.964	0.155
332	3.951	0.062
333	4.066	0.088
334	2.875	0.054
335	3.514	0.118
336	3.363	0.071
337	3.103	0.054
338	2.518	0.122
339	2.333	0.193
340	3.055	0.144
341	3.598	0.129
342	3.609	0.167
343	2.864	0.072
344	2.437	0.142
345	2.251	0.263
346	1.599	0.142
347	1.989	0.135
348	1.861	0.181
349	1.362	0.088
350	1.382	0.006
351	1.076	0.021
352	1.906	0.184
353	1.225	0.081
354	0.538	0.112
355	0.007	0.326
356	-1.020	0.196

Table B.1. cont.

Cumulative Julian Date	Average Daily Temperature	Standard Error
357	-4.802	0.665
358	-5.892	0.735
359	-1.666	0.200
360	-1.454	0.067
361	-0.710	0.080
362	-0.194	0.044
363	0.029	0.002
364	0.662	0.271
365	-0.690	0.424
366	-1.614	0.120
367	-1.279	0.497
368	-0.902	0.610
369	-0.802	0.443
370	0.243	0.119
371	0.642	0.109
372	1.101	0.263
373	1.885	0.539
374	2.429	0.200
375	1.259	0.304
376	0.255	0.066
377	1.378	0.235
378	3.674	0.379
379	3.039	0.589
380	2.163	0.700
381	1.416	0.540
382	2.664	0.435
383	3.861	0.315
384	2.247	0.254
385	2.907	0.226
386	2.972	0.217
387	3.110	0.155
388	2.367	0.143
389	3.265	0.122
390	3.218	0.158
391	2.605	0.150
392	2.685	0.129

Table B.1. cont.

Cumulative Julian Date	Average Daily Temperature	Standard Error
393	3.162	0.107
394	4.450	0.211
395	4.007	0.153
396	2.297	0.087
397	2.412	0.144
398	3.759	0.215
399	5.567	0.124
400	5.816	0.113
401	4.967	0.028
402	4.732	0.026
403	4.767	0.027
404	4.995	0.019
405	4.981	0.016
406	4.907	0.021
407	4.523	0.033
408	4.127	0.022
409	3.628	0.040
410	3.384	0.025
411	3.003	0.018
412	2.369	0.053
413	1.862	0.051
414	1.213	0.033
415	1.783	0.222
416	2.570	0.262
417	2.833	0.320
418	1.549	0.219
419	0.380	0.054
420	0.376	0.039
421	0.524	0.058
422	-0.229	0.095
423	-0.190	0.083
424	0.468	0.065
425	1.623	0.314
426	0.883	0.215
427	1.837	0.974
428	0.681	0.447

Table B.1. cont.

Cumulative Julian Date	Average Daily Temperature	Standard Error
429	1.492	0.430
430	4.031	1.519
431	0.816	1.088
432	4.547	0.853
433	4.090	0.760
434	3.805	1.866
435	4.271	1.742
436	5.295	1.833
437	6.514	1.584
438	5.673	0.445
439	4.312	0.665
440	4.319	1.321
441	2.910	0.547
442	3.123	0.431
443	5.202	1.281
444	5.801	1.529
445	4.612	0.973
446	5.528	0.710
447	5.086	1.086
448	2.555	0.689
449	3.356	1.193
450	3.411	0.790
451	5.716	0.488
452	6.627	1.110
453	6.636	1.361
454	7.590	0.891
455	6.277	1.465
456	3.825	0.813
457	3.803	1.089
458	6.221	1.270
459	5.580	0.485
460	7.161	0.551
461	8.506	0.972
462	6.432	0.700
463	7.173	0.294
464	6.950	0.125

Table B.1. cont.

Cumulative Julian Date	Average Daily Temperature	Standard Error
465	6.702	0.058
466	6.940	0.066
467	6.036	0.069
468	6.028	0.078
469	6.025	0.124
470	6.629	0.160
471	6.792	0.082
472	6.388	0.039
473	6.423	0.120
474	6.668	0.115
475	7.621	0.167
476	8.209	0.103
477	8.313	0.122
478	8.937	0.174
479	9.207	0.156
480	9.370	0.248
481	9.047	0.204
482	9.774	0.234
483	9.014	0.135
484	7.824	0.048
485	7.256	0.060
486	7.551	0.072
487	8.492	0.161
488	9.319	0.204
489	10.037	0.132
490	10.075	0.064
491	9.968	0.109
492	9.099	0.058
493	8.707	0.071
494	8.856	0.101
495	8.031	0.078
496	7.421	0.056
497	7.911	0.111
498	8.782	0.159
499	9.884	0.088
500	10.282	0.092

Table B.1. cont.

Cumulative Julian Date	Average Daily Temperature	Standard Error
501	10.217	0.059
502	9.533	0.051
503	8.600	0.040
504	9.010	0.128
505	9.860	0.146
506	10.811	0.174
507	11.350	0.145
508	11.382	0.169
509	11.917	0.228
510	11.917	0.113
511	12.850	0.191
512	12.068	0.081
513	13.112	0.244
514	13.344	0.194
515	13.675	0.172
516	12.899	0.112
517	12.651	0.141
518	12.676	0.373
519	14.533	0.229
520	13.981	0.100
521	13.966	0.273
522	15.069	0.244
523	16.020	0.174
524	15.956	0.093
525	15.085	0.107
526	13.852	0.199
527	13.996	0.177
528	14.358	0.201
529	15.310	0.189
530	14.895	0.209
531	14.867	0.191
532	14.979	0.086
533	14.889	0.137
534	15.463	0.150
535	16.668	0.170
536	17.455	0.256

Table B.1. cont.

Cumulative Julian Date	Average Daily Temperature	Standard Error
537	18.940	0.095
538	18.806	0.232
539	17.609	0.128
540	18.163	0.230
541	19.334	0.164
542	19.179	0.201
543	19.061	0.159
544	19.170	0.098
545	19.373	0.170
546	19.202	0.074
547	19.008	0.159
548	17.998	0.141
549	17.681	0.109
550	18.422	0.251
551	20.328	0.155
552	21.451	0.136
553	21.544	0.169
554	21.360	0.138
555	22.069	0.173
556	22.530	0.095
557	22.040	0.113
558	22.373	0.126
559	22.998	0.161
560	23.944	0.214
561	23.912	0.178
562	24.213	0.162
563	24.576	0.256
564	24.977	0.163
565	23.817	0.110
566	23.362	0.190
567	23.090	0.164
568	22.755	0.195
569	23.221	0.202
570	24.034	0.257
571	24.672	0.205
572	25.288	0.221

Table B.1. cont.

Cumulative Julian Date	Average Daily Temperature	Standard Error
573	25.357	0.101
574	25.074	0.134
575	25.280	0.172
576	25.447	0.167
577	25.711	0.077
578	25.092	0.095
579	24.261	0.157
580	23.235	0.164
581	23.262	0.191
582	23.696	0.183
583	23.856	0.184
584	24.123	0.221
585	24.618	0.182
586	24.814	0.177
587	25.226	0.225
588	25.013	0.159
589	23.464	0.169
590	23.159	0.174
591	23.058	0.185
592	23.107	0.189
593	22.856	0.126
594	22.702	0.147
595	23.082	0.199
596	22.933	0.129
597	21.904	0.084
598	21.722	0.241
599	22.321	0.217
600	21.953	0.122
601	21.117	0.145
602	20.503	0.158
603	19.631	0.073
604	19.169	0.127
605	19.297	0.216
606	20.038	0.186
607	20.035	0.101
608	19.920	0.170

Table B.1. cont.

Cumulative Julian Date	Average Daily Temperature	Standard Error
609	19.901	0.202
610	19.936	0.208
611	19.888	0.180
612	19.761	0.178
613	19.715	0.212
614	20.167	0.187
615	20.429	0.239
616	20.642	0.133
617	20.227	0.170
618	19.033	0.099
619	18.033	0.077
620	17.483	0.184
621	16.954	0.123
622	16.987	0.244
623	17.292	0.157
624	17.370	0.127
625	17.005	0.212
626	17.362	0.264
627	17.157	0.181
628	16.181	0.092
629	15.846	0.196
630	15.891	0.083
631	15.498	0.144
632	16.036	0.193
633	15.785	0.307
634	15.748	0.238
635	15.783	0.237
636	16.321	0.205
637	15.648	0.163
638	13.811	0.099
639	13.768	0.206
640	14.332	0.118
641	13.609	0.302
642	13.041	0.111
643	12.204	0.200
644	12.234	0.061

Table B.1. cont.

Cumulative Julian Date	Average Daily Temperature	Standard Error
645	12.084	0.145
646	12.173	0.143
647	12.095	0.083
648	11.752	0.296
649	11.380	0.243
650	11.856	0.344
651	11.490	0.274
652	10.576	0.406
653	10.303	0.399
654	10.203	0.449
655	10.568	0.466
656	10.639	0.441
657	10.866	0.484
658	11.133	0.522
659	11.011	0.550
660	10.641	0.610
661	10.644	0.529
662	11.289	0.453
663	9.943	0.403
664	11.050	0.259
665	10.689	0.449
666	9.709	0.184
667	8.231	0.274
668	7.533	0.302
669	6.397	0.101

Appendix C. *Nectopsyche albida* larval head capsule and case measurements

Table C.1. Case length, head capsule length, and head capsule width of all *Nectopsyche albida* larva measured from Chatcolet Lake from June 2017-October 2018. All measurements are in millimeters. Dashes indicate where data was not collected; in the case length column indicate a caddisfly outside of a case, and dashes in the head capsule columns indicate pupa. This data set includes measurements for 1102 individuals.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
14-Jun-17	16.904	1.121	0.842
14-Jun-17	13.347	1.005	0.841
14-Jun-17	-	0.917	0.832
15-Aug-17	11.099	0.671	0.533
15-Aug-17	10.295	0.639	0.496
15-Aug-17	9.317	0.673	0.530
15-Aug-17	9.116	0.688	0.528
15-Aug-17	11.588	0.683	0.502
15-Aug-17	10.852	0.686	0.533
15-Aug-17	10.414	0.655	0.497
15-Aug-17	10.244	0.535	0.392
15-Aug-17	9.924	0.702	0.526
15-Aug-17	10.797	0.688	0.494
15-Aug-17	7.818	0.704	0.515
15-Aug-17	9.880	0.641	0.496
15-Aug-17	8.572	0.611	0.505
15-Aug-17	11.520	0.723	0.525
15-Aug-17	7.659	0.670	0.489
15-Aug-17	12.610	0.636	0.498
15-Aug-17	7.485	0.695	0.507
15-Aug-17	9.279	0.666	0.501
15-Aug-17	7.516	0.715	0.490
15-Aug-17	12.931	0.690	0.493
15-Aug-17	6.282	0.655	0.467
15-Aug-17	12.113	0.655	0.511
15-Aug-17	9.522	0.661	0.473
15-Aug-17	10.510	0.681	0.545
15-Aug-17	10.674	0.678	0.506
15-Aug-17	10.475	0.670	0.552
15-Aug-17	10.517	0.617	0.474

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
15-Aug-17	9.871	0.639	0.552
15-Aug-17	10.661	0.553	0.451
15-Aug-17	8.657	0.685	0.528
15-Aug-17	9.694	0.641	0.511
15-Aug-17	7.827	0.653	0.531
15-Aug-17	8.765	0.649	0.519
15-Aug-17	10.439	0.692	0.504
15-Aug-17	10.712	0.677	0.528
15-Aug-17	9.430	0.701	0.491
15-Aug-17	7.221	0.670	0.504
15-Aug-17	10.839	0.647	0.534
15-Aug-17	9.378	0.656	0.504
15-Aug-17	9.956	0.717	0.549
15-Aug-17	11.36	0.709	0.474
15-Aug-17	8.306	0.648	0.492
15-Aug-17	8.300	0.662	0.511
15-Aug-17	9.966	0.693	0.527
15-Aug-17	8.964	0.647	0.549
15-Aug-17	7.883	0.632	0.489
15-Aug-17	10.506	0.669	0.519
15-Aug-17	9.176	0.669	0.489
15-Aug-17	9.952	0.694	0.534
15-Aug-17	10.927	0.715	0.511
15-Aug-17	8.657	0.699	0.489
15-Aug-17	9.415	0.677	0.504
15-Aug-17	8.226	0.655	0.507
15-Aug-17	8.899	0.684	0.542
15-Aug-17	7.126	0.714	0.556
15-Aug-17	9.843	0.694	0.513
15-Aug-17	8.379	0.677	0.481
15-Aug-17	8.871	0.656	0.512
15-Aug-17	8.652	0.669	0.504
15-Aug-17	8.513	0.692	0.571
15-Aug-17	8.226	0.656	0.496
15-Aug-17	10.516	0.677	0.526
15-Aug-17	8.536	1.023	0.850
15-Aug-17	8.736	0.625	0.521

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
15-Aug-17	7.927	0.649	0.493
15-Aug-17	11.157	0.692	0.534
15-Aug-17	8.850	0.617	0.489
15-Aug-17	9.765	0.677	0.544
15-Aug-17	6.927	0.662	0.496
15-Aug-17	9.002	0.634	0.526
15-Aug-17	11.834	0.724	0.536
15-Aug-17	8.537	0.669	0.534
15-Aug-17	10.143	0.692	0.489
15-Aug-17	11.281	0.649	0.491
15-Aug-17	10.117	0.666	0.534
15-Aug-17	9.208	0.632	0.526
15-Aug-17	8.220	0.670	0.504
15-Aug-17	9.969	0.670	0.492
15-Aug-17	10.258	0.692	0.558
15-Aug-17	10.049	0.677	0.534
15-Aug-17	10.728	0.620	0.496
15-Aug-17	10.483	0.679	0.474
15-Aug-17	9.107	0.677	0.534
15-Aug-17	10.818	0.684	0.504
8-Sep-17	-	1.086	0.910
8-Sep-17	-	0.949	0.790
8-Sep-17	-	0.941	0.767
8-Sep-17	-	1.060	0.812
8-Sep-17	-	0.971	0.820
8-Sep-17	-	0.918	0.722
8-Sep-17	-	0.986	0.812
8-Sep-17	-	1.083	0.857
8-Sep-17	-	1.068	0.880
8-Sep-17	-	0.958	0.797
8-Sep-17	-	0.994	0.805
8-Sep-17	-	0.946	0.792
8-Sep-17	-	1.050	0.872
8-Sep-17	-	1.016	0.881
8-Sep-17	-	1.046	0.842
8-Sep-17	-	1.015	0.865
8-Sep-17	-	0.970	0.797

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
8-Sep-17	-	0.932	0.797
8-Sep-17	-	1.030	0.850
8-Sep-17	-	0.967	0.744
8-Sep-17	-	1.015	0.752
8-Sep-17	-	1.116	0.850
8-Sep-17	-	0.933	0.760
8-Sep-17	-	1.040	0.859
8-Sep-17	-	1.043	0.798
8-Sep-17	-	0.988	0.767
8-Sep-17	-	0.970	0.782
8-Sep-17	-	1.091	0.850
8-Sep-17	-	1.004	0.806
8-Sep-17	-	0.977	0.797
8-Sep-17	-	1.023	0.783
8-Sep-17	-	1.008	0.820
8-Sep-17	-	0.985	0.797
8-Sep-17	9.504	1.009	0.842
8-Sep-17	14.418	1.008	0.843
8-Sep-17	17.017	1.069	0.887
8-Sep-17	10.881	1.008	0.865
8-Sep-17	12.769	1.031	0.835
8-Sep-17	14.065	1.038	0.827
8-Sep-17	13.485	0.979	0.820
8-Sep-17	13.792	1.077	0.842
8-Sep-17	13.268	1.136	0.902
8-Sep-17	11.362	0.962	0.786
8-Sep-17	16.775	1.008	0.813
8-Sep-17	11.068	1.068	0.872
8-Sep-17	11.273	0.970	0.812
8-Sep-17	14.167	1.075	0.880
8-Sep-17	11.748	0.993	0.812
8-Sep-17	9.164	1.038	0.865
8-Sep-17	10.305	0.940	0.737
8-Sep-17	8.912	0.645	0.473
8-Sep-17	15.248	1.085	0.802
8-Sep-17	15.109	1.060	0.812
8-Sep-17	9.372	0.977	0.752

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
8-Sep-17	11.130	0.631	0.521
8-Sep-17	9.184	1.008	0.805
8-Sep-17	15.880	1.053	0.836
8-Sep-17	14.760	1.038	0.866
8-Sep-17	13.798	0.963	0.794
8-Sep-17	13.379	0.993	0.812
8-Sep-17	13.244	0.872	0.669
8-Sep-17	9.941	0.985	0.790
8-Sep-17	12.865	1.059	0.860
8-Sep-17	10.728	1.061	0.850
8-Sep-17	10.941	0.897	0.759
8-Sep-17	14.563	0.995	0.797
8-Sep-17	11.710	1.038	0.797
8-Sep-17	9.709	0.684	0.526
8-Sep-17	14.438	1.105	0.865
8-Sep-17	11.010	1.135	0.902
8-Sep-17	14.273	0.999	0.798
8-Sep-17	8.529	0.970	0.737
8-Sep-17	15.608	1.068	0.805
8-Sep-17	13.378	1.076	0.835
8-Sep-17	8.556	0.993	0.799
8-Sep-17	13.155	1.031	0.829
8-Sep-17	14.412	1.113	0.865
8-Sep-17	12.425	0.993	0.790
8-Sep-17	8.061	0.920	0.790
8-Sep-17	12.488	1.024	0.848
8-Sep-17	17.064	1.045	0.835
8-Sep-17	11.304	1.068	0.813
8-Sep-17	11.408	1.000	0.812
8-Sep-17	12.974	1.045	0.925
8-Sep-17	13.242	1.023	0.797
8-Sep-17	11.168	0.970	0.790
8-Sep-17	8.894	0.684	0.505
8-Sep-17	9.970	1.006	0.791
10-Oct-17	-	1.061	0.835
10-Oct-17	-	1.068	0.843
10-Oct-17	19.654	0.970	0.782

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
10-Oct-17	15.081	1.053	0.805
10-Oct-17	16.910	1.045	0.895
10-Oct-17	15.688	1.030	0.842
10-Oct-17	17.087	1.015	0.789
10-Oct-17	16.854	1.038	0.850
10-Oct-17	18.796	1.083	0.827
10-Oct-17	14.723	1.099	0.865
10-Oct-17	15.225	1.053	0.850
10-Oct-17	16.544	1.053	0.872
10-Oct-17	14.719	1.015	0.857
10-Oct-17	18.381	1.075	0.865
10-Oct-17	13.121	0.957	0.759
10-Oct-17	18.000	1.031	0.790
10-Oct-17	18.760	0.994	0.850
10-Oct-17	16.918	1.090	0.895
10-Oct-17	18.524	1.039	0.899
10-Oct-17	16.000	1.083	0.895
10-Oct-17	14.365	1.008	0.827
10-Oct-17	14.061	0.995	0.860
10-Oct-17	16.937	1.053	0.857
10-Oct-17	14.647	1.076	0.821
10-Oct-17	16.412	1.011	0.852
10-Oct-17	16.319	1.060	0.857
10-Oct-17	18.416	0.978	0.827
10-Oct-17	18.878	1.113	0.842
10-Oct-17	13.130	1.016	0.768
10-Oct-17	16.595	1.046	0.813
10-Oct-17	15.657	0.970	0.805
10-Oct-17	12.629	0.935	0.804
10-Oct-17	16.428	1.038	0.842
10-Oct-17	12.662	0.932	0.790
10-Oct-17	18.627	1.075	0.812
10-Oct-17	17.707	1.016	0.835
10-Oct-17	17.229	0.988	0.872
10-Oct-17	18.063	1.023	0.805
10-Oct-17	16.686	0.993	0.835
10-Oct-17	18.107	1.093	0.888

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
10-Oct-17	16.850	1.135	0.857
10-Oct-17	15.341	1.045	0.797
10-Oct-17	16.232	1.084	0.858
10-Oct-17	14.050	0.977	0.760
10-Oct-17	15.821	1.053	0.875
10-Oct-17	16.214	0.963	0.782
10-Oct-17	13.884	1.060	0.839
10-Oct-17	15.765	0.935	0.833
10-Oct-17	14.465	0.933	0.790
10-Oct-17	15.727	1.032	0.827
10-Oct-17	13.265	1.075	0.880
10-Oct-17	17.255	1.091	0.850
10-Oct-17	15.956	1.008	0.782
10-Oct-17	16.280	0.996	0.820
10-Oct-17	12.806	1.038	0.812
10-Oct-17	13.128	0.993	0.812
10-Oct-17	13.827	1.008	0.783
10-Oct-17	15.380	0.985	0.784
10-Oct-17	15.966	1.030	0.835
10-Oct-17	18.058	1.075	0.835
10-Oct-17	13.081	0.926	0.782
10-Oct-17	15.811	1.038	0.857
10-Oct-17	11.507	1.091	0.858
10-Oct-17	12.668	1.016	0.850
10-Oct-17	11.301	0.932	0.767
10-Oct-17	18.059	0.978	0.820
23-Mar-18	-	1.076	0.865
23-Mar-18	18.202	0.970	0.790
23-Mar-18	15.852	1.038	0.812
23-Mar-18	16.197	1.038	0.835
23-Mar-18	16.750	1.038	0.850
23-Mar-18	15.347	1.075	0.835
23-Mar-18	19.271	1.105	0.842
23-Mar-18	16.927	1.060	0.842
23-Mar-18	16.800	1.071	0.833
23-Mar-18	18.192	1.015	0.805
23-Mar-18	21.598	1.068	0.873

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
23-Mar-18	17.819	0.955	0.812
23-Mar-18	16.121	1.068	0.812
23-Mar-18	13.895	1.068	0.842
23-Mar-18	17.126	1.120	0.880
23-Mar-18	15.906	1.083	0.850
23-Mar-18	16.305	1.108	0.858
23-Mar-18	13.262	0.986	0.797
23-Mar-18	15.247	1.008	0.842
23-Mar-18	17.323	1.053	0.828
23-Mar-18	12.971	1.053	0.842
23-Mar-18	16.843	1.114	0.910
23-Mar-18	21.825	1.096	0.853
23-Mar-18	16.467	1.098	0.880
23-Mar-18	12.826	1.008	0.789
23-Mar-18	17.630	1.105	0.805
23-Mar-18	14.888	0.842	0.669
23-Mar-18	15.767	0.986	0.797
23-Mar-18	14.060	0.962	0.759
23-Mar-18	14.590	1.046	0.860
23-Mar-18	15.615	1.030	0.820
23-Mar-18	14.874	0.971	0.857
23-Mar-18	17.337	1.030	0.865
23-Mar-18	15.733	1.060	0.805
23-Mar-18	12.631	1.015	0.797
23-Mar-18	14.290	1.024	0.850
23-Mar-18	16.190	1.015	0.782
23-Mar-18	17.815	0.941	0.760
23-Mar-18	15.184	1.053	0.812
23-Mar-18	17.663	1.053	0.872
23-Mar-18	14.407	0.989	0.842
23-Mar-18	15.124	1.002	0.805
23-Mar-18	15.452	1.068	0.865
23-Mar-18	18.231	0.995	0.842
23-Mar-18	13.39	1.068	0.797
23-Mar-18	16.311	1.053	0.812
23-Mar-18	14.718	0.971	0.850
23-Mar-18	17.604	1.045	0.782

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
23-Mar-18	16.410	1.045	0.850
23-Mar-18	17.530	1.053	0.805
23-Mar-18	14.177	1.053	0.865
23-Mar-18	13.061	0.940	0.752
23-Mar-18	12.625	1.023	0.827
23-Mar-18	17.826	1.075	0.835
23-Mar-18	16.465	1.038	0.812
23-Mar-18	11.960	1.099	0.858
23-Mar-18	16.741	1.060	0.812
26-Apr-18	-	1.064	0.862
26-Apr-18	13.140	1.060	0.888
26-Apr-18	21.598	1.015	0.865
26-Apr-18	16.346	1.105	0.887
26-Apr-18	13.554	0.994	0.850
26-Apr-18	17.731	1.038	0.857
26-Apr-18	16.584	1.046	0.836
26-Apr-18	18.372	0.985	0.850
26-Apr-18	20.970	1.038	0.842
26-Apr-18	14.777	1.031	0.812
26-Apr-18	15.235	1.091	0.858
26-Apr-18	13.909	1.098	0.873
26-Apr-18	14.837	1.107	0.918
26-Apr-18	15.048	1.120	0.872
26-Apr-18	16.615	1.090	0.850
26-Apr-18	14.524	1.083	0.857
26-Apr-18	15.884	1.040	0.844
26-Apr-18	20.322	1.023	0.880
26-Apr-18	18.958	1.083	0.850
26-Apr-18	17.669	0.994	0.872
26-Apr-18	14.601	1.015	0.820
26-Apr-18	20.453	1.053	0.820
26-Apr-18	15.819	1.092	0.880
26-Apr-18	20.184	1.075	0.842
26-Apr-18	14.797	1.090	0.850
26-Apr-18	17.398	0.948	0.782
26-Apr-18	15.893	1.113	0.940
26-Apr-18	13.726	1.053	0.798

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
26-Apr-18	18.953	1.062	0.835
26-Apr-18	19.028	1.038	0.880
26-Apr-18	16.155	1.075	0.880
26-Apr-18	21.460	1.023	0.858
26-Apr-18	14.277	1.069	0.880
26-Apr-18	14.088	1.046	0.865
26-Apr-18	15.876	1.045	0.805
26-Apr-18	15.844	1.038	0.842
26-Apr-18	15.012	0.985	0.805
26-Apr-18	15.240	1.000	0.820
26-Apr-18	13.696	1.015	0.827
26-Apr-18	21.359	0.986	0.865
26-Apr-18	18.216	1.000	0.822
26-Apr-18	18.450	1.060	0.887
26-Apr-18	16.457	1.015	0.782
26-Apr-18	19.693	1.090	0.880
26-Apr-18	14.564	1.030	0.872
26-Apr-18	16.834	1.083	0.835
26-Apr-18	15.543	1.054	0.865
26-Apr-18	13.364	1.085	0.820
26-Apr-18	20.205	1.060	0.865
26-Apr-18	20.610	1.120	0.850
26-Apr-18	18.679	1.060	0.881
26-Apr-18	15.766	1.053	0.887
26-Apr-18	15.074	1.045	0.872
26-Apr-18	16.317	1.045	0.828
26-Apr-18	17.570	1.068	0.865
26-Apr-18	15.187	1.030	0.820
26-Apr-18	16.338	1.015	0.805
26-Apr-18	14.708	1.019	0.850
26-Apr-18	18.202	1.053	0.820
26-Apr-18	16.451	0.993	0.805
26-Apr-18	16.410	1.091	0.827
26-Apr-18	17.199	1.083	0.857
26-Apr-18	15.206	1.143	0.881
26-Apr-18	14.640	1.098	0.835
26-Apr-18	17.716	1.047	0.850

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
26-Apr-18	14.939	1.060	0.820
26-Apr-18	16.039	1.068	0.820
26-Apr-18	15.949	1.060	0.827
26-Apr-18	13.980	1.045	0.857
26-Apr-18	12.725	1.053	0.782
26-Apr-18	19.467	1.076	0.843
26-Apr-18	14.039	0.993	0.805
26-Apr-18	16.621	1.098	0.828
26-Apr-18	14.542	1.053	0.850
26-Apr-18	14.253	1.060	0.820
26-Apr-18	14.299	0.987	0.759
26-Apr-18	15.196	1.015	0.872
26-Apr-18	13.258	1.061	0.812
26-Apr-18	16.821	1.100	0.895
26-Apr-18	20.427	1.000	0.812
26-Apr-18	16.173	1.105	0.820
26-Apr-18	16.781	0.995	0.828
26-Apr-18	13.117	1.053	0.858
26-Apr-18	14.430	1.098	0.827
26-Apr-18	12.699	1.083	0.797
26-Apr-18	13.709	1.083	0.805
26-Apr-18	13.754	0.986	0.782
26-Apr-18	13.398	1.053	0.866
26-Apr-18	13.205	1.000	0.812
26-Apr-18	15.922	0.977	0.760
26-Apr-18	16.659	1.090	0.827
26-Apr-18	16.484	1.030	0.797
26-Apr-18	15.108	1.084	0.827
26-Apr-18	16.855	1.084	0.888
26-Apr-18	15.541	1.038	0.827
26-Apr-18	14.718	0.957	0.850
26-Apr-18	19.482	1.069	0.895
26-Apr-18	15.612	1.054	0.805
26-Apr-18	13.485	0.963	0.812
26-Apr-18	18.175	1.060	0.842
26-Apr-18	13.325	1.015	0.775
26-Apr-18	13.491	0.978	0.895

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
26-Apr-18	16.589	0.978	0.872
26-Apr-18	13.026	1.023	0.857
26-Apr-18	17.436	1.055	0.775
26-Apr-18	17.310	1.098	0.832
26-Apr-18	15.844	0.941	0.827
26-Apr-18	14.876	1.099	0.857
26-Apr-18	17.633	1.015	0.805
26-Apr-18	15.495	1.038	0.872
26-Apr-18	17.787	1.113	0.932
26-Apr-18	16.179	1.015	0.797
26-Apr-18	14.255	1.018	0.836
26-Apr-18	16.679	1.054	0.843
26-Apr-18	17.531	1.085	0.836
26-Apr-18	16.194	0.993	0.812
26-Apr-18	15.806	0.970	0.805
26-Apr-18	14.149	1.075	0.827
26-Apr-18	12.400	1.030	0.857
26-Apr-18	17.392	1.060	0.843
26-Apr-18	13.737	1.038	0.888
26-Apr-18	14.330	1.015	0.783
26-Apr-18	13.945	1.098	0.842
26-Apr-18	16.666	1.000	0.752
26-Apr-18	16.623	0.925	0.797
8-May-18	-	1.061	0.857
8-May-18	-	0.978	0.835
8-May-18	13.251	1.084	0.843
8-May-18	14.348	1.030	0.857
8-May-18	13.612	1.143	0.970
8-May-18	15.276	1.113	0.896
8-May-18	18.330	1.083	0.865
8-May-18	13.461	1.080	0.881
8-May-18	21.399	1.113	0.887
8-May-18	19.496	1.107	0.880
8-May-18	17.478	1.038	0.940
8-May-18	16.476	1.091	0.880
8-May-18	15.924	1.053	0.910
8-May-18	20.240	1.113	0.926

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
8-May-18	19.996	1.053	0.857
8-May-18	17.235	1.015	0.827
8-May-18	13.582	1.018	0.890
8-May-18	16.315	1.039	0.852
8-May-18	20.237	1.027	0.934
8-May-18	14.896	1.023	0.857
8-May-18	16.715	0.994	0.807
8-May-18	18.996	1.061	0.865
8-May-18	19.367	0.986	0.797
8-May-18	12.759	1.038	0.805
8-May-18	13.719	1.003	0.851
8-May-18	21.988	1.050	0.872
8-May-18	18.634	1.083	0.904
8-May-18	14.368	1.038	0.850
8-May-18	15.760	1.083	0.850
8-May-18	17.601	0.948	0.827
8-May-18	21.554	1.060	0.857
8-May-18	19.960	1.068	0.865
8-May-18	15.261	1.061	0.887
8-May-18	18.563	1.093	0.850
8-May-18	14.553	1.075	0.895
8-May-18	21.362	1.091	0.895
8-May-18	16.371	1.038	0.872
8-May-18	16.327	1.060	0.865
8-May-18	14.918	1.053	0.872
8-May-18	13.726	1.090	0.887
8-May-18	19.152	1.061	0.858
8-May-18	13.827	1.053	0.880
8-May-18	17.402	0.993	0.820
8-May-18	19.208	1.075	0.842
8-May-18	16.521	1.015	0.820
8-May-18	17.044	1.068	0.850
8-May-18	13.814	0.964	0.837
8-May-18	19.029	1.113	0.872
8-May-18	19.730	1.015	0.835
8-May-18	15.535	1.068	0.857
8-May-18	14.195	0.988	0.843

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
8-May-18	21.048	1.058	0.884
8-May-18	15.883	1.030	0.842
8-May-18	20.619	0.993	0.790
8-May-18	14.757	1.121	0.858
8-May-18	13.491	1.054	0.873
8-May-18	13.902	1.083	0.903
8-May-18	17.958	1.045	0.865
8-May-18	13.939	1.040	0.799
8-May-18	16.388	1.062	0.873
8-May-18	15.518	1.063	0.903
8-May-18	16.815	1.015	0.895
8-May-18	18.073	1.031	0.881
8-May-18	17.724	1.047	0.888
8-May-18	18.937	1.061	0.857
8-May-18	14.025	1.031	0.881
8-May-18	16.746	1.076	0.865
8-May-18	17.620	1.077	0.835
8-May-18	14.063	1.038	0.850
8-May-18	14.107	1.128	0.880
8-May-18	20.645	1.085	0.933
8-May-18	14.329	1.032	0.857
8-May-18	14.835	1.061	0.850
8-May-18	16.828	0.993	0.820
8-May-18	15.653	1.016	0.850
8-May-18	17.602	1.083	0.872
8-May-18	19.496	1.053	0.842
8-May-18	17.276	1.009	0.828
8-May-18	20.893	1.023	0.843
8-May-18	16.427	0.993	0.843
8-May-18	14.871	1.009	0.880
8-May-18	13.617	1.023	0.842
8-May-18	18.022	1.075	0.827
8-May-18	18.446	1.060	0.827
8-May-18	18.868	1.083	0.827
8-May-18	17.829	0.985	0.857
8-May-18	16.825	1.025	0.844
8-May-18	15.574	1.046	0.858

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
8-May-18	17.486	1.083	0.798
8-May-18	16.134	1.024	0.820
8-May-18	19.237	1.083	0.865
8-May-18	14.387	1.045	0.887
8-May-18	13.913	1.076	0.868
8-May-18	20.356	0.977	0.865
8-May-18	17.676	0.940	0.820
8-May-18	13.829	1.075	0.857
8-May-18	17.027	1.075	0.881
8-May-18	14.956	1.023	0.813
8-May-18	12.550	1.060	0.872
8-May-18	15.184	1.030	0.835
8-May-18	13.775	1.032	0.820
8-May-18	17.041	1.008	0.820
8-May-18	15.147	0.992	0.812
8-May-18	15.726	1.030	0.872
8-May-18	18.724	1.098	0.842
8-May-18	16.612	1.076	0.895
8-May-18	20.045	1.068	0.842
8-May-18	19.383	1.040	0.882
8-May-18	18.255	0.985	0.775
8-May-18	13.903	1.045	0.812
8-May-18	19.592	1.098	0.872
8-May-18	17.553	1.076	0.904
8-May-18	15.287	1.053	0.850
8-May-18	15.318	1.092	0.888
5-Jun-18	-	1.053	0.835
5-Jun-18	15.004	0.977	0.797
5-Jun-18	16.591	1.041	0.887
5-Jun-18	15.578	1.075	0.902
5-Jun-18	13.091	1.053	0.910
5-Jun-18	18.422	1.061	0.902
5-Jun-18	14.357	1.033	0.865
5-Jun-18	14.837	1.031	0.872
5-Jun-18	17.636	1.038	0.895
5-Jun-18	17.708	1.001	0.828
5-Jun-18	14.647	1.083	0.865

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
5-Jun-18	16.251	1.050	0.838
5-Jun-18	17.826	1.023	0.820
5-Jun-18	14.440	0.965	0.903
5-Jun-18	15.106	0.910	0.835
5-Jun-18	15.844	1.083	0.827
5-Jun-18	15.985	1.000	0.857
5-Jun-18	19.841	0.977	0.880
5-Jun-18	12.405	0.978	0.820
5-Jun-18	19.851	0.925	0.880
5-Jun-18	21.634	1.076	0.842
5-Jun-18	19.443	1.098	0.820
5-Jun-18	15.185	0.986	0.820
5-Jun-18	16.931	1.083	0.850
5-Jun-18	20.250	1.008	0.940
5-Jun-18	18.168	1.098	0.857
5-Jun-18	19.872	1.038	0.850
5-Jun-18	17.671	1.054	0.850
5-Jun-18	19.222	1.046	0.844
5-Jun-18	22.684	1.061	0.866
5-Jun-18	19.970	0.957	0.872
5-Jun-18	20.941	0.927	0.843
5-Jun-18	17.767	1.061	0.827
5-Jun-18	20.976	1.068	0.850
5-Jun-18	20.471	1.068	0.858
5-Jun-18	15.178	1.077	0.902
5-Jun-18	17.340	1.061	0.888
5-Jun-18	17.209	1.030	0.918
5-Jun-18	14.488	1.101	0.868
5-Jun-18	17.361	1.046	0.858
5-Jun-18	16.935	1.077	0.850
5-Jun-18	17.983	0.985	0.790
5-Jun-18	18.304	1.045	0.842
5-Jun-18	18.642	1.061	0.806
5-Jun-18	18.357	1.099	0.872
5-Jun-18	21.409	1.122	0.828
5-Jun-18	18.846	1.053	0.888
5-Jun-18	14.755	1.030	0.805

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
5-Jun-18	20.392	1.053	0.835
5-Jun-18	16.404	1.030	0.835
5-Jun-18	13.146	0.999	0.872
5-Jun-18	13.698	0.955	0.827
5-Jun-18	15.254	1.015	0.910
5-Jun-18	15.726	0.963	0.797
5-Jun-18	15.402	1.128	0.835
5-Jun-18	13.456	1.019	0.810
5-Jun-18	14.645	1.136	0.857
5-Jun-18	13.952	1.016	0.835
5-Jun-18	13.908	1.040	0.850
5-Jun-18	15.340	1.000	0.850
5-Jun-18	15.754	1.084	0.827
5-Jun-18	21.386	1.068	0.888
5-Jun-18	19.269	1.085	0.895
19-Jun-18	-	1.083	0.865
19-Jun-18	27.767	1.030	0.850
19-Jun-18	24.900	1.038	0.902
19-Jun-18	24.404	1.120	0.850
19-Jun-18	24.353	1.045	0.820
19-Jun-18	20.651	1.000	0.910
19-Jun-18	22.600	1.105	0.895
19-Jun-18	22.055	1.090	0.872
19-Jun-18	21.201	1.084	0.896
19-Jun-18	20.854	1.068	0.911
19-Jun-18	20.510	1.060	0.887
19-Jun-18	19.496	1.099	0.842
19-Jun-18	17.439	1.019	0.880
19-Jun-18	19.226	1.024	0.753
19-Jun-18	17.288	1.083	0.880
19-Jun-18	19.592	0.940	0.820
19-Jun-18	21.787	0.993	0.835
19-Jun-18	20.785	1.045	0.827
19-Jun-18	19.234	1.023	0.872
19-Jun-18	15.070	1.000	0.812
19-Jun-18	18.772	0.970	0.813
19-Jun-18	19.031	0.974	0.850

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
19-Jun-18	15.151	1.030	0.805
19-Jun-18	15.367	1.068	0.842
19-Jun-18	17.031	0.934	0.827
19-Jun-18	16.743	1.015	0.842
19-Jun-18	15.300	1.023	0.797
19-Jun-18	18.080	0.943	0.805
19-Jun-18	17.039	0.970	0.850
19-Jun-18	16.875	1.060	0.857
19-Jun-18	15.505	1.098	0.880
19-Jun-18	20.218	1.090	0.917
19-Jun-18	16.750	0.962	0.865
19-Jun-18	16.012	1.083	0.850
19-Jun-18	16.509	1.068	0.835
19-Jun-18	16.498	1.008	0.827
19-Jun-18	14.770	1.023	0.842
19-Jun-18	16.133	1.061	0.813
19-Jun-18	14.432	1.023	0.790
19-Jun-18	15.351	1.030	0.835
19-Jun-18	15.217	1.083	0.925
19-Jun-18	18.473	1.024	0.851
19-Jun-18	15.960	1.045	0.842
19-Jun-18	14.429	0.993	0.865
19-Jun-18	17.337	1.031	0.820
19-Jun-18	15.106	1.098	0.842
19-Jun-18	15.008	1.023	0.767
19-Jun-18	14.028	1.000	0.767
19-Jun-18	15.767	1.061	0.812
19-Jun-18	14.847	1.068	0.947
19-Jun-18	17.721	1.045	0.812
19-Jun-18	15.419	1.045	0.850
19-Jun-18	17.690	0.895	0.850
19-Jun-18	11.966	1.106	0.880
19-Jun-18	16.237	1.015	0.820
19-Jun-18	15.122	1.000	0.842
19-Jun-18	18.534	0.970	0.857
19-Jun-18	17.555	1.045	0.782
19-Jun-18	16.059	0.956	0.835

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
19-Jun-18	17.249	1.113	0.872
19-Jun-18	16.391	0.977	0.820
3-Jul-18	16.271	-	-
3-Jul-18	15.195	-	-
3-Jul-18	15.491	-	-
3-Jul-18	14.861	-	-
3-Jul-18	16.290	-	-
3-Jul-18	15.137	-	-
3-Jul-18	15.431	-	-
3-Jul-18	18.256	-	-
3-Jul-18	15.572	-	-
3-Jul-18	16.859	-	-
3-Jul-18	15.904	-	-
3-Jul-18	16.234	-	-
3-Jul-18	16.327	-	-
3-Jul-18	14.471	-	-
3-Jul-18	15.693	-	-
3-Jul-18	15.343	-	-
3-Jul-18	15.968	-	-
3-Jul-18	21.708	1.060	0.767
3-Jul-18	14.604	1.030	0.812
3-Jul-18	15.808	1.032	0.865
3-Jul-18	15.557	1.018	0.865
3-Jul-18	16.561	1.015	0.872
3-Jul-18	16.083	1.098	0.888
3-Jul-18	16.906	1.024	0.813
3-Jul-18	17.242	1.098	0.902
3-Jul-18	15.228	1.045	0.857
3-Jul-18	19.067	0.993	0.850
3-Jul-18	14.478	1.075	0.820
3-Jul-18	14.508	1.060	0.850
3-Jul-18	14.081	1.083	0.835
3-Jul-18	23.571	1.033	0.842
3-Jul-18	16.506	0.986	0.850
3-Jul-18	17.095	1.090	0.895
3-Jul-18	17.087	0.994	0.835
3-Jul-18	24.150	1.038	0.782

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
3-Jul-18	14.992	0.977	0.782
3-Jul-18	16.287	0.955	0.850
3-Jul-18	16.760	1.053	0.910
3-Jul-18	15.867	1.045	0.948
3-Jul-18	17.611	0.985	0.850
3-Jul-18	19.653	1.098	0.827
3-Jul-18	15.271	1.038	0.887
3-Jul-18	14.324	0.955	0.797
3-Jul-18	15.979	1.053	0.835
3-Jul-18	15.132	0.934	0.869
3-Jul-18	17.044	0.970	0.842
3-Jul-18	14.655	0.985	0.850
3-Jul-18	16.155	0.970	0.902
3-Jul-18	14.234	1.008	0.842
3-Jul-18	16.615	1.065	0.831
3-Jul-18	16.768	0.993	0.880
3-Jul-18	16.457	0.955	0.842
3-Jul-18	14.643	1.083	0.842
3-Jul-18	17.126	1.045	0.857
3-Jul-18	15.202	0.903	0.820
3-Jul-18	15.730	0.993	0.880
3-Jul-18	17.386	0.985	0.865
3-Jul-18	15.396	1.002	0.902
3-Jul-18	14.321	1.000	0.872
3-Jul-18	16.044	1.060	0.902
3-Jul-18	16.253	1.166	0.850
3-Jul-18	17.882	0.970	0.857
3-Jul-18	17.918	1.039	0.910
3-Jul-18	14.296	1.000	0.857
3-Jul-18	16.240	0.992	0.903
28-Aug-18	11.910	1.098	0.835
28-Aug-18	13.741	1.154	0.860
28-Aug-18	11.534	1.123	0.830
28-Aug-18	12.788	1.061	0.835
28-Aug-18	14.047	1.158	0.858
28-Aug-18	14.552	1.129	0.949
28-Aug-18	11.277	1.113	0.880

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
28-Aug-18	13.602	1.116	0.889
28-Aug-18	12.586	1.134	0.828
28-Aug-18	12.152	1.159	0.874
28-Aug-18	14.564	1.145	0.875
28-Aug-18	13.859	1.113	0.844
28-Aug-18	13.455	1.159	0.895
28-Aug-18	12.175	1.158	0.903
28-Aug-18	12.276	1.098	0.813
28-Aug-18	12.727	1.158	0.902
28-Aug-18	12.121	1.120	0.902
28-Aug-18	14.545	1.143	0.918
28-Aug-18	12.092	1.174	0.910
28-Aug-18	11.553	1.075	0.850
28-Aug-18	14.212	1.105	0.820
28-Aug-18	13.641	1.092	0.895
28-Aug-18	11.730	1.030	0.865
28-Aug-18	12.380	1.086	0.865
28-Aug-18	10.091	0.677	0.534
28-Aug-18	14.261	1.090	0.880
28-Aug-18	11.012	1.150	0.910
28-Aug-18	12.623	1.090	0.887
28-Aug-18	12.061	1.092	0.888
28-Aug-18	13.243	1.105	0.857
28-Aug-18	12.636	1.113	0.842
28-Aug-18	14.733	1.090	0.872
28-Aug-18	11.403	1.113	0.782
28-Aug-18	13.042	1.173	0.880
28-Aug-18	13.825	1.143	0.835
28-Aug-18	15.249	1.106	0.902
28-Aug-18	14.194	1.143	0.872
28-Aug-18	14.429	1.128	0.902
28-Aug-18	15.183	1.128	0.902
28-Aug-18	13.061	1.053	0.880
28-Aug-18	12.283	1.129	0.865
28-Aug-18	16.076	1.068	0.842
28-Aug-18	12.516	0.722	0.542
28-Aug-18	12.554	1.080	0.918

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
28-Aug-18	10.907	1.068	0.902
28-Aug-18	11.826	0.670	0.496
28-Aug-18	14.170	1.075	0.865
28-Aug-18	13.282	0.678	0.542
28-Aug-18	12.942	1.091	0.872
28-Aug-18	11.308	1.107	0.827
28-Aug-18	12.143	1.105	0.843
28-Aug-18	12.439	1.137	0.887
28-Aug-18	12.364	0.707	0.519
28-Aug-18	13.098	1.113	0.940
28-Aug-18	15.153	1.083	0.917
28-Aug-18	13.699	1.135	0.857
28-Aug-18	11.229	1.120	0.857
28-Aug-18	13.427	1.129	0.926
28-Aug-18	12.939	1.090	0.887
28-Aug-18	13.091	1.128	0.865
28-Aug-18	12.357	1.105	0.820
28-Aug-18	10.619	0.639	0.519
28-Aug-18	12.879	0.609	0.512
28-Aug-18	14.797	1.061	0.805
28-Aug-18	11.788	1.060	0.865
28-Aug-18	12.121	0.677	0.526
28-Aug-18	11.709	1.108	0.910
28-Aug-18	11.965	1.091	0.820
28-Aug-18	13.127	1.113	0.857
28-Aug-18	11.302	0.677	0.504
28-Aug-18	11.789	0.708	0.519
28-Aug-18	11.758	0.635	0.504
28-Aug-18	12.004	1.113	0.902
28-Aug-18	10.974	1.098	0.865
28-Aug-18	14.244	1.113	0.865
28-Aug-18	11.246	0.641	0.511
28-Aug-18	13.371	1.061	0.805
28-Aug-18	12.730	0.677	0.511
28-Aug-18	13.727	1.105	0.812
28-Aug-18	11.858	0.654	0.504
28-Aug-18	10.368	0.692	0.534

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
28-Aug-18	10.970	0.639	0.496
28-Aug-18	8.716	0.654	0.527
28-Aug-18	9.425	0.692	0.489
28-Aug-18	11.280	1.083	0.805
28-Aug-18	14.138	1.091	0.865
28-Aug-18	15.012	1.120	0.827
28-Aug-18	11.939	0.671	0.512
28-Aug-18	10.345	0.602	0.489
28-Aug-18	10.909	0.685	0.511
28-Aug-18	12.351	1.060	0.827
28-Aug-18	10.035	1.090	0.835
28-Aug-18	8.912	0.692	0.526
28-Aug-18	8.128	0.639	0.526
28-Aug-18	10.220	0.632	0.549
28-Aug-18	10.833	1.062	0.873
28-Aug-18	11.577	1.123	0.876
28-Aug-18	11.978	0.677	0.489
28-Aug-18	11.415	0.678	0.527
28-Aug-18	12.266	1.075	0.842
28-Aug-18	10.489	0.707	0.534
28-Aug-18	12.155	1.121	0.827
11-Sep-18	17.980	1.045	0.850
11-Sep-18	15.248	1.090	0.872
11-Sep-18	13.861	1.068	0.857
11-Sep-18	19.234	1.061	0.872
11-Sep-18	17.928	1.115	0.837
11-Sep-18	14.993	1.046	0.911
11-Sep-18	16.761	1.062	0.933
11-Sep-18	17.364	1.121	0.895
11-Sep-18	17.914	1.068	0.827
11-Sep-18	14.757	1.045	0.842
11-Sep-18	18.265	1.105	0.827
11-Sep-18	19.123	1.143	0.872
11-Sep-18	15.916	1.090	0.842
11-Sep-18	15.378	1.120	0.917
11-Sep-18	13.849	1.143	0.917
11-Sep-18	17.674	1.120	0.895

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
11-Sep-18	17.747	1.158	0.910
11-Sep-18	16.969	1.083	0.835
11-Sep-18	18.142	1.000	0.872
11-Sep-18	14.408	1.135	0.865
11-Sep-18	15.303	1.098	0.872
11-Sep-18	16.819	1.083	0.880
11-Sep-18	17.092	1.120	0.880
11-Sep-18	18.331	1.056	0.888
11-Sep-18	18.137	1.083	0.865
11-Sep-18	13.941	1.083	0.880
11-Sep-18	18.527	1.061	0.903
11-Sep-18	14.876	1.125	0.898
11-Sep-18	14.640	1.100	0.882
11-Sep-18	15.578	1.068	0.850
11-Sep-18	16.816	1.128	0.880
11-Sep-18	18.334	1.068	0.805
11-Sep-18	16.854	1.105	0.842
11-Sep-18	20.154	1.083	0.850
11-Sep-18	18.138	1.113	0.872
11-Sep-18	17.483	1.126	0.851
11-Sep-18	13.048	1.105	0.850
11-Sep-18	16.077	1.093	0.857
11-Sep-18	16.235	1.069	0.843
11-Sep-18	17.172	1.098	0.835
11-Sep-18	16.776	1.128	0.872
11-Sep-18	16.041	1.060	0.857
11-Sep-18	16.875	1.098	0.865
11-Sep-18	14.796	1.136	0.903
11-Sep-18	11.850	1.090	0.872
11-Sep-18	17.683	1.128	0.865
11-Sep-18	16.389	1.068	0.835
11-Sep-18	16.096	1.093	0.882
11-Sep-18	16.120	1.068	0.872
11-Sep-18	17.023	1.113	0.880
11-Sep-18	16.005	1.083	0.865
11-Sep-18	15.065	1.075	0.850
11-Sep-18	14.743	1.060	0.790

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
25-Sep-18	-	1.000	0.797
25-Sep-18	17.449	1.083	0.865
25-Sep-18	19.964	1.038	0.820
25-Sep-18	17.710	1.045	0.872
25-Sep-18	19.824	1.039	0.820
25-Sep-18	20.608	1.053	0.872
25-Sep-18	14.680	1.113	0.895
25-Sep-18	20.100	1.062	0.820
25-Sep-18	17.989	1.121	0.873
25-Sep-18	20.106	1.092	0.865
25-Sep-18	22.061	1.101	0.926
25-Sep-18	19.921	1.091	0.850
25-Sep-18	21.885	1.083	0.880
25-Sep-18	17.101	1.060	0.872
25-Sep-18	13.903	1.075	0.820
25-Sep-18	19.184	1.075	0.857
25-Sep-18	20.965	1.065	0.881
25-Sep-18	19.171	1.048	0.851
25-Sep-18	16.732	1.045	0.820
25-Sep-18	19.844	1.106	0.880
25-Sep-18	22.262	1.143	0.910
25-Sep-18	19.228	1.060	0.925
25-Sep-18	20.854	1.046	0.872
25-Sep-18	17.882	1.083	0.790
25-Sep-18	19.653	1.046	0.827
25-Sep-18	17.865	1.045	0.850
25-Sep-18	21.753	1.068	0.925
25-Sep-18	22.074	1.008	0.880
25-Sep-18	17.599	1.075	0.835
25-Sep-18	20.870	1.098	0.865
25-Sep-18	18.469	1.045	0.857
25-Sep-18	19.886	1.054	0.880
25-Sep-18	20.194	1.068	0.880
25-Sep-18	20.154	1.061	0.872
25-Sep-18	18.767	1.083	0.865
25-Sep-18	20.059	1.068	0.857
25-Sep-18	20.506	1.053	0.857

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
25-Sep-18	14.061	1.075	0.857
25-Sep-18	18.526	1.060	0.857
25-Sep-18	21.022	1.098	0.888
25-Sep-18	19.591	1.030	0.857
25-Sep-18	21.630	1.038	0.911
25-Sep-18	17.983	1.068	0.805
25-Sep-18	19.885	1.038	0.857
25-Sep-18	16.992	1.008	0.887
25-Sep-18	21.155	1.060	0.917
25-Sep-18	18.798	1.083	0.880
25-Sep-18	13.398	1.060	0.887
25-Sep-18	19.146	1.091	0.873
25-Sep-18	20.231	1.045	0.827
25-Sep-18	20.970	1.038	0.911
25-Sep-18	16.700	0.994	0.828
25-Sep-18	18.049	1.083	0.827
25-Sep-18	22.229	1.105	0.910
25-Sep-18	22.187	1.071	0.895
25-Sep-18	18.562	1.038	0.827
25-Sep-18	21.515	1.023	0.857
25-Sep-18	19.686	1.108	0.890
25-Sep-18	19.499	1.030	0.820
25-Sep-18	17.044	1.091	0.827
25-Sep-18	13.514	0.963	0.835
9-Oct-18	-	1.053	0.842
9-Oct-18	-	1.166	0.917
9-Oct-18	14.350	1.083	0.895
9-Oct-18	20.076	1.090	0.902
9-Oct-18	17.554	0.985	0.865
9-Oct-18	14.990	1.023	0.865
9-Oct-18	14.489	1.038	0.872
9-Oct-18	15.919	1.056	0.828
9-Oct-18	23.051	1.083	0.835
9-Oct-18	22.550	1.060	0.865
9-Oct-18	15.962	1.060	0.872
9-Oct-18	20.116	1.090	0.887
9-Oct-18	20.504	1.068	0.857

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
9-Oct-18	13.988	1.023	0.842
9-Oct-18	21.514	1.008	0.835
9-Oct-18	22.590	1.060	0.857
9-Oct-18	14.791	1.105	0.910
9-Oct-18	22.775	1.106	0.850
9-Oct-18	22.802	1.068	0.865
9-Oct-18	13.609	1.055	0.865
9-Oct-18	15.232	1.143	0.857
9-Oct-18	15.094	1.061	0.865
9-Oct-18	20.535	1.090	0.880
9-Oct-18	14.426	1.041	0.812
9-Oct-18	21.492	1.075	0.842
9-Oct-18	16.472	1.083	0.812
9-Oct-18	23.317	1.120	0.887
9-Oct-18	15.657	1.098	0.902
9-Oct-18	15.112	1.098	0.902
9-Oct-18	15.372	1.075	0.872
9-Oct-18	15.923	1.108	0.910
9-Oct-18	14.369	1.106	0.842
9-Oct-18	16.238	1.075	0.872
9-Oct-18	22.752	1.113	0.925
9-Oct-18	14.482	1.068	0.835
9-Oct-18	24.317	1.113	0.872
9-Oct-18	15.418	1.099	0.896
9-Oct-18	13.554	1.083	0.917
9-Oct-18	14.585	1.083	0.812
9-Oct-18	17.472	1.038	0.865
9-Oct-18	21.274	1.038	0.850
9-Oct-18	20.973	1.030	0.842
9-Oct-18	17.022	1.068	0.895
9-Oct-18	15.181	1.070	0.872
9-Oct-18	15.530	1.039	0.865
9-Oct-18	20.574	1.076	0.880
9-Oct-18	16.660	1.010	0.820
9-Oct-18	14.146	1.090	0.865
9-Oct-18	20.619	1.053	0.820
9-Oct-18	15.264	1.046	0.873

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
9-Oct-18	20.854	1.128	0.895
9-Oct-18	14.830	1.105	0.880
9-Oct-18	15.161	1.106	0.858
9-Oct-18	22.370	1.068	0.887
9-Oct-18	13.594	1.060	0.932
9-Oct-18	14.215	1.060	0.850
9-Oct-18	14.689	1.106	0.880
9-Oct-18	21.478	1.083	0.857
9-Oct-18	20.845	1.053	0.865
9-Oct-18	15.339	1.011	0.850
9-Oct-18	15.799	0.985	0.857
9-Oct-18	16.389	1.084	0.880
9-Oct-18	21.678	1.038	0.865
9-Oct-18	14.800	1.083	0.880
9-Oct-18	14.990	1.106	0.881
9-Oct-18	16.431	1.062	0.837
9-Oct-18	14.914	1.106	0.881
9-Oct-18	13.689	1.053	0.857
9-Oct-18	20.533	1.030	0.902
9-Oct-18	19.661	1.070	0.865
9-Oct-18	15.812	1.040	0.851
9-Oct-18	12.041	1.008	0.759
9-Oct-18	12.909	1.032	0.813
24-Oct-18	15.384	1.068	0.907
24-Oct-18	14.876	1.046	0.910
24-Oct-18	14.398	1.083	0.933
24-Oct-18	14.081	1.061	0.823
24-Oct-18	15.615	1.107	0.829
24-Oct-18	17.882	1.083	0.859
24-Oct-18	14.195	1.030	0.820
24-Oct-18	14.612	1.083	0.874
24-Oct-18	15.498	1.070	0.905
24-Oct-18	12.786	1.053	0.775
24-Oct-18	17.281	1.038	0.881
24-Oct-18	13.137	0.994	0.814
24-Oct-18	16.210	1.105	0.881
24-Oct-18	13.826	1.098	0.835

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
24-Oct-18	14.922	1.121	0.880
24-Oct-18	12.664	1.075	0.887
24-Oct-18	13.564	1.038	0.889
24-Oct-18	13.041	1.023	0.887
24-Oct-18	13.592	1.060	0.857
24-Oct-18	13.249	1.038	0.850
24-Oct-18	15.471	1.121	0.844
24-Oct-18	13.557	1.158	0.865
24-Oct-18	15.979	1.105	0.827
24-Oct-18	15.301	1.090	0.880
24-Oct-18	12.855	1.023	0.790
24-Oct-18	15.339	1.083	0.872
24-Oct-18	13.236	1.084	0.873
24-Oct-18	15.561	1.129	0.903
24-Oct-18	14.791	1.024	0.872
24-Oct-18	15.534	1.008	0.797
24-Oct-18	12.194	0.962	0.774
24-Oct-18	14.913	1.060	0.902
24-Oct-18	14.667	1.009	0.805
24-Oct-18	15.207	1.068	0.902
24-Oct-18	14.542	1.075	0.857
24-Oct-18	14.024	0.982	0.791
24-Oct-18	13.596	1.101	0.860
24-Oct-18	14.108	1.015	0.812
24-Oct-18	14.683	1.030	0.835
24-Oct-18	15.223	0.978	0.827
24-Oct-18	13.873	1.038	0.812
24-Oct-18	13.363	1.008	0.842
24-Oct-18	14.329	1.068	0.835
24-Oct-18	14.373	1.054	0.875
24-Oct-18	14.413	1.060	0.835
24-Oct-18	13.754	0.970	0.789
24-Oct-18	14.496	0.985	0.782
24-Oct-18	14.407	1.061	0.865
24-Oct-18	15.067	1.075	0.895
24-Oct-18	14.562	1.060	0.827
24-Oct-18	15.534	1.068	0.902

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
24-Oct-18	14.865	1.048	0.792
24-Oct-18	14.214	0.994	0.790
24-Oct-18	14.651	1.076	0.887
24-Oct-18	15.380	1.023	0.827
24-Oct-18	13.232	0.993	0.798
24-Oct-18	14.114	1.038	0.850
24-Oct-18	13.031	1.030	0.797
24-Oct-18	13.869	1.030	0.797
24-Oct-18	14.504	1.030	0.812
24-Oct-18	15.000	1.023	0.850
24-Oct-18	13.818	1.106	0.858
24-Oct-18	15.444	1.076	0.882
24-Oct-18	13.294	1.090	0.872
24-Oct-18	14.085	1.038	0.850
24-Oct-18	15.397	1.113	0.887
24-Oct-18	14.126	1.042	0.865
24-Oct-18	14.012	1.068	0.850
24-Oct-18	14.012	1.083	0.872
24-Oct-18	16.121	1.068	0.842
24-Oct-18	14.855	1.038	0.842
24-Oct-18	14.198	1.045	0.842
24-Oct-18	15.903	1.060	0.865
24-Oct-18	14.384	1.105	0.850
24-Oct-18	15.364	1.030	0.827
24-Oct-18	15.328	1.106	0.857
24-Oct-18	15.000	1.046	0.851
24-Oct-18	15.031	1.001	0.827
24-Oct-18	15.738	1.053	0.827
24-Oct-18	16.229	1.075	0.857
24-Oct-18	16.121	1.098	0.880
24-Oct-18	15.369	1.121	0.850
24-Oct-18	15.881	1.113	0.895
24-Oct-18	14.716	1.068	0.887
24-Oct-18	14.638	1.046	0.866
24-Oct-18	16.103	1.061	0.820
24-Oct-18	15.977	1.031	0.835
24-Oct-18	17.725	1.113	0.902

Table C.1. cont.

Collection date	Case length (mm)	Head capsule length (mm)	Head capsule width (mm)
24-Oct-18	17.164	1.027	0.794
24-Oct-18	16.477	1.078	0.776
24-Oct-18	15.187	1.078	0.895
24-Oct-18	17.942	1.008	0.797
24-Oct-18	18.333	1.053	0.835
24-Oct-18	17.422	1.015	0.857
24-Oct-18	19.699	1.053	0.842
24-Oct-18	15.960	1.008	0.850
24-Oct-18	14.253	1.053	0.865
24-Oct-18	16.145	1.090	0.872
24-Oct-18	18.993	1.030	0.835
24-Oct-18	21.519	1.045	0.850
24-Oct-18	20.172	1.061	0.827
24-Oct-18	20.000	1.083	0.865
24-Oct-18	20.086	1.053	0.812
24-Oct-18	21.898	1.030	0.835

Appendix D. Carbon and nitrogen stable isotope values of samples from Chatcolet Lake, ID

Table D.1. All samples taken from Chatcolet Lake are listed by sampling occasion. Spring 2018 encompasses all samples taken from 26-April, 8-May, 23-May, 5-June, and 19-June. The values listed are ^{13}C:^{12}C, percent carbon, ^{15}N:^{14}N, and percent nitrogen. Values are the results of the analysis by the Washington State University Stable Isotope Core Laboratory.

Date	Sample	$\delta^{13}C_{VPDB}$ x 1000	C%	$\delta^{15}N_{AIR}$ x 1000	N%
10-Oct-17	*Nectopsyche albida*	-19.56	46.908	1.73	11.085
10-Oct-17	*Nectopsyche albida*	-20.62	47.161	3.35	9.589
10-Oct-17	*Nectopsyche albida*	-16.76	49.404	1.99	9.649
10-Oct-17	*Myriophyllum* spp.	-20.71	25.179	2.7	1.973
10-Oct-17	*Myriophyllum* spp.	-18.43	36.802	2.49	2.167
10-Oct-17	*Myriophyllum* spp.	-19.53	34.416	2.26	2.33
10-Oct-17	*Elodea canadensis*	-17.56	35.195	1.8	2.108
10-Oct-17	*Elodea canadensis*	-17.87	34.349	1.3	2.055
10-Oct-17	*Elodea canadensis*	-18.11	35.093	1.1	2.066
10-Oct-17	*Ceratophyllum demersum*	-20.78	35.892	3.14	1.8
10-Oct-17	*Ceratophyllum demersum*	-21.18	36.559	4.92	2.016
10-Oct-17	*Ceratophyllum demersum*	-19.41	34.745	1.47	2.044
10-Oct-17	Detritus	-20.81	32.215	1.24	3.245
10-Oct-17	Detritus	-21.82	37.629	1.3	3.231
10-Oct-17	Detritus	-20.56	35.561	1.31	3.367
8-May-18	*Nectopsyche albida*	-21.41	44.174	2.71	9.065
8-May-18	*Nectopsyche albida*	-20.01	45.883	2.59	9.331
8-May-18	*Nectopsyche albida*	-20.71	47.061	1.37	8.584
23-May-18	*Nectopsyche albida*	-25.39	50.192	2.44	7.28
23-May-18	*Nectopsyche albida*	-22.98	47.145	2.26	7.586
23-May-18	*Nectopsyche albida*	-20.42	42.375	2.25	9.606
5-Jun-18	*Nectopsyche albida*	-20.77	52.272	1.23	8.71
5-Jun-18	*Nectopsyche albida*	-19.67	49.658	1.6	9.925
5-Jun-18	*Myriophyllum* spp.	-21.39	39.698	1.96	3.983
19-Jun-18	*Elodea canadensis*	-16.48	31.078	0.19	2.426
26-Apr-18	Epiphytes	-25.32	4.118	1.39	0.286
8-May-18	*Potamogeton amplifolius*	-18.08	33.545	-4.95	3.547
8-May-18	*Potamogeton amplifolius*	-17.65	34.113	-3.35	3.022
8-May-18	*Potamogeton amplifolius*	-18.16	27.115	-2.54	2.122
23-May-18	Filamentous algae	-30.33	24.151	1.91	2.309
26-Apr-18	Filamentous algae	-33.34	22.827	1.58	2.623

Table D.1. cont.

Date	Sample	$\delta^{13}C_{VPDB}$ x 1000	C%	$\delta^{15}N_{AIR}$ x 1000	N%
26-Apr-18	Chironomids	-25.01	34.681	1.98	8.161
26-Apr-18	Fungus	-18.06	7.411	2.54	0.431
28-Aug-18	*Nectopsyche albida*	-18.59	47.43	-2.89	10.68
28-Aug-18	*Nectopsyche albida*	-17.17	48.47	-3.00	10.43
28-Aug-18	*Nectopsyche albida*	-18.25	48.67	-1.97	9.65
28-Aug-18	*Myriophyllum* spp.	-14.36	41.01	1.60	3.33
28-Aug-18	*Myriophyllum* spp.	-14.32	40.94	1.64	3.31
28-Aug-18	*Myriophyllum* spp.	-14.36	40.97	1.67	3.3
28-Aug-18	*Elodea canadensis*	-14.86	38.19	-1.25	2.43
28-Aug-18	*Elodea canadensis*	-14.88	38.16	-1.07	2.37
28-Aug-18	*Elodea canadensis*	-14.86	38.05	-1.09	2.43
28-Aug-18	*Ceratophyllum demersum*	-17.47	30.44	1.65	2.22
28-Aug-18	*Ceratophyllum demersum*	-17.69	30.03	1.64	2.3
28-Aug-18	*Ceratophyllum demersum*	-17.68	29.72	1.65	2.23
28-Aug-18	*Potamogeton richardsonii*	-15.48	39.33	0.75	2.02
28-Aug-18	*Potamogeton richardsonii*	-15.34	39.47	0.73	2.02
28-Aug-18	*Potamogeton richardsonii*	-15.35	39.4	0.59	2.01
28-Aug-18	*Ranunculus aquatilis*	-14.74	37.59	1.23	2.5
28-Aug-18	*Ranunculus aquatilis*	-14.59	38.11	1.25	2.48
28-Aug-18	*Ranunculus aquatilis*	-14.68	38.33	1.13	2.36
28-Aug-18	*Potamogeton pusillis*	-17.02	38.27	-3.03	2.88
28-Aug-18	*Potamogeton pusillis*	-17.1	38.47	-2.91	3.03
28-Aug-18	*Potamogeton pusillis*	-17.02	38.45	-3.09	2.79
28-Aug-18	*Najas* spp.	-16.74	37.9	-4.01	3.08
28-Aug-18	*Najas* spp.	-16.62	37.61	-4.13	3
28-Aug-18	*Najas* spp.	-16.71	37.65	-3.91	3.1
25-Sep-18	*Nectopsyche albida*	-17.94	38.77	0.71	5.18
25-Sep-18	*Nectopsyche albida*	-17.44	44.47	0.24	6.15
25-Sep-18	*Nectopsyche albida*	-18.63	50.73	0.46	6.51
25-Sep-18	*Myriophyllum* spp.	-14.67	36.68	2.37	2.91
25-Sep-18	*Myriophyllum* spp.	-14.7	36.93	2.33	2.89
25-Sep-18	*Myriophyllum* spp.	-14.94	36.74	2.38	2.97
25-Sep-18	*Elodea canadensis*	-15.73	27.04	-0.08	1.55
25-Sep-18	*Elodea canadensis*	-15.43	29.45	0.33	1.54
25-Sep-18	*Elodea canadensis*	-15.58	28.48	0.33	1.68
25-Sep-18	*Potamogeton richardsonii*	-14.95	30.61	1.66	1.4
25-Sep-18	*Potamogeton richardsonii*	-15.27	28.54	1.66	1.46

Table D.1. cont.

Date	Sample	$\delta^{13}C_{VPDB}$ x 1000	C%	$\delta^{15}N_{AIR}$ x 1000	N%
25-Sep-18	*Potamogeton richardsonii*	-14.98	31.01	1.60	1.44
25-Sep-18	*Ranunculus aquatilis*	-14.89	25.79	1.99	2.02
25-Sep-18	*Ranunculus aquatilis*	-15.06	25.13	2.22	1.92
25-Sep-18	*Ranunculus aquatilis*	-14.87	27.16	2.08	2.03
25-Sep-18	Epiphytes	-18.85	10.9664193	1.55	1.49
25-Sep-18	Epiphytes	-18.72	11.3426348	2.42	1.57
25-Sep-18	Epiphytes	-18.68	11.8400517	2.03	1.60
9-Oct-18	*Nectopsyche albida*	-19.14	49.95	0.83	8.66
9-Oct-18	*Nectopsyche albida*	-17.91	49.8	0.96	7.36
9-Oct-18	*Nectopsyche albida*	-20.09	45.56	1.66	5.28
9-Oct-18	*Myriophyllum* spp.	-15.33	27.6	3.05	2.3
9-Oct-18	*Myriophyllum* spp.	-15.57	27.43	2.99	2.46
9-Oct-18	*Myriophyllum* spp.	-15.33	28.04	2.88	2.34
9-Oct-18	*Elodea canadensis*	-16.36	23.14	0.51	1.67
9-Oct-18	*Elodea canadensis*	-16.44	24.6	0.19	1.79
9-Oct-18	*Elodea canadensis*	-16.58	21.76	0.53	1.7
9-Oct-18	*Ceratophyllum demersum*	-17.61	23.81	1.97	1.76
9-Oct-18	*Ceratophyllum demersum*	-17.69	23.21	2.00	1.75
9-Oct-18	*Ceratophyllum demersum*	-17.87	23.07	1.85	1.83
9-Oct-18	*Potamogeton richardsonii*	-16.96	24.77	2.21	1.81
9-Oct-18	*Potamogeton richardsonii*	-16.84	25.31	2.01	1.75
9-Oct-18	*Potamogeton richardsonii*	-17.02	24.89	2.07	1.8
9-Oct-18	Epiphytes	-28.08	21.0801559	4.47	4.03
9-Oct-18	Epiphytes	-28.24	19.3632371	4.61	3.75
9-Oct-18	Epiphytes	-28.03	18.8193421	4.59	3.61
9-Oct-18	*N. albida* case	-15.81	24.49	0.85	7.33
9-Oct-18	*N. albida* case	-15.56	20.98	1.46	4.37
9-Oct-18	*N. albida* case	-15.25	20.65	1.41	4.05
24-Oct-18	*Nectopsyche albida*	-19.48	48.23	2.25	7.47
24-Oct-18	*Nectopsyche albida*	-18.23	48.3	1.62	7.38
24-Oct-18	*Nectopsyche albida*	-17.44	50.86	1.14	7.1
24-Oct-18	*Myriophyllum* spp.	-14.93	22.7	2.62	2.14
24-Oct-18	*Myriophyllum* spp.	-14.66	23.51	2.82	2.24
24-Oct-18	*Myriophyllum* spp.	-14.7	22.85	2.86	2.08
24-Oct-18	*Elodea canadensis*	-14.65	26.54	-0.04	1.34
24-Oct-18	*Elodea canadensis*	-14.47	28.71	-0.31	1.49
24-Oct-18	*Elodea canadensis*	-14.61	25.92	0.09	1.28

Table D.1. cont.

Date	Sample	$\delta^{13}C_{VPDB}$ x 1000	C%	$\delta^{15}N_{AIR}$ x 1000	N%
24-Oct-18	*Ceratophyllum demersum*	-16.54	31.18	-0.40	1.84
24-Oct-18	*Ceratophyllum demersum*	-16.64	32.24	-0.52	1.9
24-Oct-18	*Ceratophyllum demersum*	-16.48	30.12	-0.36	1.86
24-Oct-18	*Potamogeton richardsonii*	-16.14	22.17	1.45	1.47
24-Oct-18	*Potamogeton richardsonii*	-16.24	21.44	1.63	1.48
24-Oct-18	*Potamogeton richardsonii*	-16.32	21.92	1.49	1.53
24-Oct-18	Epiphytes	-24.18	9.415	3.94	1.402
24-Oct-18	Epiphytes	-23.01	7.121	3.3	1.017
24-Oct-18	Epiphytes	-22.82	7.318	3.63	1.068
24-Oct-18	*N. albida* case	-17.41	18.57	1.87	5.22
24-Oct-18	*N. albida* case	-17.53	18.77	1.81	3.87
24-Oct-18	*N. albida* case	-17.48	19.13	1.78	4

Appendix E. Plots of isotope signatures by sample date

These figures are the average carbon and nitrogen isotope data from samples collected between 10-October-2017 and 24-October-2018 from Chatcolet Lake, Idaho. Each point represents an average of that species signatures, and the error bars represent standard error. The nitrogen ratio is $^{15}N:^{14}N$, and the carbon ratio is $^{13}C:^{12}C$.

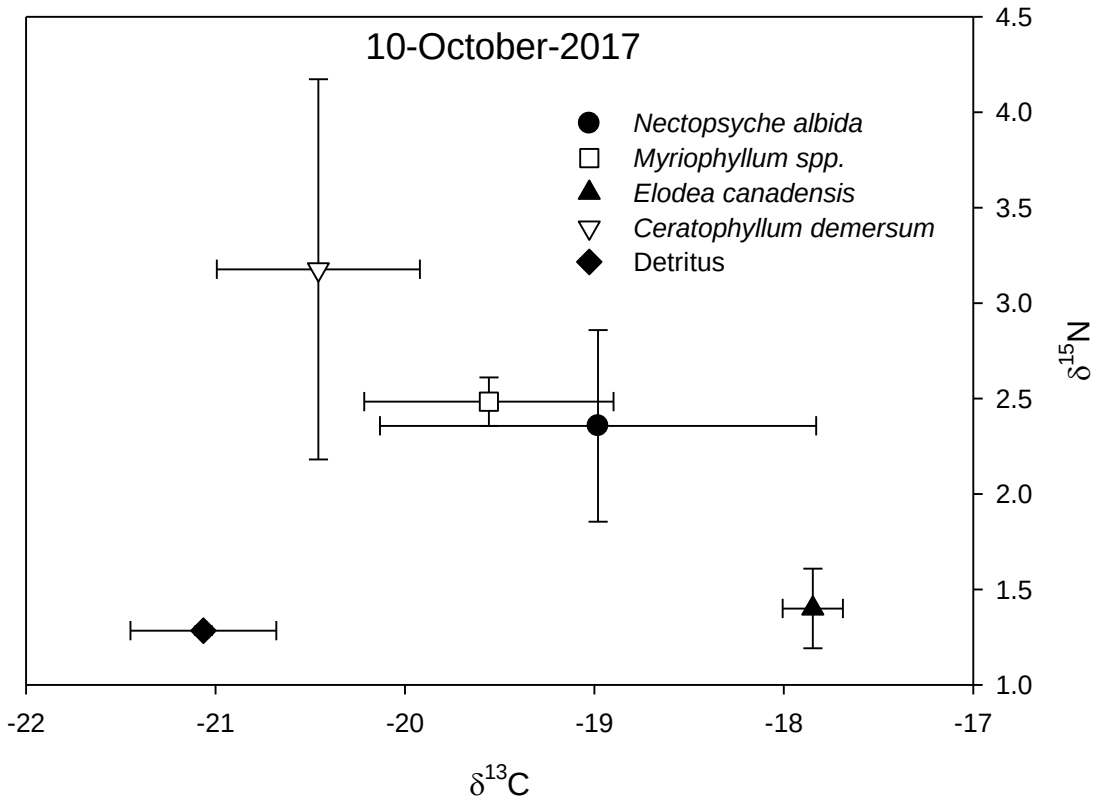

Figure E.1. Isotope signatures of samples collected on 10-October-2017 (means±SE) from Chatcolet Lake, ID.

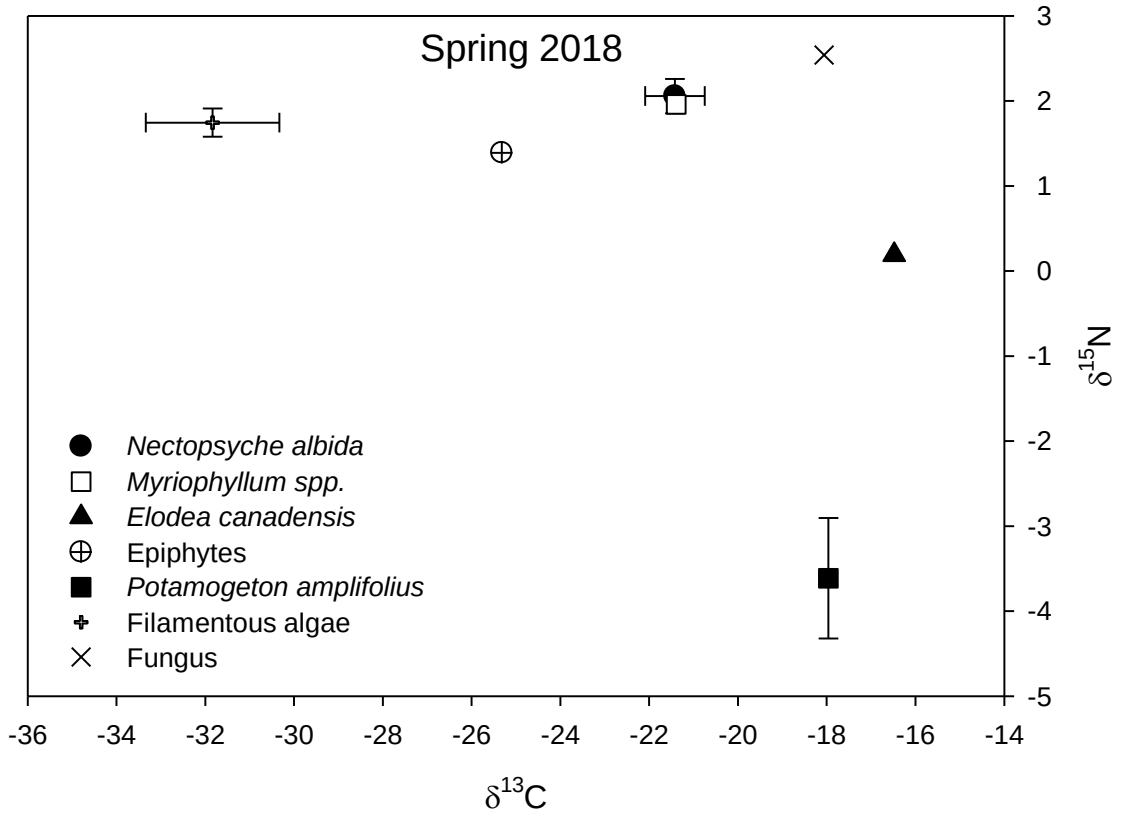

Figure E.2. Isotope signatures of samples collected in Spring 2018 (means±SE) from Chatcolet Lake, ID. Epiphytes, filamentous algae, and fungus were collected on 26-April-2018. Some *Nectopsyche albida* larva and *Potamogeton amplifolius* were collected on 8-May-2018. Some *N. albida* larva and filamentous algae were collected on 23-May-2018. Some *N. albida* larva and *Myriophyllum* spp. were collected on 5-June-2018. *Elodea canadensis* was collected on 19-June-2018.

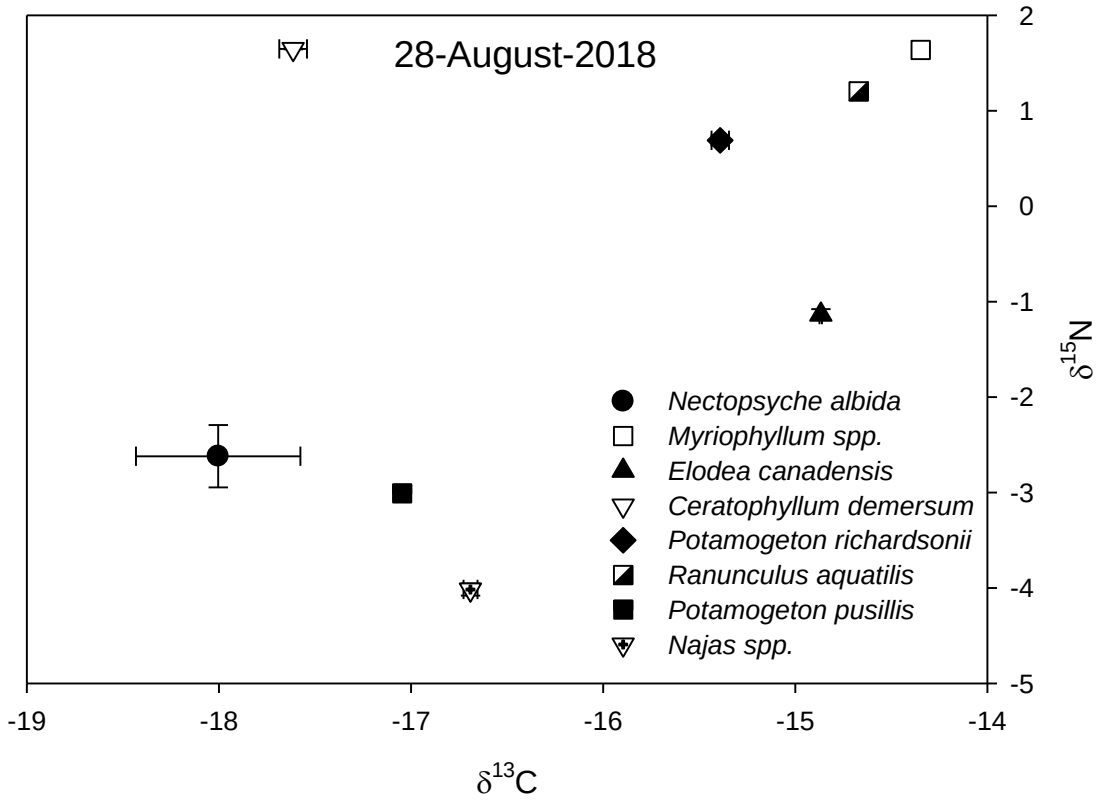

Figure E.3. Isotope signatures of samples collected on 28-August-2018 (means±SE) from Chatcolet Lake, ID.

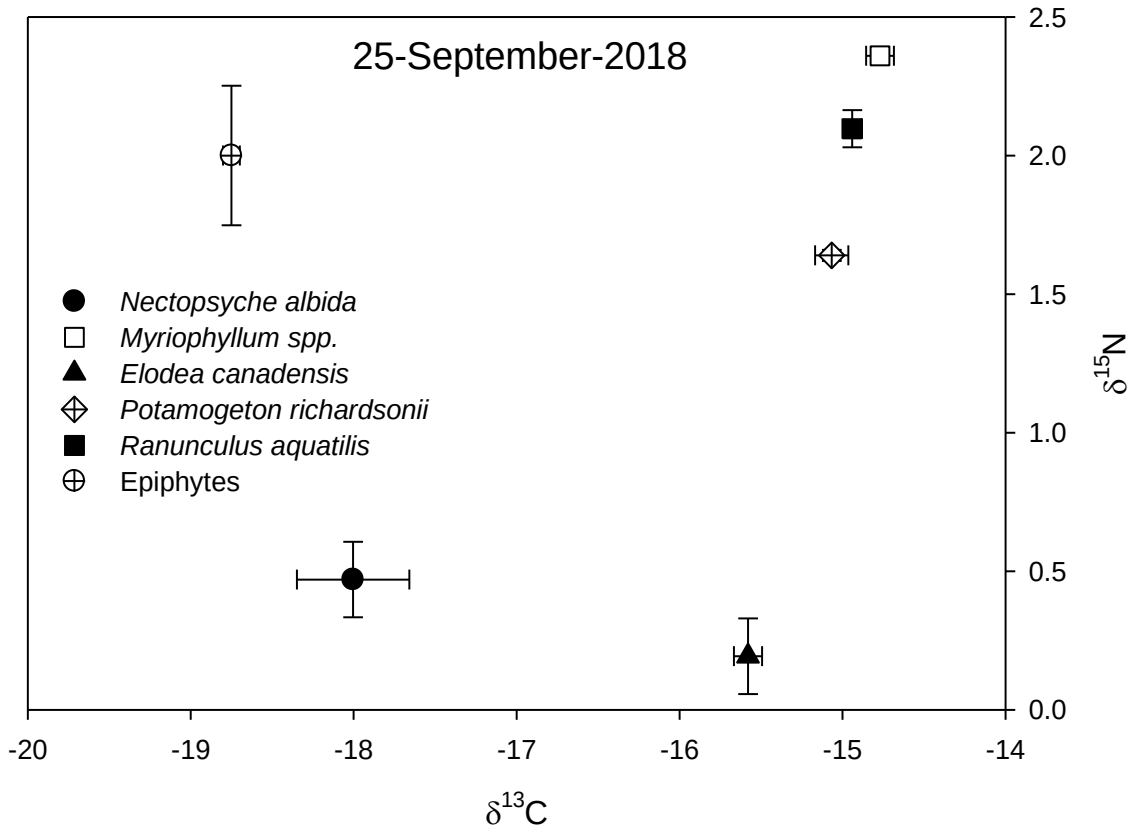

Figure E.4. Isotope signatures of samples collected on 25-September-2018 (means±SE) from Chatcolet Lake, ID.

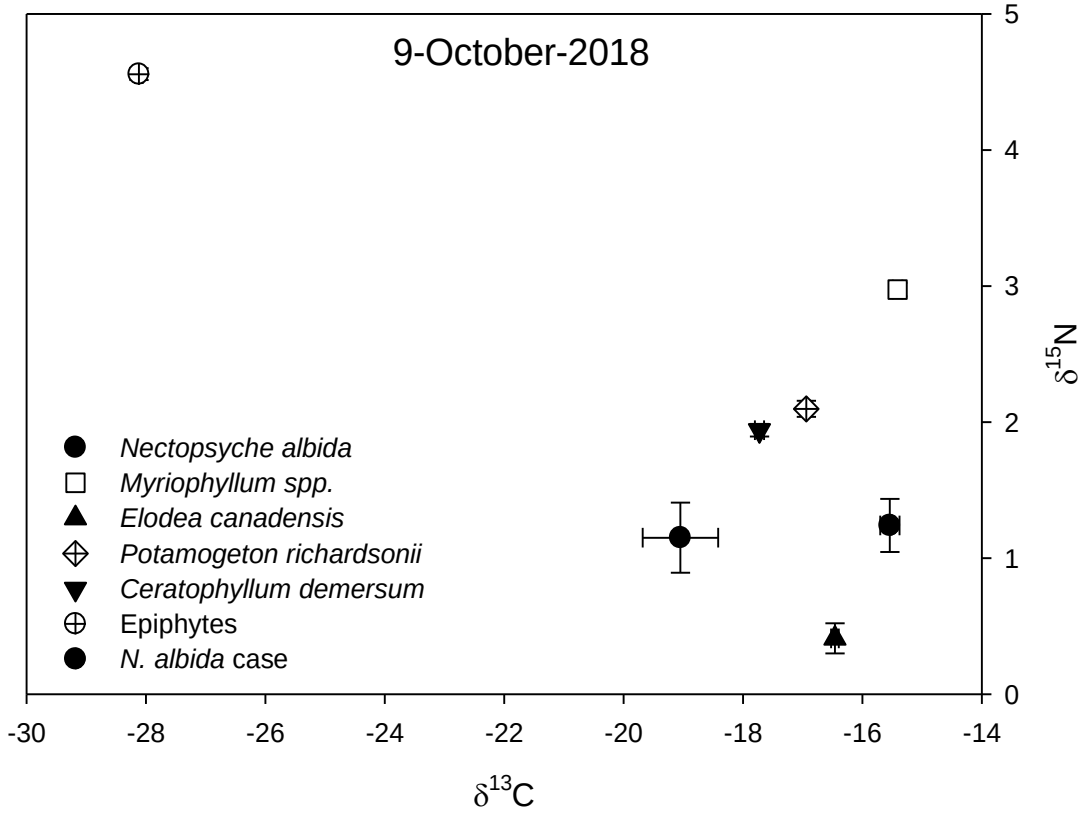

Figure E.5. Isotope signatures of samples collected on 9-October-2018 (means±SE) from Chatcolet Lake, ID.

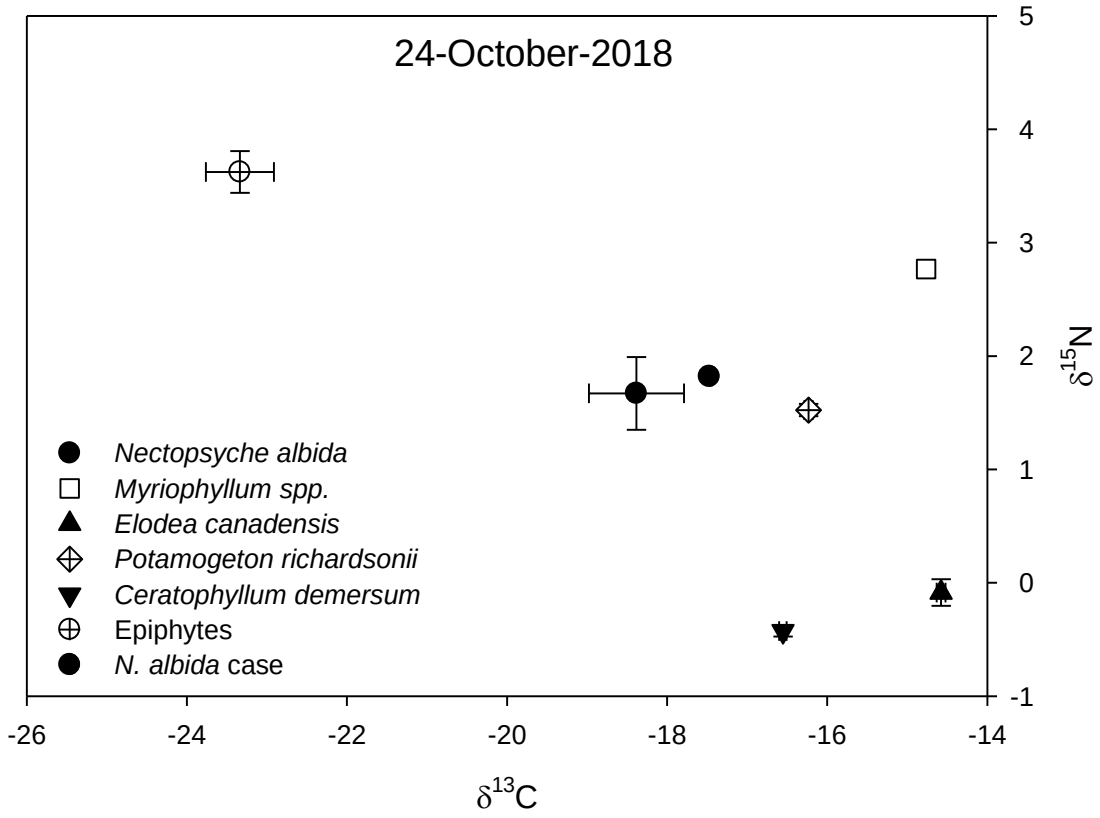

Figure E.6. Isotope signatures of samples collected on 24-October-2018 (means±SE) from Chatcolet Lake, ID.