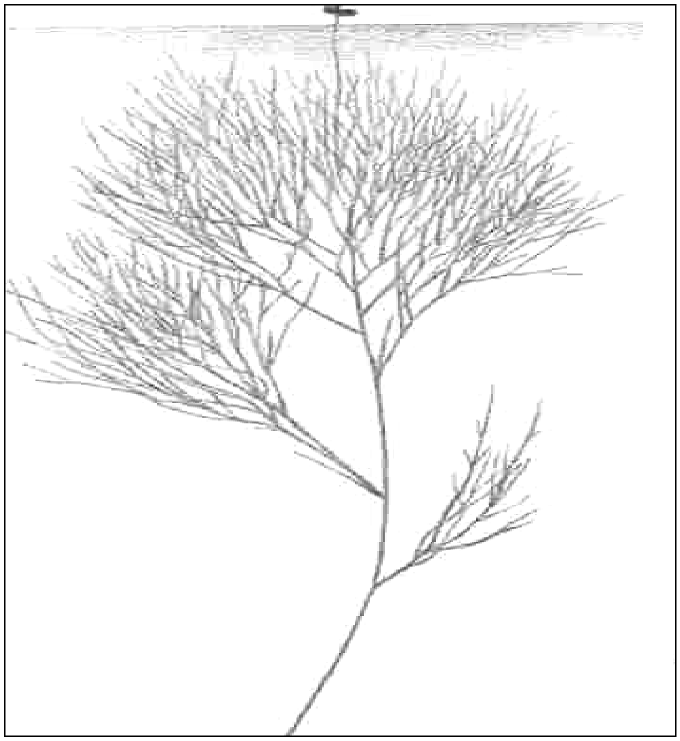

Diversity and Distribution of Aquatic Macrophytes in Swan and Middle Lakes, Nicollet County, Minnesota

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Report submitted to the Minnesota Waterfowl Association
GeoResources Institute Report 4002

October 2004

ABSTRACT

Point intercept surveys were conducted on Swan and Middle Lakes, Nicollet County, MN to quantitatively assess the aquatic macrophyte distribution and diversity. Likewise, to identify the environmental factors that are limiting the growth of these macrophytes species, especially sago pondweed (*Stuckenia pectinata* (L.) Börner) and american wildcelery (*Vallisneria americana* (Michx.). Overall macrophyte diversity decreased significantly with increasing light extinction coefficients in 2001. Diversity was different between sites with Swan Lake having more species of aquatic macrophytes present than North and South Middle Lake. Sago pondweed distribution was different between all sites and between years. Wildcelery was only found in Swan Lake and its distribution was also different between years. There was a negative relationship between the percent clay in the sediment and the presence of sago pondweed shoots. In contrast, there was positive relationship between the percent clay in the sediment and the presence of wildcelery shoots.

INTRODUCTION

Aquatic Macrophyte Ecology

One of the most dominant areas of freshwater lakes in world is the prairie pothole region of North America (Mitsch and Gosselink 1993). The prairie pothole region encompasses an area of approximately 780,000 km^2 (300,000 square miles) in the moraines and glacial till of Minnesota, Iowa, and Dakotas in the Unites States, and Alberta, Saskatchewan, and Manitoba in Canada (Mitsch and Gosselink 1993). The region is comprised of undrained depressions resulting from glacial activity during the Wisconsin stage glaciations (Stewart and Kantrud 1971). These shallow lakes being less than a couple of meters deep are very important for primary productivity, for wildlife of all species, and for human activities (Wetzel 2001). Ecology of these shallow lakes can differ greatly from that of deeper lakes such that shallow lakes often do not become thermally stratified in the summer and have a large littoral zone that can be colonized by aquatic macrophytes. In many shallow lakes the impact of macrophytes on the ecosystem can be great with productivity frequently exceeding 1,000 g m^{-2} (Mitsch and Gosselink 1993).

Aquatic macrophytes constitute an important role in aquatic ecosystems. Macrophytes contribute to the general fitness and diversity of a healthy aquatic ecosystem (Flint and Madsen 1995) by acting as indicators for water quality and aiding in nutrient cycling (Carpenter and Lodge 1986). Likewise, submersed macrophytes produce food for aquatic organisms and provide habitat areas for insects, fish, and other aquatic or semi-aquatic organisms (Madsen et al. 1996). Submersed macrophytes also aid in the anchoring of soft bottom sediments and removing suspended particles and nutrients from the water column (Madsen et al. 1996). Frequent resuspension of bottom sediments reduces water clarity resulting in low light environments which negatively affects the growth of submersed macrophytes. Similarly, submersed macrophytes can be limited by, wave action, temperature, herbivory, or disturbance by animals in shallow lakes. However, light availability is considered to be the primary factor limiting the growth of submersed macrophytes (Scheffer 1998).

A critical light level is needed for photosynthesis of all aquatic vegetation. At depths where the lake bottom does not reach this critical light level submersed macrophyte colonization is limited because of the absence of photosynthetic activity (Case and Madsen 2004). The lack of photosynthesis in aquatic macrophytes is due to low light environments caused by the resuspension of bottom sediments within the water column. The amounts of these light-attenuating materials (turbidity) are dependent upon the interactions between the benthic and pelagic regions of the lake. Shallow lakes with a loose bottom, little or no submersed plants, and a long fetch can experience frequent resuspension due to wind and waves (Blom et al. 1994) resulting in poor water clarity and reduced macrophyte production.

In large lakes regardless of light availability, littoral zones can be barren due to intense wave action caused by a large fetch. The depth of the wave-mixed zone is an important factor that determines the depth and location of water suitable for the colonization of submersed macrophytes (Kantrud 1990). In shallow lakes with a large fetch, the wave-mixed zone deepens and the effects of wave action on sediment-induced turbidity can prevent the growth of submersed macrophytes (Kantrud 1990). In general, wave action washes away finer sediments such as silts and clays leaving coarser, less fertile sediments such as sand and gravel behind (Spence 1982, Wilson and Keddy 1985). Therefore, turbulence created by a large fetch in a shallow lake will affect the distribution of submersed macrophytes directly through damage to mature plants or, indirectly by altering particle size, nutritional status, and stability of the bottom sediment inhibiting the establishment of plants (Spence 1967). Furthermore, wind and wave energy play an important role in the distribution of solar radiation within the water column aiding in the increasing or decreasing of water temperature depending on the time of year.

Temperature can influence plant performance, especially photosynthetic rates (Pilon and Santamaria 2002). During periods of cooler temperatures plant production is generally less due to the lower photosynthetic rates (Scheffer 1998). Temperature may also have an effect on propagule germination and shoot elongation in many submersed species (Spencer 1986, Madsen and Adams 1988). If water temperature is elevated to rapidly it may cause the premature senescence of plants or damage proteins in new propagules which may have an adverse affect on germination (Kantrud 1990).

Waterfowl may also have adverse affects on submersed macrophyte growth and density (Scheffer 1998) through consumption of roots, shoots, and reproductive parts. Benthivorous fish, especially the common carp (*Cyprinus carpio*) directly damage submersed plants through herbivory and uprooting and indirectly by increasing sediment resuspension and water turbidity (Robel 1961, Crivelli 1983). High densities of fish have often been associated with increased turbidity, loss of submersed macrophytes, and diminished waterfowl use (Anderson 1950, Robel 1962, Crivelli 1983).

Waterfowl use of aquatic macrophytes has been well documented in past studies. Submersed aquatic macrophytes are some of the most important food sources available for waterfowl such that migration routes of some species of waterfowl may change depending on the abundance of certain macrophyte species (Kantrud 1990). Submergent macrophyte communities serve as a direct source of waterfowl foods and indirectly as a rich environment for aquatic macro invertebrates (Baldassarre and Bolen 1994). However, two species of submersed macrophytes, sago pondweed (*Stuckenia pectinata* (L.) Börner) and american wildcelery (*Vallisneria americana* (Michx.), form a large portion of the diets of waterfowl (Korschgen and Green 1988, Kantrud 1990). Lakes that contain an abundance of these plant species are often favored as feeding areas by waterfowl (Korschgen and Green 1988).

Sago Pondweed

Sago pondweed (*Stuckenia pectinata*) is a submersed aquatic macrophyte belonging to the Potamogetonaceae family. The genus *Stuckenia* is described as a perennial, from rhizomes; leaves alternate, submersed, filiform to narrowly ribbon like, with characteristic mid-vein, septate; flowers 4-merous, borne in spikes, usually floating on the water surface; fruit drupe-like (Crow and Hellquist 2002). Sago pondweed differs from other species of pondweed by its distinctly beaked fruit and narrowly tapered leaves. Sago pondweed is classified as ruderal or a species capable of colonizing disturbed areas. The species has multiple regenerative strategies and is able to allocate resources to different plant parts depending on environmental conditions (Grime 1979, Kautsky 1987, Madsen 1991). Sago pondweed is considered a higher order aquatic plant rooted in sediment, perennially submersed except for inflorescences, and possessing long stems and small, mostly undivided leaves (Hutchinson 1975).

Sago pondweed can be found circumboreally to about 70^{o} N (Hulten 1968) and can also be found in South Africa, South America, South Eurasia, and New Zealand (Kantrud 1990). The species occurs from sea level to nearly 4,900 m above sea level in the mountains of Venezuela and Tibet (Ascherson and Graebener 1907, cited in Yeo 1965). Sago pondweed is considered a pioneering species that can quickly inhabit disturbed areas and colonizes shallow waters with relatively strong wave action (Ozimek and Kowalczewski 1984) or areas that are polluted (Haslam 1978). Davis and Brinson (1980) placed this species in a group of plants tolerant of, and able to maintain dominance in altered environments. However, optimal growth of sago pondweed occurs in submerged plant communities, and poorest growth in emergent communities where plants tend to be short in stature (Van der Valk and Bliss 1971).

In Minnesota, sago pondweed is common throughout most of the state except in the soft waters of the Archaean rock area of the northeast. However, the phenology of sago pondweed can vary greatly depending on the geographic location of the plant. In the temperate prairie pothole region, sago pondweed behaves as a herbaceous perennial, over-wintering in the form of buried tubers (Case 2003). In these temperate populations, propagules typically survive winter and resume growth the following spring (Spencer et al. 2000) with sago pondweed being one of the first submersed plants to begin spring growth.

Plant growth is usually initiated with tuber germination in the spring when water temperatures reach approximately 10^{o}C. In north temperate regions this usually occurs from late March to June (Kantrud 1990). By mid June the shoots reach the water surface. Shoot length increases between 10 and 15^{o}C (Pilon and Santamaria 2002) with water depth determining the overall shoot length (Kantrud 1990). Once the main shoot reaches the water surface branching occurs that forms a canopy at the water surface. Branching is dense with leaves growing up to 35 cm long, .25-2.5 mm wide, and .18-1.07 mm thick (Kantrud 1990). Optimal growth is attained by mid to late summer (van Dijk and van Vierssen 1991) when water temperatures are between 15 and 25^{o}C, with flowering occurring shortly thereafter. Flowering is light initiated producing light pink monoecious flowers arising from the tip of a leafy shoot (Kantrud 1990). Pollination of flowers occurs along the water surface resulting in drupelet formation. Drupelet formation tends to occur in mid-July or mid-August (Case 2003) with senescence of the plant occurring shortly thereafter when water temperatures exceed 30^{o}C (Spencer 1986).

Tuber production likely begins after peak biomass is attained (Kantrud 1990). The formation of tubers may be initiated by environmental cues in the form of depressed temperatures, decreased light intensity, changes in seasonal photoperiod length, nutrient deficiency, water deficiency, or changes in water chemistry (Sculthorpe 1967, Wiegleb and Brux

1991). Production of tubers begins when the main stem of a mature plant sends out a horizontal rhizome near the surface of the bottom substrate. The rhizome penetrates the substrate and forms branches at every other node. Specialized tissues at the tips of the branches form tubers (Kantrud 1990). Photoperiods of 10 h – 12 h, as well as shading, have been shown to increase tuber production (Spencer and Anderson 1987, van Dijk and van Vierssen 1991, van Dijk et al. 1992, Spencer et al. 1993, Spencer and Ksander 1995, Doyle 2000). Similarly, tuber size and depth within the sediment influence growth and survivorship with larger tubers having an advantage over smaller tubers (Spencer 1987). Likewise, Kantrud (1990) stated larger tubers produce larger plants with more shoots that reach the water surface earlier than plants born from small tubers.

The production from a sago pondweed propagule can be astonishing under the right environmental conditions. In a single season culture experiment, Yeo (1965) grew 36,000 subterranean tubers, 800 axillary tubers, and 6,000 drupelets from 1 tuber. Similarly, he produced 63,300 drupelets and 15,000 tubers from a single drupelet. Densities reached during this experiment were 3,308 tubers m^{-2} and 8,624 drupelets m^{-2}. However, in nature propagule production does not reach densities as those reported by Yeo (1965). For example, in North Heron and South Heron Lakes, Minnesota, tuber densities were only 41 and 26 tubers m^{-2} respectively (Case and Madsen 2004). Likewise, maximum standing crop biomass for sago pondweed was also low in these lakes reaching only 56 g m^{-2} for North Heron Lake and 36 g m^{-2} for South Heron Lake (Case 2003). Lakes with total biomass of sago pondweed less than 200 g m^{-2} indicate a number of possible factors that may be limiting the production of this plant. The most notable of these factors being light availability and temperature.

Increases in light and temperature result in increases in overall biomass, while decreases in light leads to a reduction in biomass and an earlier peak biomass (Barko et al. 1982, van Dijk and van Vierssen 1991, van Dijk et al. 1992). Similarly, colonization of sago pondweed decreases at depths where on average less than 21 percent of PAR (photosynthetically active radiation) incident on the water surface is received during the growing season. Likewise, temperature is a key factor in tuber germination and photosynthesis (Madsen and Adams 1988). For example, Pilon and Santamaria (2002) reported that increases in temperatures were correlated with an increased number of shoots per plant and can correspond to increases in tuber production and an overall abundance of sago pondweed in and area.

The abundance of sago pondweed and other submersed aquatic plants have historically been locations of substantial use by migrating and staging waterfowl (Kantrud 1990). For example, a single sago pondweed dominated lake could support a large percentage of the continental migrating waterfowl population for a month during fall staging (Kantrud 1986). As a food item sago pondweed forms a significant portion of foods consumed by fall staging populations, pre-molting birds, flightless molting ducks, and older ducklings (Bartonek and Hickey 1969, Bergman 1973, Chura 1961, Hay 1974, Keith and Stanislawski 1960). In fact, Martin and Uhler (1939) stated that, "sago pondweed is probably the most important single waterfowl food plant on the continent and is responsible for about half, or more, of the total food percentage credited to the genus *Potamogeton* [*Stuckenia*]." The importance of sago pondweed to migrating and staging waterfowl is so great that in North America, continental migration pathways of some species (most notably the diving species) of waterfowl can be determined by the locations of large bodies of water dominated by the plant (Kantrud 1990).

American Wildcelery

American wildcelery (*Vallisneria americana*) is a dioecious (bearing staminate (male) and pistillate (female) flowers on different plants) freshwater perennial aquatic plant belonging to the Hydrocharitaceae family. Crow and Hellquist (2000) describe the species as "perennial herbs, submersed; leaves basal, long ribbon-like; plants dioecious; pistillate flowers solitary, sessile, enclosed in a tubular spathe, reaching surface by peduncle elongation; staminate flowers numerous, enclosed in spathes born on short peduncles, released and floating to the surface; fruit elongate, cylindrical, peduncle recoiling after fertilization, submersing fruit." Wildcelery has linear strap shaped leaves that are either submersed or floating that can extend 2 meters or more depending on water depth (Korschgen and Green 1988). The stem is vertical having a short axis and bears stolons. Lowden (1982) described two forms of wildcelery, a narrow leaved and broad leaved form of the plant. The narrow leaved typed has leaves less than 10 mm wide with 3-5 longitudinal veins and leaf margins that are entire to finely toothed. The narrow leaf form is typical of freshwater ecosystems. The broad leaved form as leaves that are 10-25 mm wide with 5-9 longitudinal veins and leaf margins that are toothed. Broad leaf wildcelery can be found in many coastal and or brackish ecosystems.

Wildcelery occurs predominately in eastern North America. The species has been reported west from Nova Scotia to South Dakota and south to the Gulf of Mexico (Fassett 1957). Recently, wildcelery has been reported in Nebraska, New Mexico, Arizona, and as far west as Washington (Lowden 1982). Wildcelery tends to grow at intermediate depths of 0-3 meters. Hunt (1963) found the optimum depth was 0.3-1.5 meters with plants being found as deep as 3.3 meters. However, wildcelery may be at a disadvantage in deeper waters due to its limited elongation potential resulting in an inability to concentrate photoreceptive biomass at or near the water surface (Barko et al. 1984). Wildcelery may compensate for its disadvantageous morphology by being able to better adapt to low light environments (Titus and Adams 1979) by reallocating resources to other structures to promote growth under light stressed conditions (Madsen 1991).

Growth of wildcelery is typically initiated in late spring from underground turions. Turions germinate when spring water temperatures reach 10-14^{o}C (Zamuda 1976). After germination the second internode of the turion elongates to form a stolon that carries a rosette of ribbon like leaves to the sediment water interface occurring by late May (Wilder 1974). The leaves reach the water surface by mid summer after which flowering occurs. Pistillate flowers are born on a pedicel that carries the flower to the air water interface for pollination in late summer (Donnermeyer 1982). Male inflorescences are developed submersed with each inflorescence containing approximately 2,000 flowers. Once mature, the male flowers float to the surface and are dispersed by water and air currents on the surface where they may encounter a female flower.

After pollination the pedicel contracts drawing the flower underwater where fruit development takes place (Korschgen and Green 1988). In late summer or early fall the fruit capsule rupture and release a gelatinous matrix containing seeds that will eventually settle to the bottom close to the parent plant (Kaul 1978). Near the end of the growing season (late July to mid August) some of the rosettes develop one or more turions on stolons that grow down into the sediment (Titus and Stephens 1983) after which the remaining above-ground tissue breaks from the sediment and decomposes (Titus and Adams 1979). Wildcelery is capable of both sexual (seed forming) and asexual (turion forming) reproduction, however due to the environments it grows in, asexual reproduction is favored (Titus and Stephens 1983).

Asexual and sexual reproduction of wildcelery can be limited by a number of factors of which light availability and temperature are the most limiting environmental factors for this species. Wildcelery is light adaptable by acclimating rapidly to increasing light levels and also by efficiently using low light environments (Titus and Adams 1979). In general, the depths at which submersed plants can grow are a direct function of water clarity and light intensity (Meyer et al. 1943, Chambers and Kalff 1985). Wildcelery exhibited an ability to grow in deep water where light intensities are only 4.5 percent of the surface intensities (Spence and Chrystal 1970). However, this plant displays a constant decrease in photosynthetic rate with an increase in water depth (Meyer et al. 1943) due to low light intensities and possible thermal stress. Production of wildcelery is severely limited when water temperature falls below 20^{o}C (Barko et al. 1982, 1984). The temperature optimum for this species is between 30 and 36^{o}C with arrested growth below 20^{o}C and plants becoming limp above 40^{o}C (Wilkinson 1963) resulting in early senescence and reduced biomass production.

Production of wildcelery is very important as a food source of waterfowl, such that all parts of the plant are consumed; however the turions and rootstocks are the most favored. Both puddle and diving species of waterfowl alike feed on wildcelery, however the later group of ducks is better adapted to feeding on this submersed plant. Martin and Uhler (1939) reported that wildcelery accounted for approximately 2 percent of the total volume of food consumed by waterfowl, making it the seventh most popular plant food. Similarly, this plant was the most important food used by ducks in the Lower Detroit River (Hunt 1963). Likewise, wildcelery and the pondweeds were the most important plant species used by 47 greater scaup (*Aythya marila*), 44 lesser scaup (*Aythya affinis*), and 39 common goldeneye (*Bucephala clangula*) in the Detroit River during the winters of 1980 and 1981 (Jones and Drobney 1986). However, the canvasback (*Aythya valisineria*) has been the most notable for its use of wildcelery.

Cottam (1939) stated that the name of the canvasback (*Aythya valisineria*) derives itself from the close association of the canvasback and wildcelery plants. Similarly, McAtee (1917) wrote "the names wildcelery and canvasback duck have been closely associated in the annals of American sport. To a certain extent this association is justified, since the canvasback is very fond of the subterranean propagating buds of this plant." Historically canvasback ducks have been obligated to two foods during fall migration, sago pondweed and wildcelery (Cottam 1939, Perry and Uhler 1982). For example, canvasbacks fed primarily on the turions of wildcelery and consumed 40% of the standing crop in Lake Onalaska in 1980 (Korschgen et al. 1988). Wildcelery is so important that in the 1960's and 1970's, canvasbacks shifted their migration routes to respond to the production of wildcelery on the upper Mississippi River (Korschgen and Green 1988). An estimated 75 percent of the canvasback population in the three eastern flyways utilizes this food resource each fall (Korschgen et al. 1988).

The primary production by submersed macrophytes constitutes an important source of organic material for an aquatic system (Howard-Williams and Allanson 1981). The spatial distributions and overall productivity of submersed macrophytes are often regulated by the availability of light (Congdon and McComb 1979, Barko et al. 1986). The primary environmental factor that limits the growth and distribution of aquatic macrophytes, most notably the submersed species, is light availability (Barko et al. 1986, Scheffer 1998, Case and Madsen 2004). A critical light level is needed for photosynthesis of all aquatic vegetation. At depths where the lake bottom does not reach this critical light level submersed macrophyte colonization is limited because of the absence of photosynthetic activity (Case and Madsen 2004). Even in shallow waters light levels at the plant canopy are often insufficient to saturate photosynthesis (Wetzel and Penhale 1983). Declines in photosynthesis and distribution of submersed macrophytes are often related to water clarity associated with increases in phytoplankton densities and other suspended materials (Zimmerman and Livingston 1976, Carpenter 1980). The amounts of these light-attenuating materials (turbidity) are dependent upon the interactions between the benthic and pelagic regions of a lake. Shallow lakes with a loose bottom, little or no submersed plants, and a long fetch can experience frequent resuspension due to wind and waves (Blom et al. 1994).

Littoral zones are often barren due to intense wave action caused by a large fetch. The depth of the wave-mixed zone is an important factor that determines the depth and location of water suitable for the colonization of submersed macrophytes (Kantrud 1990). In shallow lakes with a large fetch, the wave-mixed zone deepens and the effects of wave action on sediment-induced turbidity can prevent the growth of submersed macrophytes (Kantrud 1990). In general, wave action washes away the finer sediments leaving coarser sediments behind (Spence 1982, Wilson and Keddy 1985). Therefore, turbulence created by a large fetch in a shallow lake will affect the distribution of submersed macrophytes directly through damage to mature plants or, indirectly by altering particle size, nutritional status, and stability of the bottom sediment inhibiting the establishment of submersed macrophytes (Spence 1967).

Swan Lake has historically been a favored location of migrating waterfowl due to its extensive and diverse population of aquatic macrophytes, especially sago pondweed and wildcelery. Aquatic macrophyte distribution has declined in recent years as result of poor growing conditions within the lake. To assess macrophyte distributions surveys were conducted on Swan and Middle Lakes to quantitatively assess the effects on environmental factors (e.g. light availability, water depth, and soil characteristics) on the distribution and diversity of aquatic macrophytes, most notably sago pondweed and wildcelery. The majority of past studies of environmental factors have been spatially limited in design. The objective of this study was to determine the effects of light availability, water depth, and sediment characteristics on the distribution and diversity of aquatic macrophytes, especially sago pondweed and wildcelery, at the whole lake scale. We predict, (1) decreases in light availability will decrease the overall diversity of macrophyte species present in a given lake; (2) increases in water level will increase light attenuation resulting in a decrease in overall macrophyte diversity; and (3) sediment characteristics will affect the distribution of sago pondweed and wildcelery.

MATERIALS AND METHODS

Site Description

Swan Lake (Lat. 44.30^{o}N Long. 94.25^{o}W) is located in Nicollet County, Minnesota approximately 1.6 km north west of the town of Nicollet (Figure 1). Swan Lake is the largest prairie pothole in North America encompassing 37.82 km^2. The lake is comprised of meandering shorelines with many points and islands. The lake has a maximum depth of approximately 2 meters with a mean depth of 1.2 meters. Five county ditches and two streams drain into Swan Lake and a ditch at the south end of the lake serving as the only outlet (Schultz 1985). Swan Lake is intensively managed for waterfowl and has served as a major feeding and resting area for migrating birds due to its diverse population of aquatic macrophytes.

Middle Lake (Lat. 44.30^{o}N Long. 94.18^{o}W) is located directly east of Swan Lake and approximately 8.0 km north east of the town of Nicollet (Figure 1). Middle Lake is divided into two basins (North Middle and South Middle) by extensive cattail (*Typha* spp.) growth in the center of the lake. The north basin tends to be shallower and more turbid with a less diverse population of aquatic macrophytes. The south basin generally has deeper water depths, better water clarity, and a more diverse macrophyte population. Middle Lake is not managed as intensively as Swan Lake however it is used extensively by waterfowl for feeding and resting during migrations.

Vegetation Surveys

To assess the distribution of aquatic macrophytes among lakes and between years, surveys of the aquatic vegetation were conducted on Swan Lake, North Middle, and South Middle Lake during July of 2001 and 2002. Macrophyte distribution was evaluated using a point intercept survey method using a 400 m grid following methods outlined by Madsen (1999). A 200 m grid was used on North and South Middle Lake. The grids were constructed using ArcView GIS software and maps of Swan and Middle Lake to obtain Universal Transverse Mercator (UTM) coordinates.

The UTM coordinates were used to navigate to each sample point with the aid of a Garmin GPSMAP76 Versatile Navigator (Olathe, KS). At each sample point a rake was tossed into the water and retrieved to determine the presence or absence of aquatic macrophytes species. Macrophyte species were identified using Crow and Hellquist (2000) as the taxonomic authority. Voucher specimens of each species were collected and are housed in the herbarium at Minnesota State University, Mankato. In addition, water depth was taken at each point using a 2.54 cm PVC pipe labeled in centimeters. At three points along the survey underwater light intensity was measured using a LiCor LI-1400 (Lincoln, NB) meter with surface and submersible photosynthetically active radiation (PAR) quantum sensors in 0.25 m intervals from the water surface to the lake bottom. Light measurements were not conducted in 2002 on any of the lake basins.

Regression analysis was used to test the effects of light extinction and water depth on the number of species found at each point. The change in the number of species per point in between years was assessed using a one way Analysis of Variance. Likewise, the change in the number of species per point between sites was assessed using a Kruskal-Wallis test was used as an alternative to a one way ANOVA because the data were not normally distributed. The change in distribution of all aquatic macrophytes and specifically sago pondweed and wildcelery were assessed using a Chi^2 analysis from presence/absence data. All statistical analyses were conducted at the $p < 0.05$ level of significance.

Tuber and Sediment Surveys

To evaluate sago pondweed tuber production and distribution and also sediment characteristics in each lake surveys were conducted in each lake basin during October 2002. The survey was conducted using a point intercept method following methods outlined by Madsen (1999). October was chosen as the time for the tuber survey because tuber production is completed. Samples were taken at every other point of the grid used in the vegetation survey.

Again, the UTM coordinates were used to navigate to each sample point with the aid of a Garmin GPSMAP76 Versatile Navigator (Olathe, KS). At each point tubers and sediment core were collected. Tubers were collected by using a 0.018 m^2 PVC coring device placed into the bottom sediment (Madsen 1993). Tubers were gathered by rinsing the sediment through a 19 L pail with a 0.25 cm^2 wire mesh bottom. Collected tubers were placed in labeled Ziploc bags and stored in a cooler for transportation to the lab. Likewise, a sediment core was collected using the same 0.018 m^2 coring device, placed into a labeled Ziploc bag, and stored in a cooler for transportation to the lab. Water depth at each sample point was also recorded using the same 2.54 cm PVC pipe as the vegetation surveys.

In the lab, tubers were rinsed, counted, and dried to a constant weight at 55^{o}C for at least 48 hours in a VWR Scientific 1390 FM (Cornelius, OR) constant temperature oven. The dry weight of each tuber was found using an analytical balance to the nearest ± 0.0001 g. Tuber weight and number were used to calculate total tuber biomass and tuber density per square meter for each sample point on the lake.

Sediment cores were analyzed using the Bouyoucos hydrometer method for particle size to determine the percent sand, silt, and clay (Bouyoucos 1962). Core samples were dried to a constant weight at 105^{o}C using a VWR Scientific 1390FM (Cornelius, OR) constant temperature oven. Two grams of the dried sediment core were placed in a crucible of known weight and again placed back in the oven to ensure the removal of any soil moisture. The crucible and sediment were weighed using a Mettler Toledo AB104-S (Greifensee, Switzerland) analytical balance after which they were placed in a Thermolyne 6000 (Dubuque, IA) muffle furnace at 550^{o}C for two hours to ash the contents. The crucible was removed from the furnace and placed in a desiccating jar to avoid the absorption of ambient moisture. The crucible and its contents were again weighed with the difference of the previous weight being the amount of organic matter in the sediment.

A Kruskal-Wallis test was used to test the differences in tubers found, tuber density, and tuber biomass between lakes. To test for differences in sediment characteristics between lakes a one way Analysis of Variance was used. Logistic regression analysis was used to assess the effects of sediment composition on the presence of sago pondweed and wildcelery shoots. Again, all statistical analyses on tuber and sediment data were conducted at the $p < 0.05$ level of significance.

RESULTS

Vegetation Surveys

Aquatic Macrophytes The number of macrophyte species observed per point (diversity) had a negative relationship with increasing light extinction coefficients in 2001 ($F = 41.312$, d.f. = 210, $p < 0.0001$) (Figure 2). Macrophyte diversity was affected by increasing water depth in both 2001 and 2002. Swam Lake macrophyte diversity had a negative relationship with increasing water depth ($F = 32.442$, d.f. = 117, $p < 0.0001$). Species diversity in North Middle Lake had a slight negative relationship with increasing water depth ($F = 3.269$, d.f. = 51, $p = 0.077$). Macrophyte diversity in South Middle Lake did not have a relationship with water depth ($F = 0.320$, d.f. = 34, $p = 0.575$). Diversity of macrophytes between the three sample sites was different ($H = 83.064$, d.f. 437, $p < 0.0001$) however macrophyte diversity between years was only marginally significant ($F = 2.863$, d.f. = 436, $p = 0.091$).

Diversity was greatest in Swan Lake with a total of 25 species of macrophytes identified during 2001 and 19 species identified in 2002 with *Myriophyllum sibiricum* (northern water-milfoil) being the most frequently observed species in both years (Table 1). It was located at 69.0 and 73.8 percent of the sites sampled in 2001 and 2002 respectively for Swan Lake. During the vegetation survey on North Middle Lake 13 species of macrophytes were identified in 2001 and 10 species identified in 2002 with northern water-milfoil being the most observed species in 2001 and *Ceratophyllum demersum* (coontail) being the most observed species in 2002 (Table 2). South Middle Lake had 12 species identified during 2001 with sago pondweed being the most frequently observed species at 73.7 percent of the points (Table 3). In 2002 there were 11 species of macrophytes observed on South Middle Lake with *Chara* spp. (muskgrass) being the most frequently observed species at 58.3 percent of the points.

Sago pondweed and Wildcelery The percent frequency of occurrence for sago pondweed in Swan Lake was 60.7 and 50.0 in 2001 and 2002 respectively (Table 1 and Figure 3). In North Middle Lake the percent frequency of occurrence was18.2 in 2001 and 36.1 in 2002 (Table 2 and Figure 3). South Middle Lake had a percent frequency of occurrence of sago pondweed of 73.7 and 44.4 in 2001 and 2002 respectively (Table 3 and Figure 3). The distribution of sago pondweed was different between sites (X^2 = 27.802, d.f. = 2, p < 0.0001) and marginally significant between years (X^2 = 2.123, d.f. = 1, p = 0.087) when taking all the sites into account. Individually, the only change in sago pondweed distribution was in North Middle Lake (X^2 = 10.051, d.f. = 1, p =0.003) between 2001 and 2002. The distribution of sago pondweed did not change between 2001 and 2002 in Swan and South Middle Lakes (X^2 = 0.318, d.f. = 1, p = 0.573; X^2 = 0.059, d.f. = 1, p = 0.809) respectively.

Sago pondweed distribution did not appear to be affected by water depth in Swan Lake. The depth distribution of sago pondweed in Swan Lake was similar between 2001 and 2002 (Figure 4). Sago pondweed was observed in the same depth range 0.6 m to 1.8 m and at relatively the same frequencies between years for North Middle Lake (Figure 5). The interval of 1.5 m in 2002 had only one point representing it and subsequently sago pondweed was observed at that point resulting in a 100 percent frequency of occurrence. Sago pondweed in South Middle Lake was observed in relatively the same depth interval 0.9 m to 1.4 m in both 2001 and 2002 (Figure 6) Water depth in 2002 was slightly lower than that of 2001 in South Middle Lake.

Wildcelery was only found in Swan Lake during both years of the vegetation survey. It had a percent frequency of occurrence of 9.0 and 22.2 in 2001 and 2002 respectively (Table 1 and Figure 3) The distribution of wildcelery changed (X^2 = 9.293, d.f. 1, p = 0.002) in Swan Lake between 2001 and 2002. The depth range that wildcelery was observed in was narrower and shallower in 2001 (1.4 m to 1.6 m) than in 2002 (0.6 m to 1.8) (Figure 4).

Tuber and Sediment Survey

Sago pondweed Tuber number, tuber density, and tuber biomass were not different between Swan and Middle Lakes (H = 1.389, d.f. = 1, p = 0.238; H = 1.389, d.f. = 1, p = 0.238; H = 1.647, d.f. = 1, p = 0.199). Swan Lake had the greatest mean tuber density of 64.33 ± 18.06 N m^{-2} as opposed to Middle Lake which had a mean tuber density of 33.63 ± 14.74 N m^{-2} (Table 4). Likewise, mean tuber biomass was greater in Swan Lake than in Middle Lake, 4.27 ± 1.35 g m^{-2} and 1.43 ± 0.62 g m^{-2} respectively. Tuber production did not appear to be affected by sediment characteristics in either lake. Sediment characteristics (percent sand, silt, and clay) were not different between lakes (F = 0.579, d.f. = 94, p = 0.449; F = 1.752, d.f. = 94, p = 0.189; F = 1.360, d.f. = 94, p = 0.246) respectively. Mean sediment characteristics are compared in (Table 5).

Sago pondweed and Wildcelery Sediment particle size had very little effect on the presence of sago pondweed shoots in either lake. There was no relationship between the presence of sago pondweed shoots and the percent sand or silt in the sediment (W = 0.492, d.f. = 1, p = 0.483 and W = 1.866, d.f. = 1, p = 0.172) respectively. There was a slight negative relationship between the presence of sago pondweed shoots and the percent clay in the sediment (W = 3.551, d.f. = 1, p = 0.060). Similarly, there was no relationship with between the percent of sand and silt in the sediment and the presence of wildcelery (W = 0.021, d.f. = 1, p = 0.885 and W = 0.786, d.f. = 1, p = 0.375) respectively. A positive relationship (W = 3.988, d.f. = 1, p = 0.046) existed between the percent clay in the sediment and the presence of wildcelery.

DISCUSSION

Vegetation Surveys

Aquatic Macrophytes Swan and Middle Lakes have the potential to support a diverse and healthy population of aquatic macrophytes. During the surveys of these lakes emergent, submergent, and floating species were all observed. However, the growth of these macrophytes, most notably the submersed species, exhibited potential signs of light stress. It is this light stress that appears to limit the growth of macrophytes almost exclusively in these lakes. Indeed, the diversity of macrophytes in Swan and Middle (North and South) Lakes decreased significantly as light extinction in the water column increased. Similarly, light attenuation as a function of water depth and turbidity also had negative effects on the growth of submersed macrophytes.

Increasing water depths in Swan and North Middle Lakes resulted in a decrease in macrophyte diversity. However, Swan Lake had a greater diversity of macrophytes than North Middle due primarily to increased water clarity resulting in increased photosynthetic activity. The water depths to which aquatic macrophytes can grow are a direct function of water clarity (Meyer et al. 1943, Chambers and Kalff 1985). Decreased water clarity was likely the main factor restricting light availability to macrophytes in these lakes especially at deeper water depths resulting in declines in macrophyte diversity. The stress caused by decreased light availability limits the growth of macrophytes within an aquatic environment (Barko et al. 1986) with turbidity being an important factor limiting light availability (Madsen et al. 2001). Similarly, light attenuation in the water column was found to be the best single environmental variable explaining the growth and distribution of aquatic macrophytes (Hansel-Welch et al. 2003).

Sago pondweed and Wildcelery The growth of sago pondweed was different between the lakes sampled in this study. Swan and South Middle Lakes had the greatest population of sago pondweed. Again, the difference in sago pondweed growth between the three sites may be attributed to decreased light availability as a result of turbidity. Swan Lake has a greater distribution of sago pondweed due to its greater water clarity. The depth distribution of sago pondweed in Swan and South Middle Lakes did not appear to change significantly between years indicating that the increased turbidity in South Middle Lake likely exacerbated light extinction resulting in decreased sago pondweed growth in South Middle especially at deeper depths. Turbidity is the factor that most frequently limits the growth of sago pondweed (Kantrud 1990). In contrast, North Middle had a significant increase in sago pondweed growth in 2002. Water depth in North Middle appeared to increase approximately 30 cm between 2001 and 2002. The rise in water depth likely increased the littoral zone allowing sago pondweed to colonize new shallow areas resulting in the slight increase of sago pondweed depth distribution and observance in 2002. Sago pondweed is considered a pioneering species that can quickly inhabit disturbed areas and colonize shallow waters (Ozimek and Kowalczewski 1984). Davis and Brinson (1980) placed this species in a group of plants tolerant of, and able to maintain dominance in newly altered environments. However, sago pondweed was likely light limited in the deeper depths of North Middle Lake.

Wildcelery often grows in a more stable environment and is less tolerant to turbid conditions as opposed to sago pondweed. Swan Lake with its larger surface area may be able to tolerate more environmental perturbations without significant changes to its macrophyte community which may explain why wildcelery was only found in this lake. Likewise, Swan Lake has greater water clarity with light penetration to the bottom in most locations unlike North and South Middle Lake where light seldom penetrates to the bottom sediments; which explains why wildcelery was only found in Swan Lake. Similarly, wildcelery tends to grow at intermediate depths of 0-3 meters and can colonize deeper depths more efficiently than that of other submersed species. Wildcelery is able to better adapt to deeper water depths (Meyer et al. 1943, Titus and Adams 1979) by reallocating resources to other structures to promote growth under reduced light conditions (Madsen 1991). Clearly, this is evident by the depth distribution of wildcelery in Swan Lake. Wildcelery had a deeper depth distribution than that of sago pondweed and appears to be able to colonize most if not all of Swan Lake. Likewise, it was observed more frequently than sago pondweed in 2002 at the deeper water sites. The significant change in growth and distribution of wildcelery is attributed to greater water clarity in Swan Lake that allows deeper light penetration resulting in a more widely distributed wildcelery population.

Tuber and Sediment Survey

Tuber Survey Sago pondweed tuber production was not different between Swan and Middle Lakes. However Swan Lake had greater mean tuber biomass and greater mean individual tuber weight than did Middle Lake. A result that indicates Swan Lake may be producing larger tubers than those being produced in Middle Lake however Swan Lake is not producing significantly more tubers. The small tubers in Middle Lake likely are not surviving season to season which when taking both the North and South basins into account results in no net change in tuber production or new sago pondweed growth. The survival of tubers is greater at larger sizes and the overall survival of small tubers is negligible (Santamaria and Rodriquez-Girones 2002). Similarly, the growth rate of shoots was greater in plants grown from larger tubers, indicating that small tubers are at a disadvantage in terms survival, germination, and production of new plants (Spencer 1987). Poor tuber production can be a symptom of light stressed plants (van Dijk et al. 1992, Doyle 2000). Light stress results in plants reallocating more resources towards shoots and leaves than to tubers (Madsen 1991). The poor tuber production in both Swan and Middle Lakes coincides with the high light extinction coefficients experienced throughout the growing season. The low light environments are preventing sago pondweed plants from producing tubers.

Sediment Survey Sago pondweed tuber density and biomass were not affected by sediment characteristics in either lake. Similarly, tuber density and location were not correlated with depth or sediment characteristics in Heron Lake, MN (Case and Madsen 2004). Sediment characteristics were not different between Swan and Middle Lakes likely due to low wave energy and particle sorting resulting in a more stable substrate for macrophyte growth (Scheffer 1998). However, particle sorting is inevitable in an aquatic system with wave energy washing away the finer clays and silts leaving the coarser, less fertile sediments behind (Spence 1982, Wilson and

Keddy 1985, Scheffer 1998). These coarser sediments are unfavorable for macrophyte growth (Keddy 1985, Doyle 1999). The negative relationship between sago pondweed presence and the percent clay in the sediment likely exists as a result of the clay particles being the first to wash away leaving coarse sand particles behind. The relationship is further exacerbated in shallow water sites when wave energy damages sago pondweed shoots (Spence 1982, Engel and Nichols 1994, Doyle 1999). In contrast, there was a positive relationship with the percent clay in the sediment and the presence of wildcelery. Wildcelery colonized deeper sites within Swan Lake, sites likely composed mainly of clay. These deep sites escape the effects of wave energy and particle sorting leaving the fine clay sediments at the bottom. The lack of wave energy in these deep sites allows wildcelery to grow in the fertile clays and silts without being directly damaged by the waves (Doyle 1999). The dense growth of wildcelery at the deeper sites also increases the sedimentation rates resulting in greater water clarity (Madsen et al. 2001).

Conclusion

Aquatic macrophyte distribution and growth in North and South Middle Lakes were shown to be limited by light availability and to some degree water depth. Light availability was the main factor that influenced the growth of submersed macrophytes at these sites. In general as light extinction increased overall species diversity decreased as a result of turbidity in the water column. Likewise, as water depth increased macrophyte diversity decreased as a function of water clarity, a direct limiting factor to light availability. The maximum depth distribution of sago pondweed appears to be between 1.2 m and 1.6 m for both lakes. Having water depths at or below these levels will promote the colonization of new areas thus increasing the distribution of sago pondweed and submersed macrophytes in North and South Middle Lake. Increased growth of submersed macrophytes will also lead to greater water clarity by stabilizing bottom sediments and increasing sedimentation rates within dense plant beds. Greater water clarity will also benefit those species of submersed macrophytes that reproduce via the production of under ground tubers, namely sago pondweed. Lower water depths and increased light availability should allow these plants to allocate more resources in the fall to tuber production. Increases in resource allocation to below ground biomass results in higher plant biomass and the production of larger tubers (Santamaria and Rodriguez-Girones 2002). To ensure the proliferation of aquatic macrophytes in these lakes management efforts should be directed towards techniques to improve water clarity. Also, future research should be conducted to establish a long term data set to enable the analysis of the effects of environmental factors on the distribution and production of aquatic macrophytes.

ACKNOWLEDGEMENTS

This project was funded by a grant from the Minnesota Waterfowl Association to Minnesota State University, Mankato with additional support from the Minnesota Department of Natural Resources.

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Table 1. Species list of macrophytes found in Swan Lake during the vegetation surveys in June 2001 and 2002.

Site	Year	Species Name	Common Name	% Frequency
Swan Lake	**2001**	*Carex* spp.	Sedge	7.0
		Carex rostrata	Beaked sedge	1.0
		Ceratophyllum demersum	Coontail	32.0
		Chara spp.	Muskgrass	5.0
		Elodea canadensis	Canadian waterweed	2.0
		Lemna minor	Common duckweed	15.0
		Lemna trisulca	Star duckweed	3.0
		Myriophyllum sibiricum	Northern water-milfoil	69.0
		Najas flexilis	Common naiad	10.0
		Nuphar advena	Spatterdock cowlily	1.0
		Nymphaea odorata	Fragrant waterlily	2.0
		Phragmites communis	Common reed	2.0
		Potamogeton foliosus	Leafy pondweed	20.0
		Potamogeton natans	Floatingleaf pondweed	6.0
		Potamogeton robinsii	Robbins' pondweed	34.0
		Potamogeton zosterformis	Flat-stemmed pondweed	44.0
		Sagittaria americana	Arrowhead	10.0
		Scirpus americanus	American bulrush	1.0
		Scripus validus	Softstem bulrush	1.0
		Sparganium spp.	Burreed	2.0
		Stuckenia pectinata	Sago pondweed	60.7
		Typha angustifolia	Narrowleaf cattail	31.0
		Ultricularia vulgaris	Common bladderwort	3.0
		Vallisneria americana	American wildcelery	9.0
		Zosterella dubia	Water star-grass	1.0
Swan Lake	**2002**	*Ceratophyllum demersum*	Coontail	55.6
		Elodea Canadensis	Canadian waterweed	7.1
		Myriophyllum sibiricum	Northern water-milfoil	73.8
		Najas flexilis	Common naiad	7.1
		Nuphar advena	Spatterdock cowlily	1.6
		Nymphaea odorata	Fragrant waterlily	5.6
		Potamogeton foliosus	Leafy pondweed	4.0
		Potamogeton natans	Floatingleaf pondweed	1.6
		Potamogeton robinsii	Robbins' pondweed	9.5
		Potamogeton zosterformis	Flat-stemmed pondweed	36.5
		Sagittaria americana	Arrowhead	5.6
		Scirpus americanus	Leafy pondweed	0.8
		Scirpus validus	Softstem bulrush	7.9
		Stuckenia pectinata	Sago pondweed	50.0
		Typha angustifolia	Narrowleaf cattail	32.5
		Ultricularia minor	Lesser bladderwort	2.4
		Ultricularia vulgaris	Common bladderwort	34.1
		Vallisneria americana	American wildcelery	22.2
		Zosterella dubia	Water star-grass	9.5

Table 2. Species list of macrophytes found in North Middle Lake during the vegetation surveys in June 2001 and 2002.

Site	**Year**	**Species Name**	**Common Name**	**% Frequency**
N. Middle	**2001**	*Carex* spp.	Sedge	1.8
		Ceratophyllum demersum	Coontail	34.5
		Chara spp.	Muskgrass	5.5
		Lemna minor	Common duckweed	5.5
		Myriophyllum sibiricum	Northern water-milfoil	47.3
		Potamogeton foliosus	Leafy pondweed	1.8
		Potamogeton robinsii	Robbins' pondweed	3.6
		Sagittaria americana	Arrowhead	3.6
		Scirpus validus	Softstem bulrush	1.8
		Stuckenia pectinata	Sago pondweed	18.2
		Typha angustifolia	Narrowleaf cattail	25.5
		Ultricularia vulgaris	Common bladderwort	16.4
		Zosterella dubia	Water star-grass	1.8
N. Middle	**2002**	*Carex* spp.	Sedge	6.6
		Ceratophyllum demersum	Coontail	49.2
		Chara spp.	Muskgrass	6.6
		Myriophyllum sibiricum	Northern water-milfoil	42.6
		Potamogeton foliosus	Leafy pondweed	3.3
		Potamogeton robinsii	Robbins' pondweed	9.8
		Sagittaria americana	Arrowhead	8.2
		Stuckeina pectinata	Sago pondweed	36.1
		Typha angustifolia	Narrowleaf cattail	26.2
		Ultricularia vulgaris	Common bladderwort	1.6

Table 3. Species list of macrophytes found in South Middle Lake during the vegetation surveys in June 2001 and 2002.

Site	Year	Species Name	Common Name	% Frequency
S. Middle	**2001**	*Ceratophyllum demersum*	Coontail	44.7
		Chara spp.	Muskgrass	57.9
		Lemna minor	Common duckweed	2.6
		Myriophyllum sibiricum	Northern water-milfoil	21.1
		Potamogeton foliosus	Leafy pondweed	44.7
		Potamogeton nodosus		2.6
		Potamogeton robinsii	Robbins' pondweed	28.9
		Sagittaria americana	Arrowhead	31.6
		Stuckenia pectinata	Sago pondweed	73.7
		Typha angustifolia	Narrowleaf cattail	36.8
		Ultricularia vulgaris	Common bladderwort	2.6
		Zostrella dubia	Water star-grass	2.6
S. Middle	**2002**	*Ceratophyllum demersum*	Coontail	52.8
		Chara spp.	Muskgrass	58.3
		Myriophyllum sibiricum	Northern water-milfoil	41.7
		Potamogeton foliosus	Narrowleaf pondweed	27.8
		Potamogeton nodosis		8.3
		Potamogeton robinsii	Robbins' pondweed	30.6
		Potamogeton zosterformis	Flat-stemmed pondweed	5.6
		Sagittaria americana	Arrowhead	27.8
		Stuckenia pectinata	Sago pondweed	44.4
		Typha angustifolia	Narrowleaf cattail	50.0
		Ultricularia vulgaris	Common bladderwort	22.2
		Zosterella dubia	Water star-grass	2.8

Table 4. Mean tuber data (±1 SE) for Swan and Middle Lakes during the tuber surveys conducted in October 2002.

	Swan Lake	**Middle Lake**
Mean Tuber Number (per sample)	1.16 ± 0.33	0.61 ± 0.27
Mean Tuber Density (N m^{-2})	64.33 ± 18.06	33.63 ± 14.74
Mean Tuber Weight (g)	0.07 ± 0.02	0.04 ± 0.01
Mean Tuber Biomass (g m^{-2})	4.27 ± 1.35	1.43 ± 0.62

Table 5. Mean (±1 SE) percent sediment composition for Swan and Middle Lakes collected during the sediment survey in October of 2002.

	Swan Lake	**Middle Lake**
Sand (%)	39.70 ± 1.53	41.63 ± 2.07
Silt (%)	51.54 ± 0.29	48.92 ± 0.40
Clay (%)	8.54 ± 1.36	9.18 ± 1.84

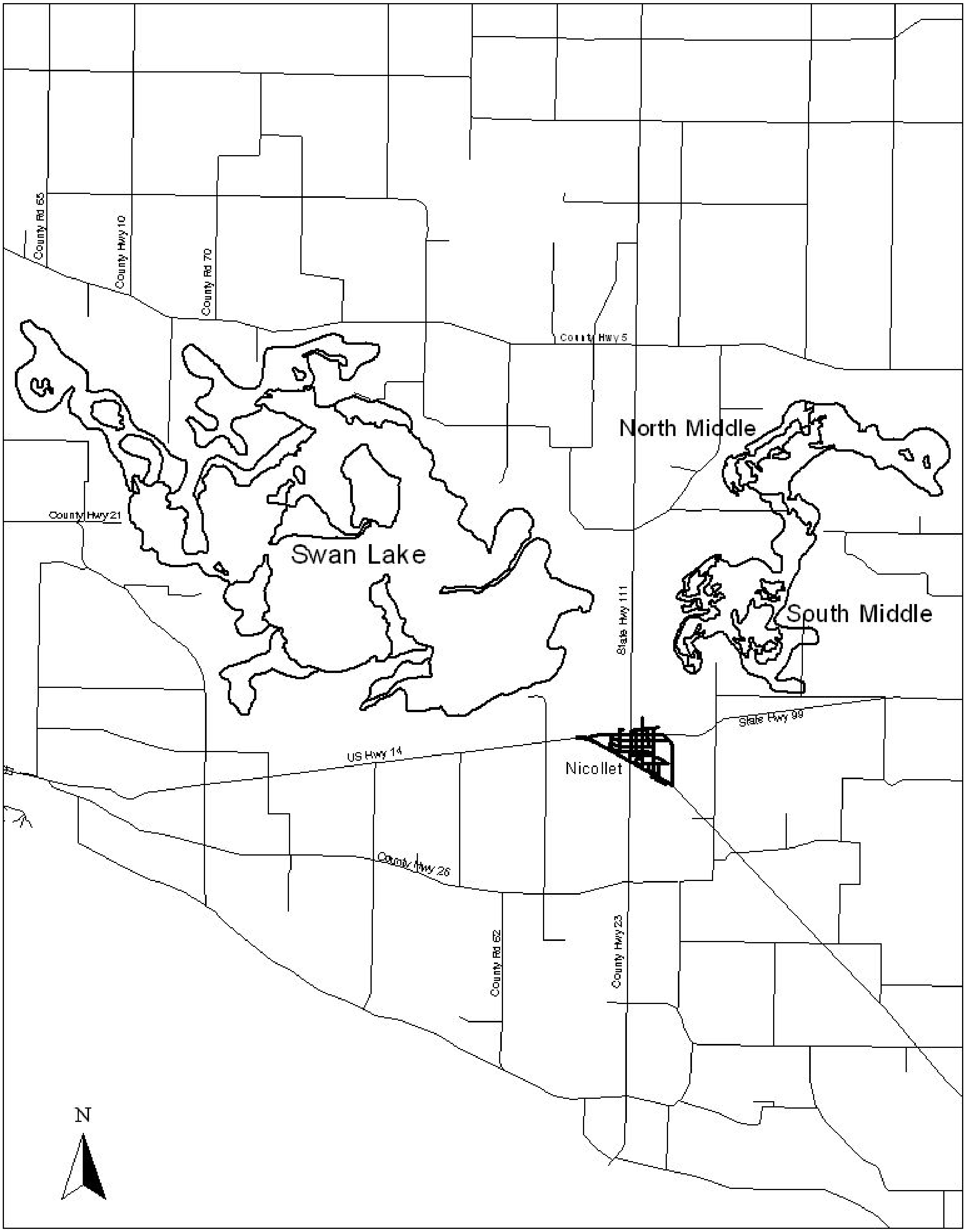


Figure 1. Map of Swan and Middle Lakes showing the north and south basins of Middle Lake and surrounding area.

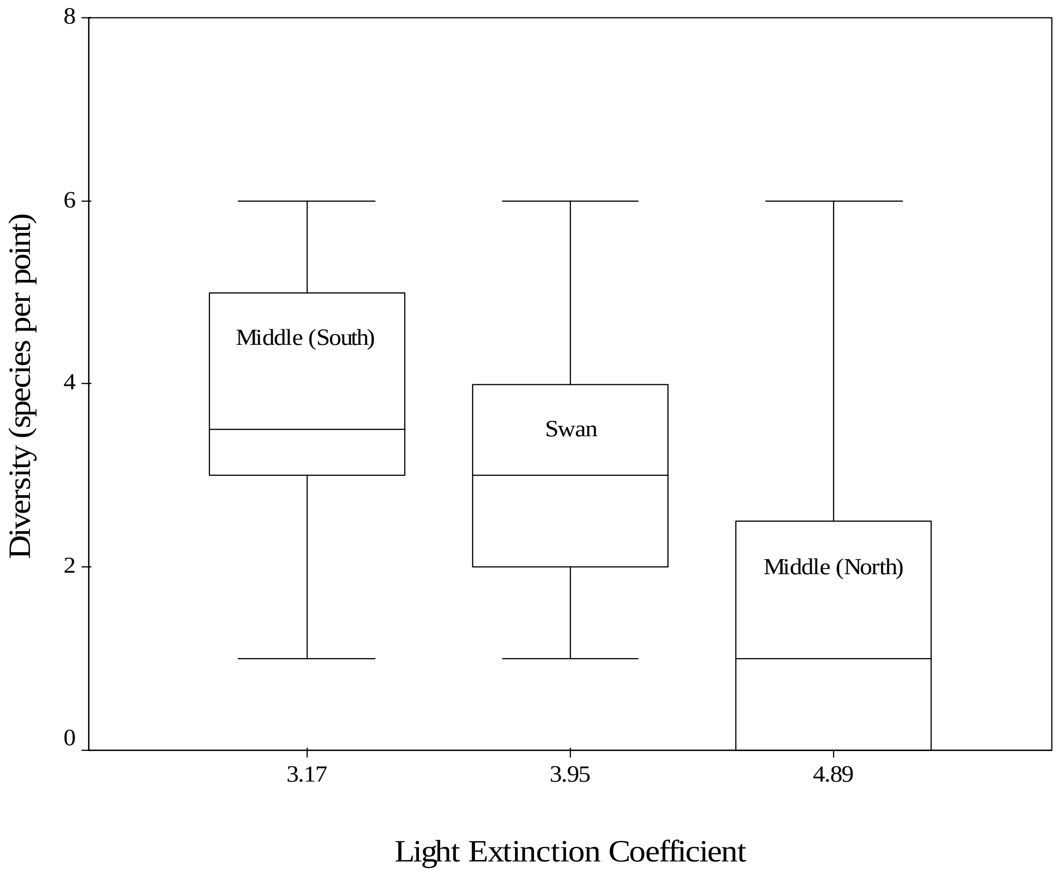


Figure 2. Number of aquatic macrophytes found within Swan and Middle Lakes in relation to light extinction coefficients. The light extinction coefficients are based on light intensity (PAR) measurements during July of 2001.

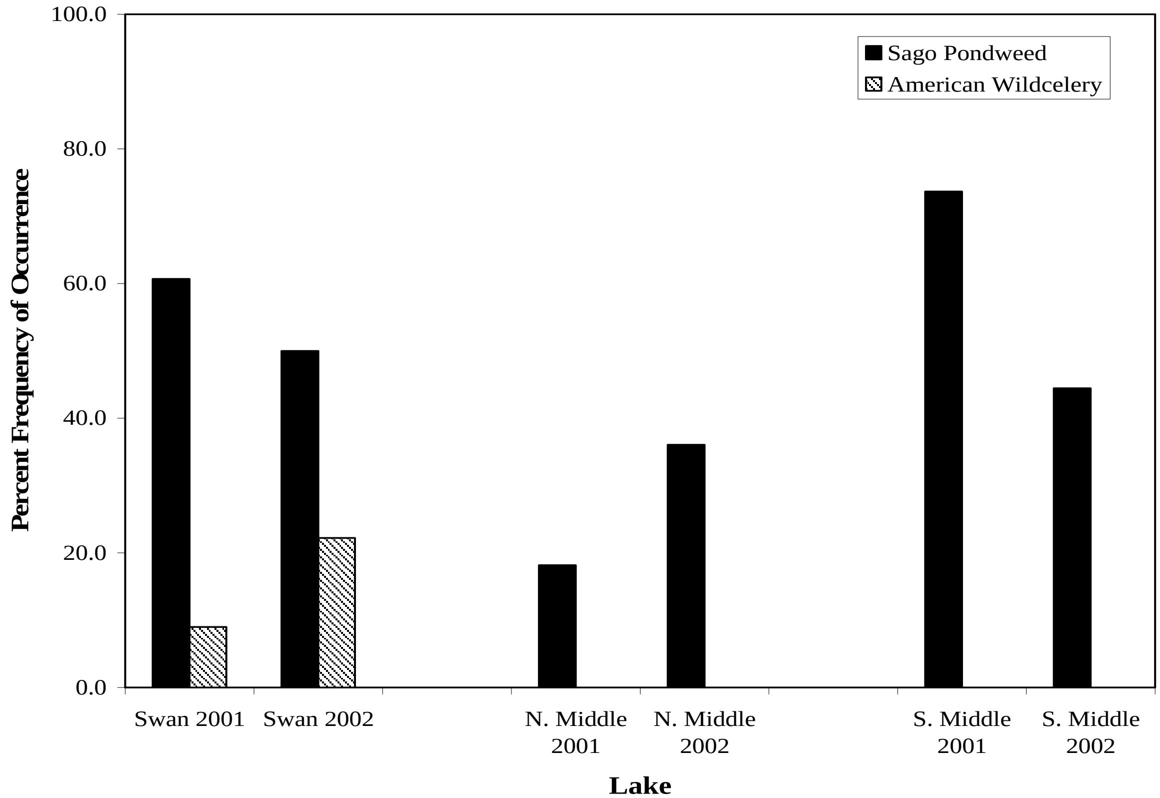


Figure 3. Percent frequency of occurrence of sago pondweed and wildcelery found within Swan and Middle Lakes during the vegetation surveys in July 2001 and 2002.

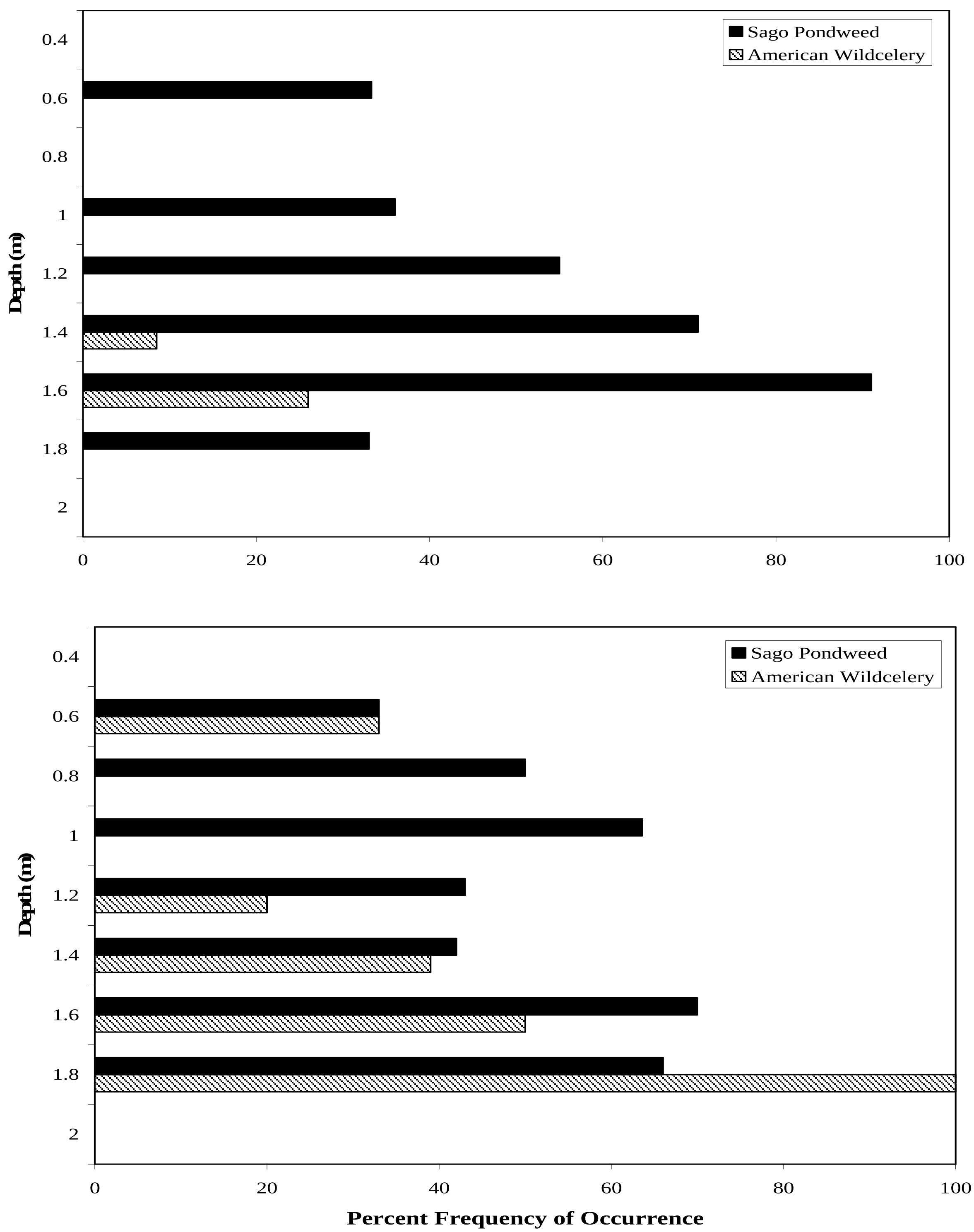


Figure 4. Depth distribution (percent frequency of occurrence of sago pondweed and wildcelery within Swan Lake during July 2001 (top) and 2002 (bottom).

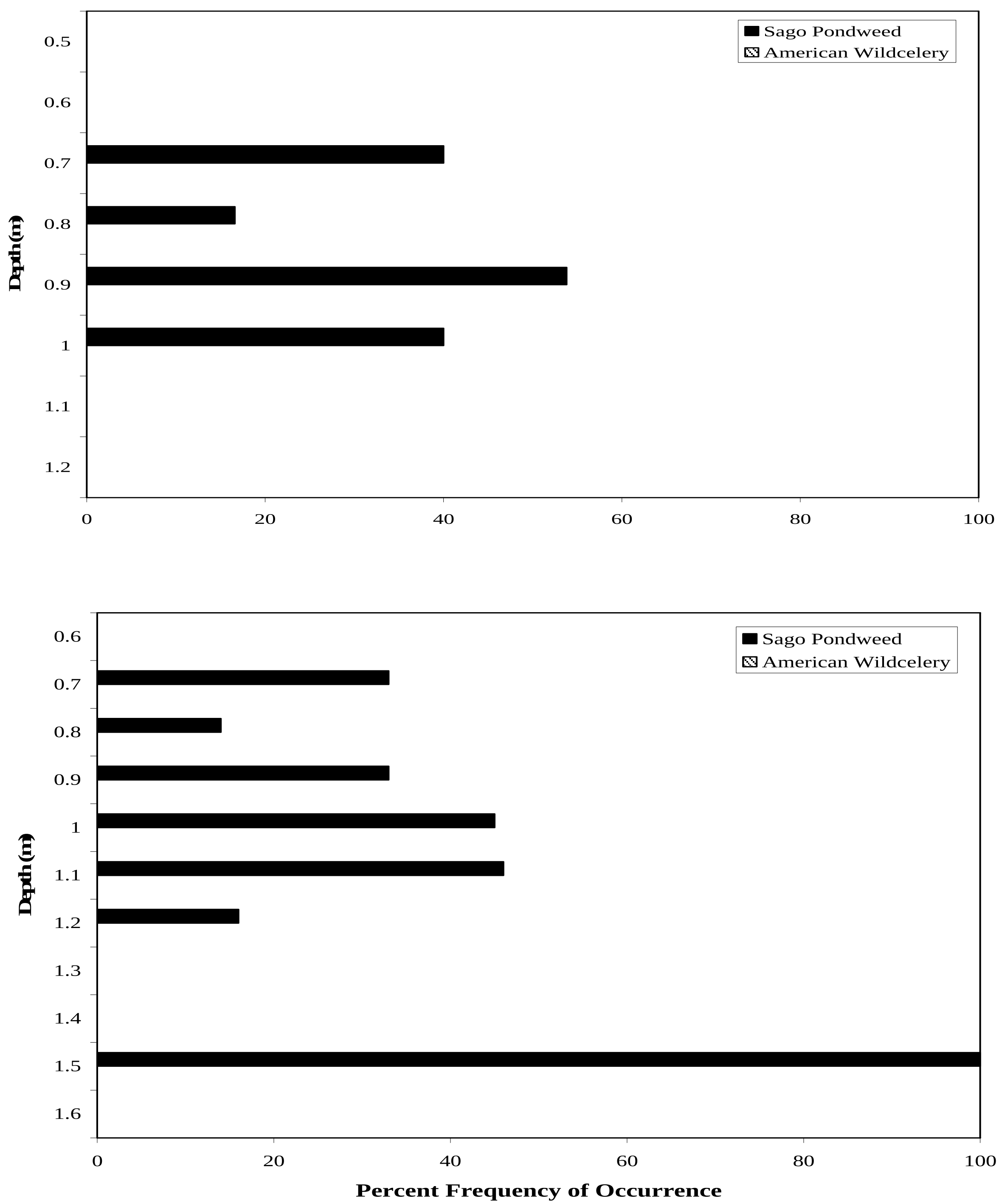
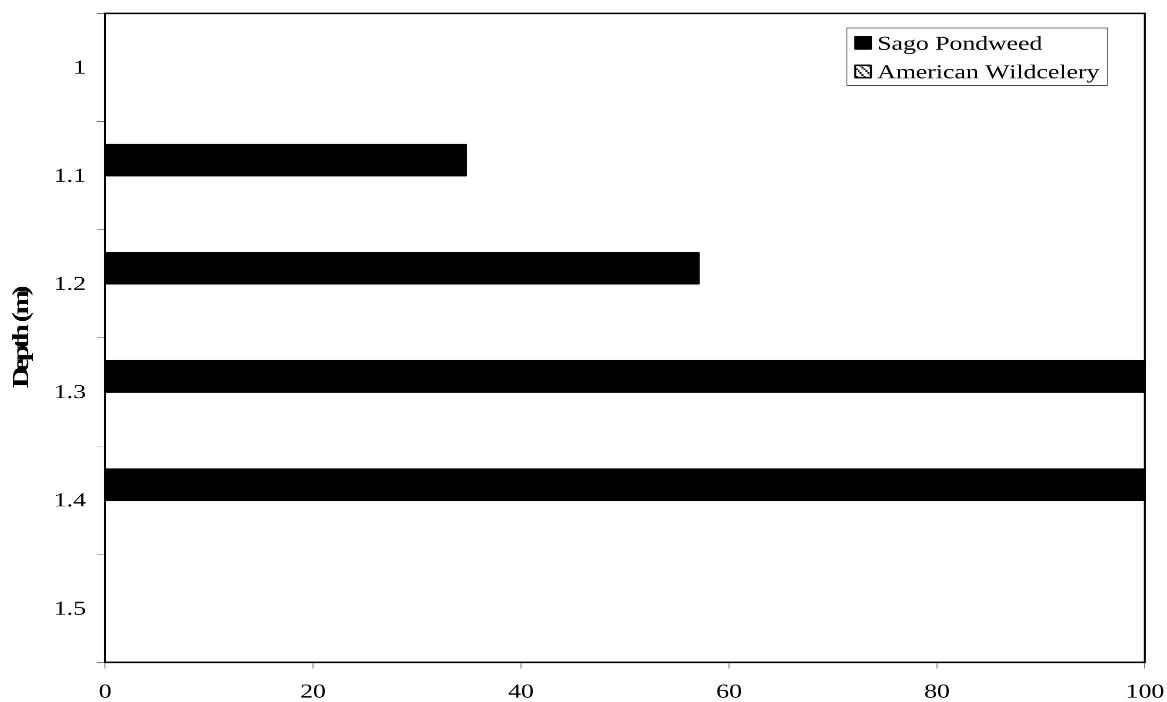


Figure 5. Depth distribution (percent frequency of occurrence of sago pondweed and wildcelery within North Middle Lake during July 2001 (top) and 2002 (bottom).



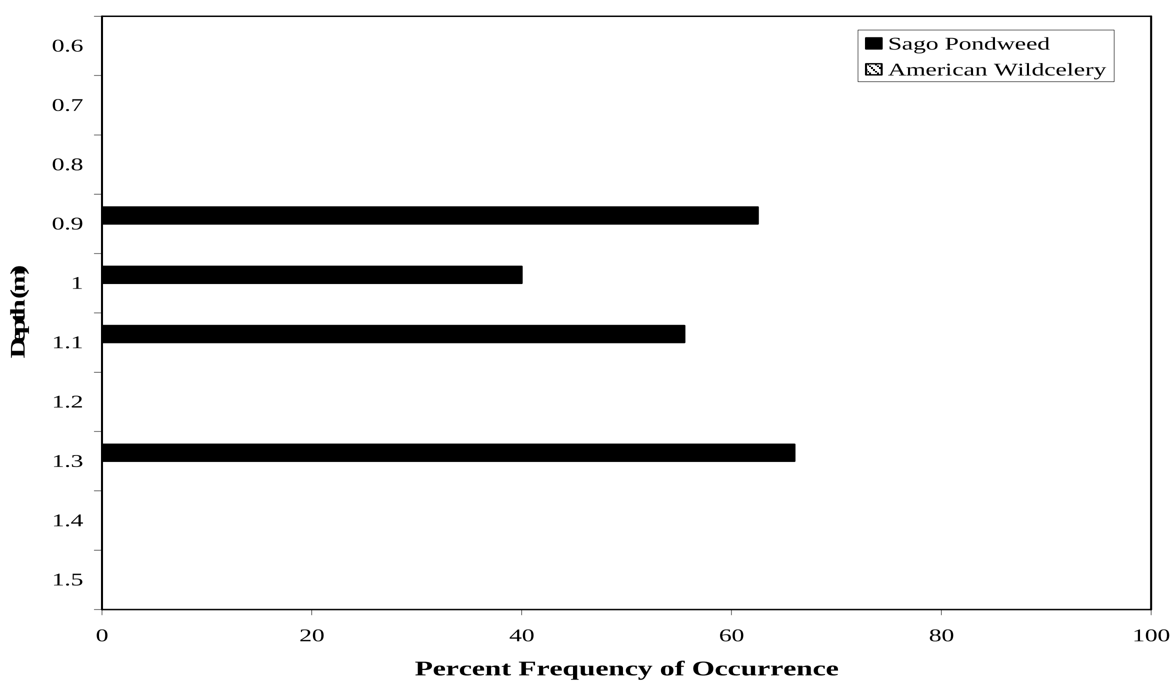


Figure 6. Depth distribution (percent frequency of occurrence of sago pondweed and wildcelery within South Middle Lake during July 2001 (top) and 2002 (bottom).