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Water Clarity During the Establishment of Zebra
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Bay, Lake Huron

presented by

John Phillip Skubinna

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Major professor

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THE RESPONSE OF SUBMERSED MACROPHYTES TO INCREASED WATER
CLARITY DURING THE ESTABLISHMENT OF ZEBRA MUSSELS, *DREISSENA*
POLYMORPHA PALLAS, IN SAGINAW BAY, LAKE HURON

By

John Phillip Skubinna

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ABSTRACT

THE RESPONSE OF SUBMERSED MACROPHYTES TO INCREASED WATER CLARITY DURING THE ESTABLISHMENT OF ZEBRA MUSSELS, *DREISSENA POLYMORPHA* PALLAS, IN SAGINAW BAY, LAKE HURON

By

John Phillip Skubinna

Submersed macrophyte communities and water clarity were monitored from 1991-1993 to determine if changes in light availability, expected with the arrival of *Dreissena polymorpha* in Saginaw Bay, corresponded with changes in macrophyte distribution. Turbidity, Secchi disk depth, and extinction of photosynthetically active radiation (PAR) were measured in inner Saginaw Bay to monitor changes in light availability. Macrophyte relative abundance (RA), maximum depth of colonization (ZMAX), and the area of plant coverage were measured late in the growing season to determine the distribution of the macrophyte assemblages in each summer. Turbidity, Secchi disk depth, and the extinction coefficient of PAR decreased at sites in northern littoral regions from 1991-1993, but not at southern littoral sites. Macrophyte RA, ZMAX, and the area of plant coverage increased in Saginaw Bay from 1991-1993. Increases were greater in northern littoral regions than southern littoral regions. Filamentous chlorophytes, charophytes, and *Vallisneria americana* increased most at transects where ZMAX increased.

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INTRODUCTION

Saginaw Bay is one of the more productive ecosystems in Lake Huron and is a valuable resource to the surrounding regions (Jaworski and Raphael 1978). It appeared poised for major ecological changes due to the appearance in 1990 of the zebra mussel, *Dreissena polymorpha* Pallas. Not only was there a need to monitor ecological change to protect this valuable resource, change in Saginaw Bay also provided an opportunity to describe the importance of water clarity in the regulation of macrophyte distribution at the ecosystem level.

Historically, Saginaw Bay has had the largest coastal wetlands in the North American Great Lakes. In 1856, 15,100 hectares of coastal wetlands were present (Jaworski and Raphael 1978). By 1973, 7,200 hectares remained. Still, today it remains the largest and most valuable, both economically and ecologically, contiguous coastal wetland in the Great Lakes (Herdendorf et al. 1981).

The invasive ability of the zebra mussel is renowned in Europe, Asia (Stanczykowska 1977), and the U.S. (Ohio Sea Grant College Program (OSGCP) 1993). Lakes St. Clair and Erie have been particularly vulnerable, and have begun to

show important changes in the ecology of endemic plant and animal communities since the appearance of mussels in 1988 (e.g., Wormington and Leach 1992; Haag et al. 1993; Leach 1993). These impacts were also expected to occur in Saginaw Bay, because it is similar in thermal, nutrient, and pH regimes to western Lake Erie (Schelske and Roth 1973). Therefore, the invasion of zebra mussels into Saginaw Bay increased the need to expand knowledge of the structure and function of the bay ecosystem so that management agencies could anticipate and manage the ecological impacts of this exotic species on Saginaw Bay and other vulnerable systems.

Beginning in 1990, scientists at the Great Lakes Environmental Research Laboratory (GLERL) undertook a systematic study of the Saginaw Bay ecosystem, with particular focus on documenting zebra mussel impacts. Their work was centered on the limnetic environment of the bay, and included monitoring of water quality, and of planktonic, benthic, and fish populations. This study focused on changes which occurred in the littoral regions of Saginaw Bay.

Although the causal relationships between zebra mussels and water clarity have not been demonstrated, it is generally believed that recent increases in water clarity and macrophyte abundance in Lake St. Clair and Lake Erie corresponded with the establishment of zebra mussels in these systems. Regardless of the mechanisms of water

clarity change, it was assumed that the arrival of zebra mussels in Saginaw Bay would provide an opportunity to describe the importance of water clarity in determining macrophyte distribution in the littoral regions of the bay.

Shoemaker (1982) demonstrated the importance of water clarity in determining macrophyte abundance in Wildfowl and Sebawaing Bay regions of Saginaw Bay. However, the arrival of zebra mussels provided the opportunity to confirm these results at the bay wide scale.

Therefore, the objectives of this study were to describe the changes in the light environment encountered by aquatic macrophytes in Saginaw Bay during the growing season to verify the assumption that water clarity would change from 1991-1993, and to describe changes in the relative abundance, composition, and depth distribution of the macrophyte assemblages over this period.

Specifically, it was hypothesized that water clarity would increase, i.e. Secchi disk depths would increase, and turbidity and the extinction coefficients of photosynthetically active radiation (PAR) would decrease from 1991-1993. It was also predicted that as water clarity increased, the relative abundance of macrophytes, the maximum depth of macrophyte colonization, and the area of macrophyte coverage would increase. We chose to monitor the maximum depth of colonization, because this was the region

in the vertical distribution of macrophytes that was likely to be most limited by light (Rørslett 1987).

LITERATURE REVIEW

I. The Invasion of Zebra Mussels into Saginaw Bay.

The invasive ability of zebra mussels is well known, as is the history of their worldwide dispersal. Based upon what is known of their invasibility, the history of their worldwide dispersal, the limnology of Saginaw Bay, and its similarity to systems with high mussel densities, e.g. western Lake Erie, it is believed that high densities, which have been established in Saginaw Bay, will remain there in the foreseeable future. Once established, populations of zebra mussels have demonstrated the remarkable ability to filter large volumes of water. This ability is believed to be the cause of increased water clarity (e.g. Hubert 1989). The ecological significance of increased water clarity is the primary focus of this study.

A. Zebra Mussel Invasibility. Zebra mussels are an opportunistic species, and have three characteristics that are believed to contribute to their invasiveness.

First, it is a member of the class Bivalvia (Pelecypoda), and family Unionidae, therefore it has a free-swimming immature stage, known as a veliger, that is microscopic and easily transported passively by water

currents. This immature stage has traveled great distances in the ballast water of ocean going ships (Carlton 1993). In addition, as adults they attach to solid substrates, but have shown the ability to detach and move to more favorable substrate. Therefore, they can move through a watershed by attaching to boat hulls in the first year of their life cycle, then detach and settle onto other substrates (e.g. Carlton 1993; Morton 1993).

Second, once populations become established, growth is very rapid compared to other Unionids (McMahon 1991), especially immediately after introduction into productive ecosystems. Production rates range from 0.05-14.7 g C/m²/yr in systems in which they were recently introduced. Typically, annual production rates of most native Unionids are <0.05 g C/m²/yr (McMahon 1991).

Lastly, mussels have high fecundity. A female mussel, over a five year lifespan, can produce 150,000 eggs (Stanczykowska 1977). Although this is similar to some native Unionids, zebra mussels usually mature sooner and produce the same number of eggs over a shorter life span (McMahon 1991). Veligers appear in the water when it reaches 14°C. The immature veligers mature rapidly especially at temperatures of 18-22°C which are optimum (Stanczykowska 1977; Garton and Haag 1993).

B. A History of Zebra Mussel Invasions. The dispersal of zebra mussels throughout the world is well documented.

Although population densities vary, they often disperse quickly over continents and become a common constituent of most aquatic ecosystems.

1. European and Asian Invasion. Zebra mussels were first described in the northern portion of the Caspian Sea and in the Ural River by Pallas in 1769 (Stanczykowska 1977). The expansion of their geographic range into Eurasia lakes and rivers was remarkably fast. Grossinger reported them in Hungary in 1794 (Clarke 1952). Kerney and Morton (1970) described their establishment in the British Isles between 1820 and 1835. Morton (1979) described their rapid spread through Germany from 1827 to 1840. Most recently, zebra mussels had spread to the Scandinavian peninsula, Switzerland, and Italy by the mid-1970s (Stanczykowska 1977).

The invasion through the former USSR was not as swift, but they became as ubiquitous in Asia as in Europe. They were first reported in the Dvina River Basin in 1845 (Stanczykowska 1977). They spread throughout eastern Europe, and by the 1960s were reported in the Oginski and Moscow canal system by Kuchina in 1964 (Stanczykowska 1977) and Kachanova in 1963 (Zhdanova and Gusynskaya 1985).

2. North American Invasion. Hebert et al. (1989) reported that the first North American collection of zebra mussels was made in Lake St. Clair in June 1988. By December 1993 they had moved throughout the Great Lakes with

occurrences in all lakes from Duluth Harbor, Minnesota, to the St. Lawrence River (OSGCP 1993).

The ability of zebra mussels to invade inland lakes and rivers was well documented in Europe and Asia before their introduction to North America. Therefore, it is reasonable to believe that they have the capability to spread just as rapidly into the inland lakes and rivers of North America from the Great Lakes. In fact, they have already been found in the Mississippi River, from St. Paul, Minnesota, to New Orleans, Louisiana, and the Illinois, Hudson, Ohio, and Tennessee Rivers. In 1993, the first collection of zebra mussels west of the Mississippi River was made in the Arkansas River, and several inland lakes in Michigan, Ohio, New York, and Ontario were reported to have established populations (OSGCP 1993).

C. The Limnology of the Inner Portion of Saginaw Bay.
Saginaw Bay is the second largest bay in Lake Huron. It is frequently divided into an inner and outer portion, because of the difference in depth-volume characteristics between the two portions. They are generally separated by a line between Point Lookout and Sand Point.

The inner portion is contained within an area bounded approximately by 43°35'00"N and 44°04'00"N and 83°22'00"W and 83°00'00"W. It has a mean depth of 4.6 m and maximum depth of 14.0 m. Eighty percent of its volume is in depths of 5.5 m or less. The outer portion of Saginaw Bay has a maximum

depth of 35 m and approximately 70% of its volume is in depths 5 m or more (Beeton et al. 1967).

1. Thermal and Oxygen Stratification. Thermal stratification occurs during summer in the inner bay, however, it is often episodic and limited to calm periods. This portion of Saginaw Bay is well mixed by strong winds, especially those in a southwesterly and northeasterly direction (Schelske and Roth 1973). Schelske and Roth (1973) report a difference of 7°C between 0 m and 10 m depth (22°C, 15°C) at the deepest point of the inner bay. Minor dissolved O₂ stratification can occur during summer, but only reaches a minimum of 92% saturation above the sediments at 10 m (Schelske and Roth 1973).

2. Current Patterns. Currents originating in Lake Huron and directed from the Saginaw River determine the distribution of sediments and nutrients in the inner bay's near-shore environments. Water moves into the inner bay along the northwestern shore past Point Lookout and Point Au Gres. It continues into the bay until it reaches the southwestern shore near the mouth of the Saginaw River. Currents move water northeasterly, out of the inner bay, along the southeastern shore between Charity Island and Sand Point (Beeton et al. 1967). Input from the Saginaw River is the major contributor to outflow currents in the inner bay. (Johnson 1958; Ayers 1959; Beeton et al. 1967; International Joint Commission (IJC) 1979).

Current patterns, however, are episodic and are dependent on weather patterns of the Great Lakes region. Weather systems which produce southwesterly and westerly winds change prevailing current patterns in the lake proper. Inflow and outflow circulation is generally reduced, and the currents at any given point in the bay depend on fetch and strength of the wind. Northerly, northeasterly, and northwesterly winds, which force water into Saginaw Bay from the lake proper, contribute to the prevailing pattern of circulation in the bay (Johnson 1958; Ayers 1959; Beeton et al. 1967). With changes in the direction of the wind, shoreline elevations can fluctuate as much as 20-30 cm within 24 hours (Batterson et al. 1991).

3. Water Inputs. The Saginaw River contributes most surface water discharge into Saginaw Bay (Johnson 1958; Ayers 1959; IJC 1979). Fourteen small rivers flow into Saginaw Bay, but none, except the Rifle and Au Gres rivers, have mean discharge of ≥ 1.7 m³/sec. The Rifle, Au Gres, and Kawkawlin combined only discharge 8% of the mean annual discharge of the Saginaw River (Beeton et al. 1967).

4. Water Chemistry. Ion concentrations in the inner bay vary among seasons, however there is a consistent pattern of concentration followed by most nutrients and ions in all seasons (Beeton et al. 1967). Total conductivity, and concentrations of Na⁺, Ca²⁺, SO₄²⁻, Mg²⁺, K⁺, and total P are greatest in three regions located between the mouths of

the Saginaw and Quanicassee Rivers, the island region near Sebewaing, and the region between Nayanquing Point and the mouth of the Pinconning River.

A thermal and solute concentration gradient occurs during summer months. Temperature and solute concentrations are greatest as stated above in water ≤ 4 m. Coldest water and lowest solute concentrations occur in the deepest water between Point Lookout and North Charity Island (Beeton et al. 1967).

5. Sediments. The composition of sediments in Saginaw Bay is well documented (Schelske and Roth 1973; Robbins 1986; Ullman and Aller 1989). Sand predominates in near-shore environments. Robbins (1986) reported <10% silt, <3% organic matter, and >50% sand in all areas ≤ 4 m deep. He reported that highly mobile sediments presented difficulty in the determination of accumulation rates, but estimated an annual sedimentation rate of organic and mineral sediments of 0.07 to 0.24 g/cm²/yr, respectively, where the highest rates were found in the southwest corner of the inner bay, near the mouth of the Saginaw River.

D. A Comparison Between Lake Erie and Saginaw Bay. Zebra mussels have become well established in western Lake Erie and Saginaw Bay (OSGCP 1993). They are expected to persist in the inner portion of Saginaw Bay, as they have in western Lake Erie, because of the limnological similarities between these two bodies of water (Schelske and Roth 1973).

1. Summer Temperature Regimes. Average depth in western Lake Erie is greater than the inner portion of Saginaw Bay, 7.3 m and 4.6 m, respectively. However, the mean summer surface temperature, important to zebra mussel reproduction, is similar, 23°C in western Lake Erie, and 22°C in the inner portion of Saginaw Bay (Schelske and Roth 1973). Both systems have optimal temperature regimes for veliger maturation, which occurs between 20-22°C. Also, Saginaw Bay reaches or exceeds 14°C, the temperature at which adult mussels release gametes, approximately May through September. The duration over which western Lake Erie attains these temperatures is approximately the same (Schelske and Roth 1973).

2. Nutrient Regimes. Soluble reactive PO_4^{3-} concentration is also similar in both aquatic systems, 3-5 ppb in Saginaw Bay and 1-10 ppb in western Lake Erie. Average Ca^{2+} concentration, essential for shell development (Stanczykowska 1977), is higher in Saginaw Bay, 46 ppm, than western Lake Erie, 32 ppm. pH in both systems ranges between 7.8-8.2 (Schelske and Roth 1973).

II. Zebra Mussel Filtration and Water Clarity.

During the first year the veligers change into an adult form and must become attached to a solid substrate. Often they attach to the shells of other zebra mussels and colonies as dense as 82,000 individuals/m². Once attached,

their nutritional requirements are met through filtration of water drawn in and out through an inhalant and exhalant siphon. They filter particles between 1 and 200 μm , digest palatable organisms, primarily planktonic algae, and eject the unpalatable material in a mucosal sphere called psuedofeces (Stanczykowska 1977).

Hubert (1989) reported that water clarity in western Lake Erie improved from Secchi depths of 1.5 m in mid-May 1988, before the rapid increase of zebra mussels, to 3.6 m in mid-May 1989. This increased light penetration was attributed to the ability of mussels to filter suspended solids out of the water column. Likewise, the increased transparency of the water has been implicated in the increases in abundance and depth distribution of aquatic macrophytes in Lake St. Clair and Lake Erie (Griffiths 1992), however no one has tested the latter hypothesis.

III. Light and Changes in Macrophyte Assemblages.

The ecological significance of light to aquatic plant assemblages is well documented (Hutchinson 1975; Kirk 1983). Light is reflected, absorbed, and scattered at a significantly greater rate in water than in air, therefore the transparency of the water greatly affects the opportunity for photosynthesis, especially for submersed plants and algae.

Macrophytes have evolved many different physiological, and morphological strategies to compensate for the light constraints presented to them in aquatic systems (Kirk 1983). Some strategies are common to all aquatic macrophytes. Therefore, any change in the aquatic light environment should result in changes in the macrophyte communities at the ecosystem level. However, many strategies are unique to a few or even one species. Hence, any change in the aquatic light environment also should result in changes in species composition and distribution at the community level.

A. The Nature of Underwater Light. The characteristics of light in aquatic media are well understood, and an excellent review is presented by Kirk (1983).

Incident solar radiation, i.e. irradiance reaching the surface of the water, is a function of transmission of solar radiation through the Earth's atmosphere, diurnal variation in solar irradiance, and variation of irradiance by latitude and season. It is greatest at midday, at summer solstice, and during clear, dry atmospheric conditions. Incident solar radiation is lower as time, season, and atmospheric conditions deviate from these maxima (Kirk 1983).

The proportion of light that is available to submersed plants and algae for photosynthesis changes as a function of light reflection and scattering at the air-water interface, and the reflection, absorption, and scattering of light by

the water color and suspended particles. Immediately below the water surface, irradiance is greatest when the surface is undisturbed, i.e. no wave or current movement, and the angle of incidence is 90° . Any deviation from undisturbed water or incident light less than 90° results in reduced irradiance.

At all depths below the surface, irradiance is dependent on light absorbance by water itself, and absorbance, scattering, and reflection by dissolved organic matter, particulate matter, both organic and inorganic, and the phytoplankton present. Any deviation from pure water decreases irradiance at depth.

Pure water absorbs red light (680-720 nm) much faster than it does green and blue light (400-550 nm). Therefore, the spectral content of incident solar radiation shifts from the full visible spectrum to blue light with depth. Dissolved organic matter is comprised of many different organic compounds which absorb light in a diversity of ways. However, they generally absorb wavelengths of light in the red region of the spectrum weakly and increase absorption as wavelengths decrease beyond 550 nm. Absorption by particulate matter is also highly variable, but it generally absorbs light in the same region of the visible spectrum as dissolved organic matter.

Phytoplankton absorb wavelengths throughout the spectrum, however, most light is absorbed in the same

regions critical to macrophytes, i.e. 450-500 nm and 670-700 nm, because they share many of the same photosynthetic pigments. Of the three largest divisions of phytoplankton, Chlorophyta, Cyanophyta, and Chrysophyta, all have two absorption maxima at 440 nm and 680 nm. These are the same wavelengths most aquatic macrophytes exhibit absorption maxima (Prescott 1980; Kirk 1983; Wetzel 1983).

B. Ecosystem Level Changes in Abundance and Depth Distribution. Limited light is a consequence of life underwater common to all submersed macrophytes. Therefore, ecosystem level changes in light availability should result in changes in submersed macrophyte abundance and depth distribution at an ecosystem level.

Macrophytes have evolved common strategies at two levels of biological organization to compensate for the limited light environment present underwater. Physiologically, pigment concentrations change in response to different light conditions. Morphologically, most submersed aquatic macrophytes show great heterophyllous capabilities, especially in leaf form (Sculthorpe 1967; Hutchinson 1975).

1. Common Adaptations Found in Freshwater Macrophytes.

Most freshwater macrophytes show an ontogenic ability to change the relative concentration of photosynthetic pigments in response to different light conditions. This is in contrast to many marine macrophytes which have

phylogenetically fixed concentrations of photosynthetic pigments specifically adapted to light with different proportions of blue, green, and red light, and hence, are restricted to growing at a specific range of depths (Kirk 1983).

Spence and Chrystal (1970a) were the first to show that the adaptation to decreasing light intensity was ontogenic adaptation in freshwater macrophytes. They concluded that aquatic plants and algae exposed to lower light intensity produced more chlorophyll a and b per leaf area.

Recent studies, however, have shown that *Potamogeton gramineus* and *P. pectinatus* do not produce more chlorophyll per leaf area (Spencer 1986; Spencer and Ksander 1990). Instead, as light intensity decreases accessory pigments, such as carotenoids and anthocyanin, decrease per leaf area. This increases chlorophyll concentrations relative to accessory pigments.

Leaf thickness and surface area increase dramatically in many macrophytes, e.g. *Ranunculus flabellaris*, as light intensity decreases. This causes extreme changes in leaf shape, i.e. heterophylly, in some species (Hutchinson 1975). Gas exchange, ion availability, temperature, and day length have all been hypothesized as the controlling mechanism. But Bodkin et al. (1980) has demonstrated that high ratios of red light (660 nm) to far red light (730 nm) absorbed by *Hippuris* leaves induced thick leaves with large surface

area, and low ratios induced thin leaves with small surface area. Because longer wavelength light is disproportionately absorbed in shallow depths, low ratios and the associated leaf form are found near the surface of the water column.

2. Changes in Macrophyte Abundance and Depth

Distribution.

a. Relationship Between Abundance and Light Intensity.

Macrophyte production has been related to light intensity. Duarte and Kalff (1987) found a negative relationship between biomass of individual plants and plant stem density for a macrophyte assemblage which included *E. canadensis*, *Isoetes lacustris*, *Myriophyllum spicatum*, *Najas flexilis*, *Potamogeton crispus*, *P. praelongus*, and *Vallisneria americana*, and light intensity. They concluded that light competition decreased production for individuals as density increased. They also suggested that macrophyte abundance increased with light intensity, because they observed an increase in abundance with decreased latitude. However, this relationship was probably confounded by the influence of length of growing season and temperature.

The relationship between light intensity and abundance has been confirmed for one species, *P. pectinatus* (Scheffer et al. 1992; Van Dijk et al. 1992). Tuber density was positively correlated to light intensity. *P. pectinatus* stem density was positively correlated to tuber density. Scheffer et al. (1992) suggested that changes in abundance

in *P. pectinatus* can be a yearly measure of changes in water transparency, because few tubers remain dormant for more than one winter. Models constructed by Scheffer et al. (1992) found that 50% of the variability in *P. pectinatus* presence could be explained by light intensity and depth. However, the other 50% of the variability remained unexplained.

b. Relationship Between Light Intensity and Depth Distribution. Depth is the simplest measure of the influence of light on distribution. Maristo (1941 in Hutchinson 1975) was the first to demonstrate that Secchi disk depth was linearly related to the lower limit of macrophytes in 27 Finnish lakes. Belonger (1969), Modlin (1970), Canfield and Hodgson (1983), Canfield et al. (1985), and Chambers and Kalff (1985) have all conducted similar studies with the same conclusion.

Depth distribution is often directly related to light transmittance, because the maximum depth of macrophyte colonization is often determined indirectly by the compensation point (Kirk 1983). The compensation point is the depth at which the rate of photosynthesis equals the rate of respiration (Wetzel 1983). Most sources agree that this point ranges from 5-15% of full incident sunlight for most angiosperms, but can be as low as 1-3% for non-vascular plants (Spence 1976, 1982; Bowes et al. 1977; Moeller 1980; Agami et al. 1980).

Spence and Chrystal (1970b) demonstrated the relationship between light tolerance and the depth of colonization. Barko and Smart (1981) explained that this occurred, because low light adapted species lowered their individual compensation points by reducing respiration rates.

A unique study by Rørslett (1987) has shown that the vertical niche of deep water macrophytes could be modelled from data collected in Norwegian lakes. A persistent domain, i.e. where macrophytes were present >1 growing season, and a transient domain, i.e. where they were present ≤ 1 growing season, could be predicted in the spatial niche of each species. Shifts in macrophyte distribution were a result of shifts in the transient domain. These shifts were determined by stochastic changes in the physical environment.

C. Community Level Changes in Species Composition.

Freshwater macrophytes, however, also have many adaptations that are unique to one or just a few species.

Physiologically, the degree to which a species can adjust relative concentrations of chlorophyll a and b is variable. Morphologically, the growth form of the mature aquatic plant varies by the proportion of biomass that is near to sediment or the water surface.

1. Unique Adaptations Found in Macrophyte Species. The physiological ability to change accessory pigment per leaf

area varies among freshwater macrophytes. *E. canadensis* does not significantly adjust relative concentrations of chlorophyll a and b with changing light conditions (Wolff and Senger 1991). In fact, this species is adapted for a narrow range of light intensities. *P. pectinatus* and *P. gramineus* can use a wider range of light intensities than *E. canadensis*, especially immediately after germination (Spencer 1986).

Spence and Chrystal (1970b) found that macrophytes could be categorized by their ability to exist in low or high intensity of light. They found that *Potamogeton praelongus* and *P. obtusifolius* began photosynthesizing at lower light intensities than *P. polygonifolius*, but were also light saturated at lower intensities. *P. polygonifolius* could not photosynthesize at the same low light intensities as the other two species, but was light saturated at much higher intensities.

Pigment assemblies, which include photosystem I and II proteins and their electron transfer components, do not increase in number, only in size. The slower saturation rates, however, are associated with a decrease in the concentration of ribulose biphosphate carboxylase in the leaf (Kirk 1983). This enzyme is the rate-determining enzyme in the photosynthetic pathway (Zubay 1988).

Sand-Jensen (1978) confirmed this relationship for high light adapted *Littorella uniflora* and low light adapted *I.*

lacustris. She also found lower respiration rates associated with low photosynthetic rates to compensate for slow production.

Although these abilities are physiologically determined, low light macrophytes are not strictly confined to deep water (Hutchinson 1975). This variation in distribution can be explained morphologically through adaptations in growth and germination strategies to different light environments.

Biomass per unit volume, i.e. biomass density, is a quantitative descriptor of growth form. It can be used to determine the proportion of production at a given depth (Duarte and Kalff 1990). High light-adapted species, such as *P. pectinatus* and *M. spicatum*, have the ability to grow successfully in water with low transparency by increasing biomass density as the plant nears the water surface (Titus and Adams 1979; Van Der Bijl et al. 1989). These species grow and increase branch number apically, i.e. new tissue is formed at an apical meristem. Therefore, photosynthesis takes place near the surface of the water and decreases in leaves that are deeper.

Inversely, *V. americana*, which is low-light adapted, can grow successfully in shallow water. *V. americana* produces tissue from basal meristems and has greater biomass density near the sediments (Titus and Adams 1979). This strategy is often observed in low-light adapted plants which

comprise the understory in shallow water macrophyte assemblages (Hutchinson 1975).

Germination of seeds can be related to many stimuli, e.g. day length, temperature, sediment redox potential, animal ingestion, etc. Asexual reproduction, however, is often temperature and day-length dependent for macrophytes which are found in shallow water and low light-adapted macrophytes in deep water (Hutchinson 1975). Asexual sprouting in high light-adapted plants growing in deep water can be determined by light intensity, day-length, and temperature if the species have broad tolerances to light levels, e.g. *M. spicatum* (Titus and Adams 1979), or strictly temperature-dependent if light tolerance is not broad, e.g. *P. pectinatus* (Spencer 1986; Van Wijk 1988, 1989a).

P. pectinatus is not able to photosynthesize until its stems rise to a critical depth where light intensity is high enough. Therefore, most reproduction in this species occurs from tubers which contain large starch reserves (Van Wijk 1988, 1989a).

2. Changes in Macrophyte Assemblage Composition. The extent to which species composition of macrophyte assemblages is determined by light intensity and spectral quality is poorly understood. The myriad of competitive interactions possible within simple assemblages often confound data interpretation. A few studies have attempted to correlate assemblage composition to characteristics of

the light environment, however comprehensive mechanistic models of interspecific relationships between aquatic macrophytes are far from being developed. The most recent studies have measured light tolerances in vitro, and then extrapolated to patterns observed in natural communities.

Sand-Jensen (1978) has reported the competitive exclusion of *Isoetes lacustris* by *Littorella uniflora* in high light intensity and vice versa in low light intensity in the oligotrophic Lake Kalgaard in Denmark. Light intensity tolerances were determined in vitro and extrapolated to field data.

Titus and Adams (1979) reported the lack of competitive exclusion of *V. americana* by *M. spicatum*, which are low and high light-adapted species, respectively, in lakes near Madison, Wisconsin. *V. americana* was not excluded, because biomass density is concentrated near the sediments while the biomass density of *M. spicatum* was concentrated near the water surface. *V. americana* was capable of photosynthesis underneath the *M. spicatum* canopy.

Agami et al. (1980) and Fair and Meeke (1983) have demonstrated how broad light intensity tolerances have enabled biological invader species *Najas marina* and *Ceratophyllum demersum* to dominate assemblages in the Yarkon River, Israel, and a pond in England, respectively. They concluded that light intensity tolerances of aquatic plants in these systems determined the composition of the

assemblages, because the efficiency of light absorbance by *N. marina* and *C. demersum* created a severely light limited environment for all other species.

IV. Other Factors Controlling Macrophyte Abundance and Distribution.

There are other physical and chemical factors that control the distribution of macrophytes. Stochastic changes in temperature, nutrient availability, pressure, and direct disturbance due to high wind, waves, and currents are potential agents of control in aquatic systems (Hutchinson 1975; Wetzel 1983).

Production, metabolism, germination, and species richness of macrophyte assemblages have been shown to be controlled by temperature. Barko et al. (1982) demonstrated that biomass increased with increasing light intensity and temperature in *E. canadensis*, *Potamogeton nodosus*, and *V. americana*. Madsen and Adams (1989) have demonstrated increased rates of photosynthesis and respiration with increased light and temperature in stream populations of *P. pectinatus*. Madsen and Adams (1988) demonstrated increased tuber germination in *P. pectinatus* with increased light and temperature, and Spencer and Ksander (1991) have demonstrated increased shoot elongation in *P. gramineus* with increased light and temperature. Pip (1989) has shown a

relationship between species richness with increased water temperature over 345 sites in central North America.

Many nutrients have been implicated in the control of macrophyte populations. For example, phosphorus availability is implicated in the control of populations of *M. spicatum*, *P. pectinatus*, and *Nitella flexilis* (Forsberg 1965; Barko and Smart 1980; Huebert and Gorham 1983; Van Wijk 1989b, 1989c). Nitrogen, S, K, Ca, Mg, NH_4^+ , and HCO_3^- are implicated as potential control nutrients for *P. pectinatus* (Huebert and Gorham 1983; Van Wijk 1989b, 1989c).

Physical perturbation due to wind and waves, currents, and sediment movement have also been implicated in the control of macrophyte distribution. Wind and waves have been implicated as controlling factors for submersed, floating-leaved, and emergent macrophytes (Anderson 1978; Duffy et al. 1987). Most species are adversely affected by wind and waves, and some show specific adaptation to these forces, e.g. Wetzel (1983). Currents as slow as 0.3 m/sec are known to be detrimental to many submerged macrophytes, and control their distribution (Nilsson 1987; Chambers et al. 1991). Sediment grain size and composition also is known to control distribution, e.g. Chambers and Kalff (1987), and changes in sediments due to movement can also re-distribute macrophytes.

Finally, pressure has been implicated in the control of vascular macrophytes. Bodkin et al. (1980) have

demonstrated that pressure can crush lacunar air spaces in plant tissue and reduce photosynthesis. Dale (1981) has demonstrated that some species, e.g. *M. spicatum*, have a competitive advantage, because they can resist crushing. However, lacunae are rarely crushed at depths <7-10 m (Dale 1981). In Saginaw Bay, the influence of pressure on plant distribution would not be likely, because macrophytes did not grow deeper than 5 m.

METHODS

Transect Model. A transect model, based on the most common pattern of macrophyte distribution found in Saginaw Bay littoral regions, was used to measure macrophyte assemblages and their associated light environment (Figure 1). Each transect extended shoreward from the bay, and perpendicular to offshore depth contours. Typically, each transect could be divided into three zones. Zone 3 extended from the shoreline through a plant assemblage in which emergent species were most abundant. Zone 2 extended through an assemblage in which submersed species were most abundant. Zone 1 was the uncolonized sediments beyond the submersed assemblage. Transects ended at 1.5 m depth unless macrophytes were present in 1991 at depths greater than 1.0 m. For these exceptions, the transect was extended to 1.5 times the maximum depth of macrophyte occurrence. Transect location and zone boundaries were originally assigned in 1991 and were re-located thereafter by use of LORAN C. The original locations were repeatable within ≤ 30 m using LORAN C. All boundaries remained fixed throughout the study period.

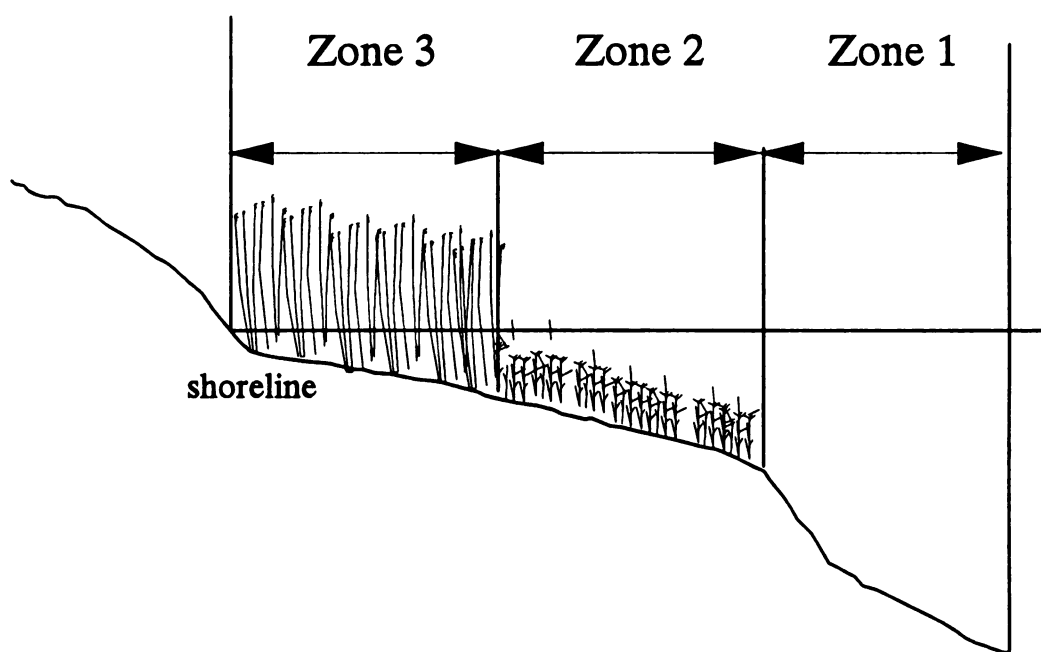


Figure 1. Sampling model for five primary transects based on the typical littoral region in the inner portion of Saginaw Bay.

Study Sites. Saginaw Bay can be divided into two hydrographic regions. The inner region is relatively shallow and productive compared to the rest of Lake Huron. It is distinguished from the deeper outer region of the bay and the rest of Lake Huron by a line between Point Lookout and Sand Point (Figure 2).

Five primary transects were established in the inner portion in 1991 to monitor light conditions and plant assemblages (Figure 2). They are referred to as Au Gres, near the mouth of the Au Gres River; Pinconning, at Pinconning County Park; Bay City, at Bay City State Park; Quanicassee, near the mouth of the Quanicassee River, and Sand Point, near the tip of Sand Point. Macrophyte distribution patterns at Au Gres, Pinconning, and Quanicassee conformed well to the transect design. The Bay City site had no emergent assemblage (zone 3). Therefore, Bay City was divided only into zones 1 and 2. Sand Point had no macrophytes present in 1991, and the entire transect was contained in zone 1. LORAN C coordinates for the primary transects are listed in Appendix A.

Twenty-seven secondary transects were established in 1992 (Figure 2). The secondary transects and four of the primary transects, excluding Sand Point, were used to determine the maximum depth of macrophyte colonization and the area of macrophyte coverage in Saginaw Bay (Table 1). The secondary transect locations were selected by a line

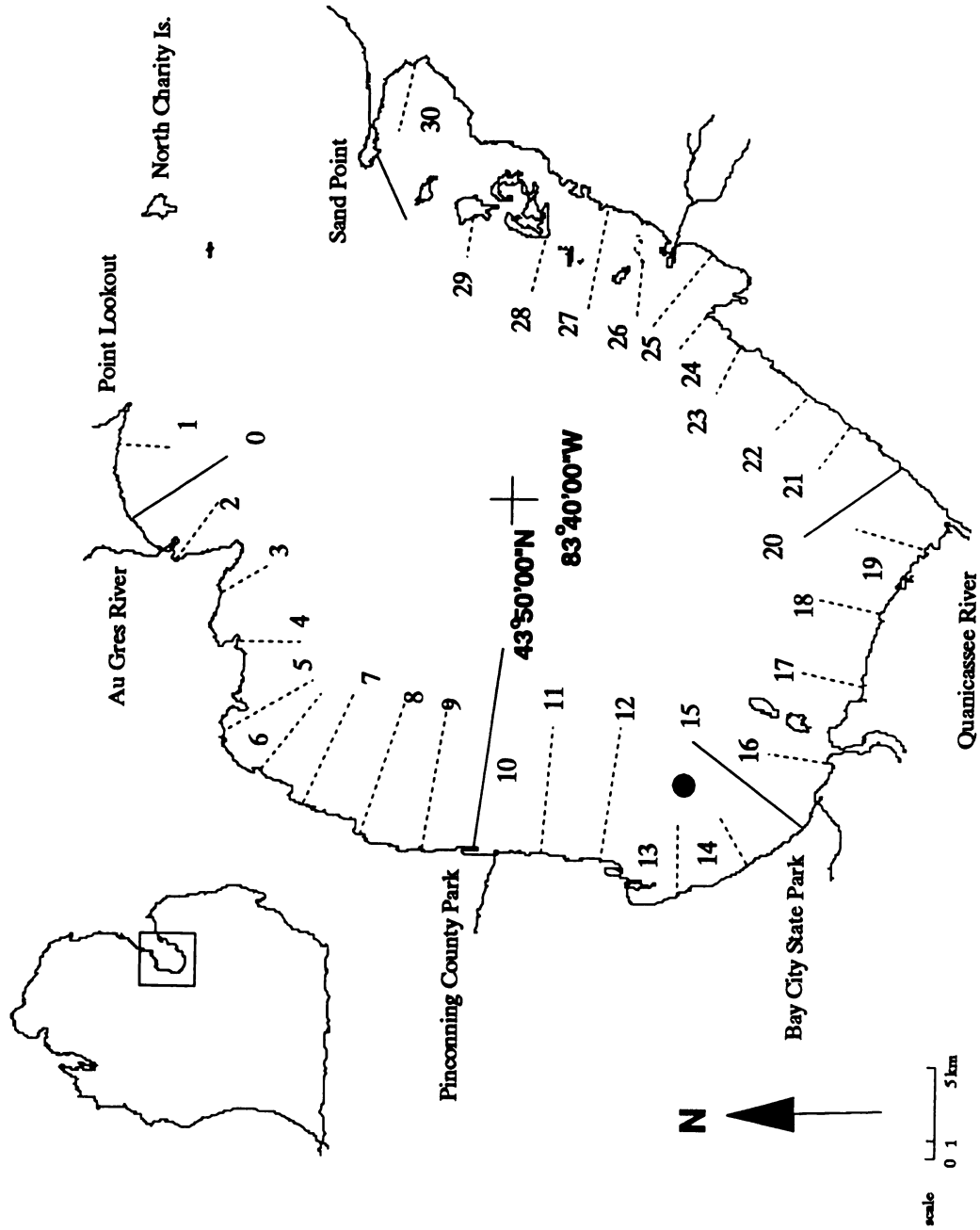


Figure 2. Locations of primary transects (solid lines) and secondary transects (dashed lines), and the Bay Metropolitan Water Treatment Plant intake (●) in the inner portion of Saginaw Bay.

Table 1. Calendar for field sampling in the inner portion of Saginaw Bay.

Measurement	Year		
	1991	1992	1993
Turbidity [†]	April-August	April-August	April-August
PAR extinction [†]	April-August	April-August	April-August
Secchi depth [†]	April-August	April-August	April-August
Temperature [†]	April-August	April-August	April-August
Water depth [†]	April-August	April-August	April-August
Macrophyte [†] relative abundance	July	June-July	June-July
Maximum depth of <0.01 relative abundance	July [†]	August [‡]	August [‡]
Max. depth of 0.14 relative abundance	July [†]	August [‡]	August [‡]

[†]Primary sites only were sampled.

[‡]Primary and secondary sites were sampled.

extending from the approximate center of the inner bay, at 43°50'00"N and 83°40'00"W, to a point intersecting the shoreline on a 1992 National Oceanic and Atmospheric Administration (NOAA) nautical chart #14863. Lines were drawn at every 10° arc. Each transect extended into the bay perpendicular to depth contours. These transects were separated by 2.5-3.3 km of shoreline. LORAN C coordinates for all secondary transects are listed in Appendix A.

Light Environment Sampling. To measure the light environment associated with the littoral regions of Saginaw Bay, three common measures of water clarity were used: 1) light extinction (k) of photosynthetically active radiation (PAR), 2) turbidity, and 3) Secchi disk depth. The light environment was sampled between one and four times each month throughout the growing season (Table 1).

The irradiance (I) of photosynthetically active radiation (PAR) was measured at the water surface and at three depths to determine the rate of extinction of light intensity (k) with respect to depth with a LI-COR LI-188 integrating quantum photometer. k is defined as:

$$k = [\ln(I_0) - \ln(I_z)] / z; \quad (1)$$

where k is the extinction coefficient with units m^{-1} , z is depth in m, I_0 is the irradiance, in microeinsteins/ m^2 /sec, at the surface, and I_z is the irradiance at z . $\ln(I_0) - \ln(I_z)$ is linearly related to z with a slope of k (Kirk 1983). PAR is the range of electromagnetic radiation with wavelengths

between 400 and 720 nm which are important for photosynthesis (Kirk 1983). k was measured at the deep end of each transect and at the boundary between zones 1 and 2 (Figure 1).

At least 5 water samples were collected in each zone at each site on each sample date. Samples were stored for less than 48 hours in an opaque cooler immediately after sampling. Samples were analyzed for turbidity using a Hach 2100A Turbidimeter and results expressed in Nephelometric Turbidity Units (NTU). Turbidity of water samples taken from a zone was averaged to obtain a single estimate for that zone. Secchi disk depth was measured at the deep end of each transect (Figure 1). Turbidity, k , and Secchi disk depth were compared between years with four-way analysis-of-variance (ANOVA). Log transformations were used to improve the homogeneity of the variance of each data set. Variance was analyzed with respect to the variables year, month, site, and zone. Some nesting of effects and separation of analysis were needed to account for interactions between effects.

Water Temperature, Wind, and Water Level. Water temperature, wind direction, and water level in Saginaw Bay were monitored to account for their potential impacts on macrophyte distribution and abundance. Temperature was measured *in situ* at each site and in each zone from one to four times per month from April to September (Figure 1;

Table 1). Water depth was measured at the boundaries between zones 1 and 2, 2 and 3, and at the deep end of each transect from one to four times per month. Temperature and water depth were analyzed with four-way ANOVA to test for a difference between years. Water depth data were log-transformed to improve the homogeneity of the variance, but transformation was not needed for water temperature.

Saginaw Bay water elevation also was monitored by the NOAA at Essexville, Michigan. Elevation was recorded as 24 hour means for each day. All data collected from April 1 to August 31 in 1991-1993 are reported.

Water temperature and wind direction also were measured by staff of the Bay Metropolitan Water Treatment Plant (BMWTP) in Bay City, Michigan. Water was collected continuously from the Bay Metro water intake located at 43°43.96N and 83°54.07W in Saginaw Bay (Figure 2). Water temperature was measured continuously and recorded as 24 hour means (John DeKam, pers. comm.). Cumulative degree days were calculated for each year for days with water temperatures above 6°C. This base temperature was used, because this is a conservative estimate of the water temperature when ice cover disappeared in the spring. Wind direction was measured from a weather station above the level of the roof of the on-shore facility. The facility is located near the Saginaw Bay shoreline by Bay City State Park. Wind direction was recorded as 12 hour means for each

day from 1991 to 1993. Only data collected during the 1991, 1992, and 1993 growing season (April 1 to August 31) are reported.

Wind direction observations were grouped into four quadrants: 1) NNE to E; 2) ESE to S; 3) SSW to W; and 4) WNW to N. Chi-square contingency analysis was used to test for independence in the distribution of wind observations among quadrants and across years.

Macrophyte and Species Abundance. The term macrophytes, in this study, included all vascular hydrophytes, charophytes, and several species of benthic, macroscopic filamentous chlorophytes. Genera with benthic filamentous forms, e.g. *Cladophora*, *Spirogyra*, *Zygnema*, *Hydrodictyon*, and *Oedogonium*, were included in the filamentous algae classification. Three genera in the family Characeae, i.e. *Chara*, *Nitella*, and *Tolypella*, were also included in the analysis. Vascular hydrophytes were identified by use of Fasset (1968). The Characeae were identified by use of Wood (1965). The other chlorophytes were identified in the field only to Division by color and form, according to Prescott (1978).

Macrophyte relative abundance was measured in each zone along each of the five primary transects by use of a petite Ponar grab, an Ekman grab, or a manual sampling technique. In zones deeper than 1.0 m, samples were taken from a boat with a petite Ponar or Ekman sampler, both of which sample

an area 15 cm X 15 cm. In zones shallower than 1.0 m, sediments and macrophytes were manually removed within an area approximately 15 cm X 15 cm. Locations where the manual samples were taken were determined by movement of the sampler a random number of steps in a random direction from a previous location within the zone.

In deep zones (>1.0 m), ten or more equi-distant points along the transect line were located by use of LORAN. Five grab samples were taken at randomly selected locations within a 10 m radius of each point on the transect line. At least 50 samples were taken in each zone deeper than 1.0 m, within a 20 m wide corridor along the transect. In zones shallower than 1.0 m, at least 33 points were randomly chosen along a corridor that was approximately 6.5 m wide and was centered on the transect. At least 33 randomly chosen points within two immediately adjacent corridors of the same width and parallel to the transect line on either side were also sampled. In this manner, 100 samples were taken from shallow zones in a 20 m corridor, as well. Grab samples were collected once monthly during the growing season (June-July) of each year (Table 1).

Data from macrophyte samples were recorded as follows: presence or absence of macrophytes, and presence or absence for all species collected. Relative abundance (RA) was calculated as follows:

$$RA = P/T \quad (2)$$

where P is the number of samples with macrophytes present, and T is the total number of samples taken.

Differences between years were tested bay-wide by Cochran-Mantel-Haenszel (CMH) Chi-square tests for general association between two variables: 1) year and 2) the frequency of presence or absence, while controlling for variables: 3) site and 4) zone. Zones 1 and 2 were combined to eliminate zero frequencies.

Differences between years of the bay-wide frequency of samples with *Potamogeton pectinatus*, *P. richardsonii*, *P. illinoensis*, *Elodea canadensis*, *Vallisneria americana*, *Najas* spp., Charophytes, and filamentous algae were tested with Pearson chi-square test for general association between two variables: 1) year and 2) presence or absence. Sites and zones were combined to eliminate zero frequencies. Each month was tested separately.

Maximum Depth of Colonization and Area of Macrophyte Coverage. The maximum depth of colonization and the area of macrophyte coverage in Saginaw Bay was determined by sampling along the 5 primary transects established in 1991 and 28 secondary transects established in 1992 (Figure 2). In July 1991, the maximum depth of colonization was determined once at each primary transect by use of grab samplers to determine the deepest end of each transect (Table 1). To increase the sample size, in August 1992 and 1993 maximum depth measurements were determined once at each

primary and secondary transect by use of double-headed rake samplers (Table 1).

In 1991, Ekman and petite Ponar dredge samplers were used to determine the maximum depth at which the proportion of samples with macrophytes present, i.e. RA, was <0.01 . In 1992 and 1993, a double-headed rake tied to a 10 m rope was used to determine the maximum depth at which the proportion of samples with macrophytes present was 0.20 and 0.40. These two depths were chosen because they were within the theoretical transient and persistent domains of the macrophyte community, respectively (Rørslett 1987).

Maximum depth was determined with the grab samplers in 1991, or rakes in 1992 and 1993 at 25 cm depth intervals along each transect until the depth at which samples were <0.01 , or 0.2 and 0.4 successful were found, respectively. Rakes were thrown in five non-overlapping directions, or 10 grab samples were taken within a 10 m radius of a point on the transect. Samples were recorded as macrophytes present or absent. Samplers then moved parallel to the depth contour 20 m to both sides of the transect and took five more rake, or 10 more grab samples. In this manner, 15 rake, or 30 grab samples were taken in a 60 m long X 20 m wide corridor perpendicular to and centered on the transect. The depth and latitude and longitude coordinates were recorded for the depth intervals at which $<1\%$ grab, or 20% and 40% rake samples yielded macrophytes.

Maximum depth of 20% and 40% successful rake samples was compared between 1992 and 1993 by Paired Student's t-tests. Maximum depth of <1% RA determined by use of the grab samplers at the primary transects in July 1991 was not compared to August 1992 and 1993 maximum depth measures, because they were measured in a different month. The area of the inner Saginaw Bay basin covered with macrophytes was estimated by plotting both maximum depth variables on a 1992 NOAA nautical chart #14863 by use of longitude coordinates. Area was then measured the area contained within each polygon bounded by lines connecting the maximum depth of 20% success or 40% success and the shoreline. Areas were measured with a standard planimeter.

Rake and grab sampling methods did not sample with the same efficiency. Therefore, comparisons were made between the proportion of successful rake samples to the proportion of successful grab samples to determine the relative sampling efficiencies of the two methods.

This relationship was determined by sampling plants at the same location with either the petite Ponar or Ekman grab samplers, and the rakes. Both sampling methods were used within three 10 m radius circles immediately adjacent to one another, and on the same depth contour. Rakes were dragged in five evenly distributed directions 10 m to the center of the circle. Ten grab samples were randomly taken within the circle, as well. If the grab sampler fell on the sediments

sampled by the rakes, it was re-located. Standardization sampling was done only where it could be certain that the two devices did not sample the same sediments.

RESULTS

Primary Transect Characteristics. The maximum depth of colonization was deeper than 1.0 m only at Pinconning during July 1991. Therefore, the Pinconning transect was extended approximately 2 times longer, and 3 times deeper than the other transects (Table 2). Au Gres, Pinconning, and Quanicassee had smooth, low-sloping bottom topography. Although slopes were low at Bay City and Sand Point, as well, these two sites had several shallow sand bars which intersected the transect and shifted several times during the study period.

Light Environment. Significant site by month (within year) interactions were present in turbidity data, therefore it was necessary to test each site separately to determine if a year effect occurred (Table 3).

Turbidity decreased from 1991 to 1993 in all zones at Au Gres, Pinconning, and Sand Point (Table 3; Figure 3). No significant decrease in turbidity was evident at Bay City and Quanicassee. The variances among the sites were not homogeneous (Table 4). Quanicassee and Bay City showed higher variability in turbidity than Pinconning, Au Gres, and Sand Point. The failure to find a significant decrease

Table 2. Transect characteristics of the five primary sites in inner Saginaw Bay.

Site	Length	1991 Maximum depth of <0.01 relative abundance	Transect maximum depth	Bay Basin Slope
Au Gres	1.3 km	0.5 m	1.5 m	115 cm/km
Pinconning	2.8 km	2.7 m	4.3 m	154 cm/km
Bay City	0.8 km	0.6 m	1.5 m	175 cm/km
Quanicassee	1.3 km	0.9 m	1.4 m	108 cm/km
Sand Point	1.4 km	0.0 m	1.5 m	107 cm/km

Table 3. Analysis of Variance tests for year and zone effects in log(turbidity) data at five site in littoral Saginaw Bay, 1991-1993. Probabilities marked with symbols were considered significant.

Site	Main Effects	N	Degrees of Freedom	F	Probability
All Sites	Month*Year	448	7,26	3.93	P=0.0004 [†]
	Site*Month(Year)	448	47,56	2.90	P<0.0001 [†]
Au Gres	Year	79	2,9	4.53	P=0.0435 [†]
	Zone	79	2,18	15.17	P<0.0001 [†]
Pinconning	Year	101	2,10	4.99	P=0.0313 [†]
	Zone	101	2,18	7.92	P=0.0008 [†]
Bay City	Year	78	2,10	1.06	P=0.3824
	Zone	78	2,10	5.60	P=0.0218 [†]
Quanicassee	Year	86	2,11	1.88	P=0.1985
	Zone	86	2,21	2.65	P=0.0815 [†]
Sand Point	Year	104	2,10	3.17	P=0.0857 [†]

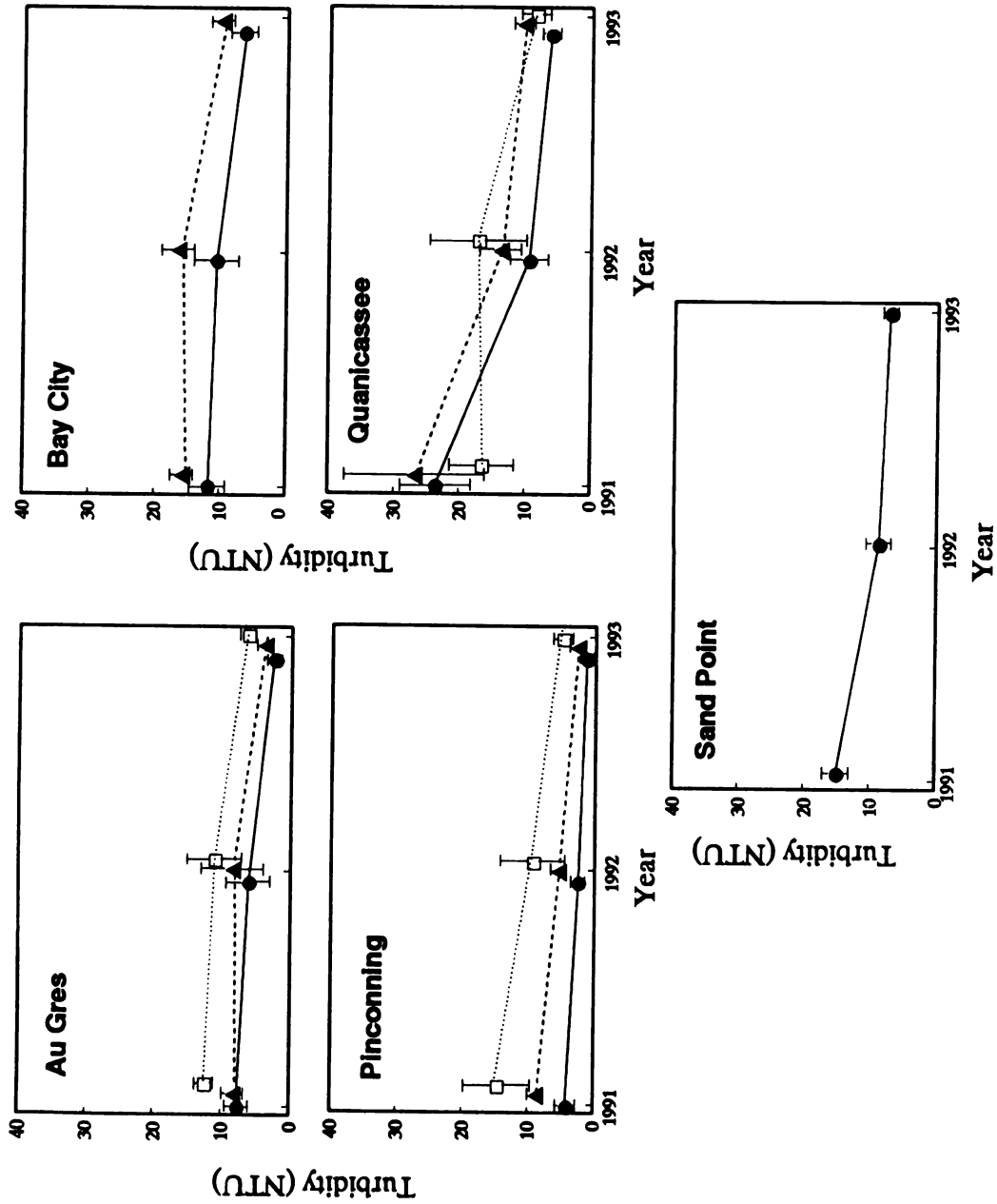


Figure 3. Mean annual turbidity (April-August) at five sites in Saginaw Bay. Error bars represent ± 1 SE. Lines represent zone 1 ($\bullet$), zone 2 ($\blacktriangle$), and zone 3 ($\square$). Bay City had no zone 3, and Sand Point had only zone 1.

Table 4. Variance estimates (s^2) of non-transformed turbidity measurements at five sites in littoral Saginaw Bay. Variance was not homogeneous among sites (Levene's test for homogeneity; $F=12.37$; $df=4,439$; $P<0.0001$).

Site	s^2	N
Au Gres	33.2	79
Pinconning	48.2	101
Bay City	86.6	78
Quanicassee	188.1	86
Sand Point	58.8	104

in turbidity at Quanicassee and Bay City was probably due to the greater variability of turbidity at these sites.

Multiple comparisons were made between years where a significant year effect was present in turbidity by use of Tukey's studentized range test for main effects (Table 5). Mean turbidity across all zones at Au Gres and Sand Point was greatest in 1991 and 1992, and least in 1993 (Table 5; Figure 3). Turbidity at Pinconning decreased sequentially each year.

There was, however, a significant year by month interaction in all zones at all sites (Table 3). This interaction reflected differences in the length of time and magnitude to which turbidity was depressed (Figure 4). In 1991, turbidity decreased throughout the sampling period. However, it did not decrease from April to May 1991 as much as it did in 1992 and 1993. In 1992, turbidity remained low from May through June, and in 1993, low turbidity values persisted from May through August.

A second four-way ANOVA was used on log-transformed turbidity data to test for a difference between sites. Zones were nested within sites due to significant zone by site interactions. Months were tested separately due to significant month by site interactions. Years were tested separately for months April, June, and July due to significant year by site interactions.

Table 5. Tukey's Studentized Range tests for year effects in log(turbidity) data at five sites in littoral Saginaw Bay, 1991-1993. $P < 0.10$ was considered significant for all multiple comparisons. Years marked with the same symbol were not different. Means are reported as actual values in NTU, and 1 SE is in parentheses.

Site	Mean		
	1991	1992	1993
Au Gres	9.2 (1.1) [†]	8.3 (2.3) [†]	3.7 (0.5) [‡]
Pinconning	10.9 (2.3) [†]	5.8 (1.4) [‡]	3.1 (0.5) [‡]
Bay City		No effect	
Quanicassee		No effect	
Sand Point	15.0 (1.9) [†]	8.7 (1.8) [†]	7.1 (0.7) [‡]

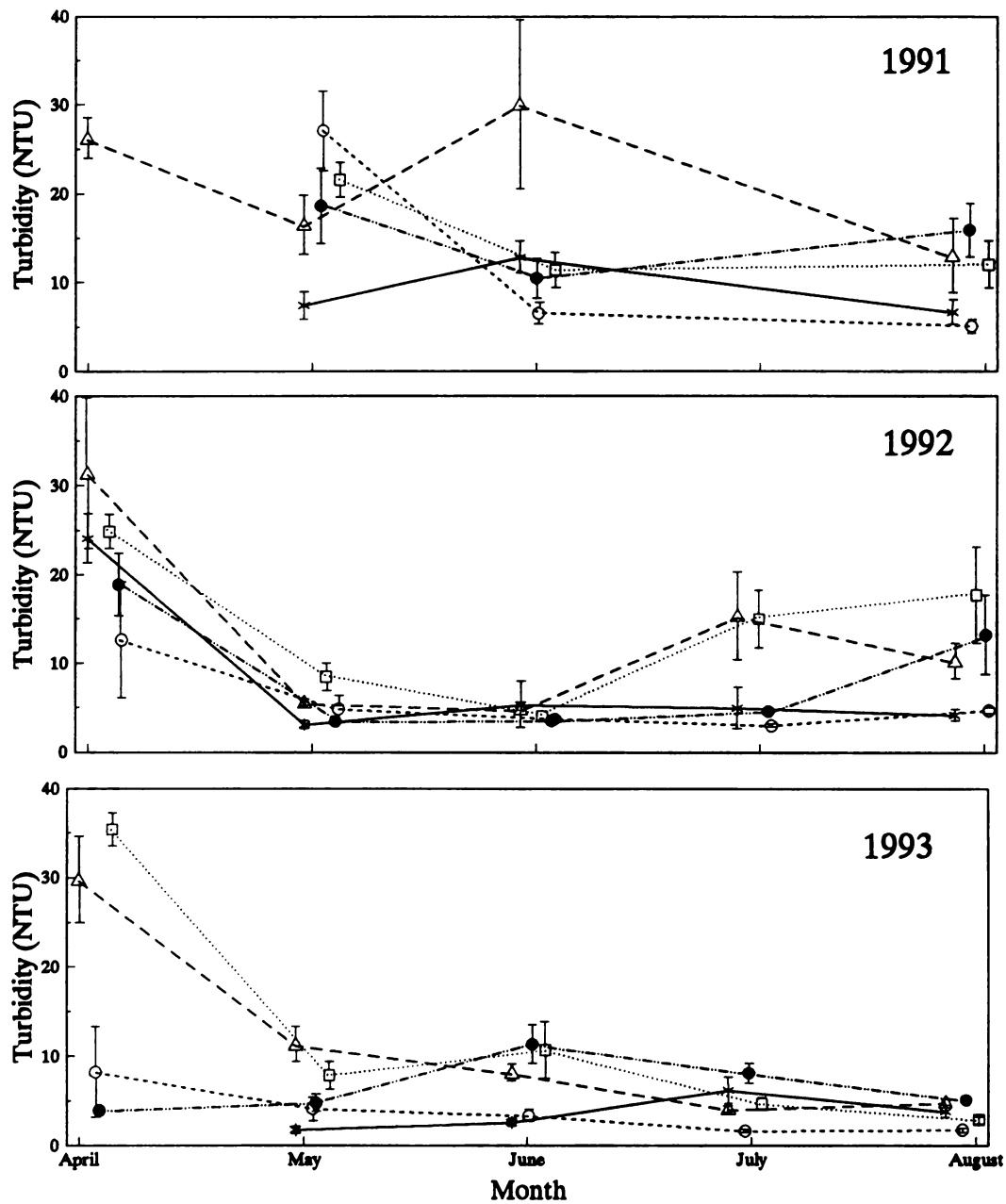


Figure 4. Mean monthly turbidity during the growing season at five sites in Saginaw Bay 1991-1993. Error bars represent ± 1 SE. Lines represent Au Gres (*), Pinconning (○), Bay City (□), Quanicassee (Δ), and Sand Point (●). No samples were taken at Au Gres, Pinconning, Bay City and Sand Point during April 1991, at all sites during July 1991, and at Au Gres during April 1993.

A significant site effect was detectable in data collected during all months, except April and June 1992 (Table 6; Figure 4). Multiple linear comparisons were made between log-transformed turbidity data at sites during each month and each year where significant site effects were present. The null hypothesis that turbidity at the southern most sites, i.e. Bay City and Quanicassee, were not different from the turbidity at the northern most sites, i.e. Au Gres, Pinconning, and Sand Point was tested. Comparisons were not estimable during May for all three years, because sampling was not balanced across months and sites in 1991. Therefore, 1991 was treated separately from 1992 and 1993.

The southern group of sites were significantly more turbid than the northern group of sites in every month with a significant site effect, except July 1993 (Table 7; Figure 4). In July 1993, the opposite pattern, in which Au Gres and Sand Point were more turbid than Pinconning, Bay City, and Quanicassee, was evident (Multiple Linear Comparison, $N=72$, $d.f.=1,7$, $F=7.05$, $P=0.0327$).

There was a significant zone effect in data collected at Au Gres, Pinconning, Bay City, and Quanicassee (Table 3). Multiple comparisons were made between zones where a significant zone effect was present in turbidity data using Tukey's studentized range test for main effects. The shallowest zones were more turbid than the deeper zones at

Table 6. Analysis of Variance tests for site effects in log(turbidity) data at five site in littoral Saginaw Bay, 1991-1993. Probabilities marked with symbols were considered significant.

Date	Main Effects	N	Degrees of Freedom	F	Probability
All Years	Site*Zone	448	5,26	4.32	P=0.0008 [†]
	Month*Site	448	16,26	2.23	P=0.0046 [†]
April	Site				NA
	Site*Year	36	3,6	4.74	P=0.0191 [†]
1992	Site	18	4,7	1.10	P=0.4253
1993	Site	14	3,5	4.97	P=0.0583 [†]
May	Site	98	4,7	3.03	P=0.0954 [†]
June	Site				NA
	Site*Year	121	8,13	3.36	P=0.0021 [†]
1991	Site	40	4,6	4.33	P=0.0551 [†]
1992	Site	17	4,7	0.16	P=0.9496
1993	Site	64	4,7	7.73	P=0.0104 [†]
July	Site				NA
	Site*Year	89	4,7	7.81	P<0.0001 [†]
1992	Site	17	4,7	4.19	P=0.0481 [†]
1993	Site	72	4,7	4.48	P=0.0412 [†]
August	Site	104	4,7	5.13	P=0.0300 [†]

Table 7. Multiple Linear Comparisons for site effects in log(turbidity) data from April through August 1991-1993 in littoral Saginaw Bay. The northern group includes Au Gres, Pinconning, and Sand Point, and the southern group includes Bay City and Quanicassee. Groups marked with the same symbol were not different. Means are reported as actual values in NTU, and 1 SE is in parentheses. Comparisons were not estimable in May, all three years combined, because sampling was unbalanced. Therefore, 1991 was treated separately from 1992 and 1993.

Month	Year	Mean		Probability
		Northern Group	Southern Group	
April	1992		No effect	
	1993	6.0 (2.5) [†]	32.5 (2.7) [†]	P=0.0122
May	1991	16.4 (2.6) [†]	19.0 (2.0) [‡]	P=0.0515
	1992 & 1993	3.7 (0.5) [†]	8.7 (1.0) [‡]	P=0.0104
June	1991	9.9 (1.1) [†]	20.7 (5.3) [‡]	P=0.0163
	1992		No effect	
	1993	5.5 (0.9) [†]	9.3 (1.7) [‡]	P=0.0211
July	1992	4.1 (0.6) [†]	15.2 (2.7) [‡]	P=0.0054
	1993	5.5 (0.7) [†]	4.3 (0.4) [†]	P=0.8983
August	All Years	6.2 (0.7) [†]	8.6 (1.3) [‡]	P=0.0973

all sites, except Quanicassee (Table 8; Figure 3): at Au Gres, zone 3 was more turbid than zones 1 and 2; at Pinconning, turbidity sequentially increased from zone 1 to zone 3; and at Bay City zone 2 was more turbid than zone 1. Although a significant zone effect was detectable in data collected at Quanicassee, no discernable pattern was evident, probably due to the high variability at this site (Tables 4 and 8). Sand Point only had one zone (Figure 3).

Significant site by year interactions were present in light extinction coefficient (k) data, therefore it was necessary to test each site separately for a year effect (Table 9). k decreased significantly from 1991 to 1993 only at Au Gres and Pinconning zone 2 (Table 9; Figure 5). No detectable change occurred in k from 1991 to 1993 at Bay City, Quanicassee, Sand Point, and Pinconning zone 1. A significant zone by year interaction prevented analysis of Pinconning data as one unit (Table 8).

A trend towards decreased light extinction coefficients was evident at all sites except Sand Point from 1991 to 1993 (Figure 5). However, the lack of statistically detectable differences was probably due to small sample size and high variability. The sample size for turbidity data was approximately twice the sample size for k data (Tables 3 and 9). Variances of k at each site were not homogeneous (Table 10). High variability in water transparency was evident at

Table 8. Tukey's Studentized Range tests for zone effects in log(turbidity) data at four sites in littoral Saginaw Bay, 1991-1993. $P < 0.10$ was considered significant for all multiple comparisons. Zones marked with the same symbol were not different. Means are reported as actual values in NTU, and 1 SE is in parentheses.

Site	Mean		
	Zone 1	Zone 2	Zone 3
Au Gres	4.2 (0.9) [†]	5.3 (1.2) [†]	8.8 (1.1) [‡]
Pinconning	2.0 (0.3) [†]	4.5 (0.6) [‡]	9.0 (2.0) [‡]
Bay City	8.6 (1.5) [†]	12.1 (1.4) [‡]	
Quanicassee	11.8 (2.3) [†]	14.5 (3.0) [†]	13.0 (2.5) [†]

Table 9. Analysis of Variance tests for year and zone effects in $\log(k)$ data at five sites in littoral Saginaw Bay, 1991-1993. Probabilities marked with symbols were considered significant.

Site	Main Effects	N	Degrees of Freedom	F	Probability
All Sites	Month*Year	260	7,10	9.46	P<0.0001 [†]
	Site*Year	260	8,20	1.84	P=0.0741 [†]
Au Gres	Year	50	2,8	4.21	P=0.0563 [†]
	Zone	50	1,8	0.20	P=0.6448
Pinconning	Year				NA
	Zone*Year	71	2,9	2.86	P=0.0673 [†]
	zone 1 Year	22	2,9	2.46	P=0.1408
	zone 2 Year	49	2,10	4.55	P=0.0393 [†]
Bay City	Year	36	2,10	0.67	P=0.5324
	Zone	36	1,4	4.40	P=0.0511 [†]
Quanicassee	Year	51	2,10	0.38	P=0.6943
	Zone	51	2,9	3.65	P=0.0672 [†]
Sand Point	Year	52	2,10	2.64	P=0.1200

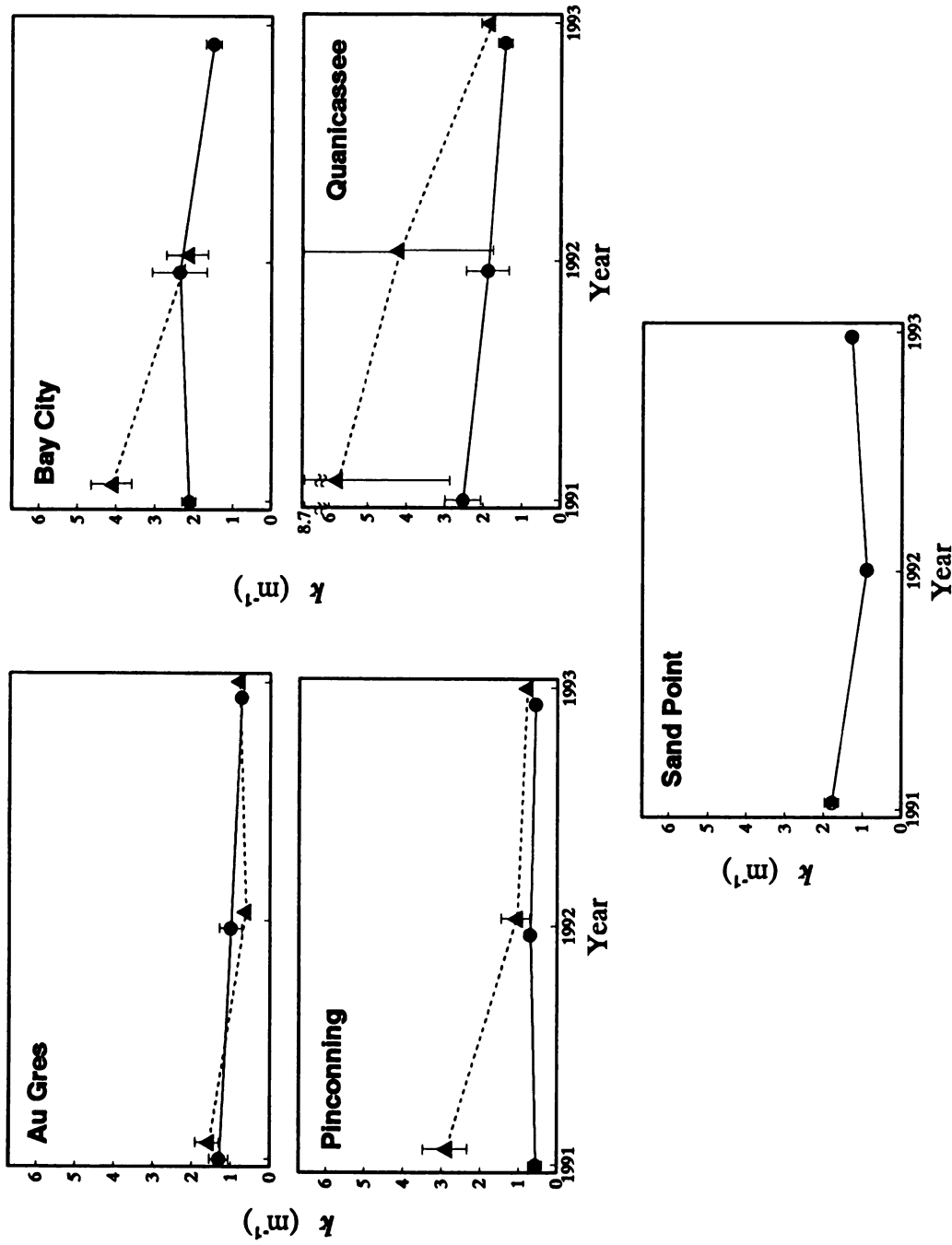


Figure 5. Mean annual light extinction (k) (August-April) for five sites in Saginaw Bay. Error bars represent ± 1 SE. Lines represent zone 1 ($\bullet$) and zone 2 ($\blacktriangle$). Bay City zone 2 1993 was not sampled. Sand Point only had zone 1.

Table 10. Variance estimate (s^2) of non-transformed light extinction (k) measurements at five sites in littoral Saginaw Bay. Variance was not homogeneous among sites (Levene's test for homogeneity; $F=6.94$; $df=4,255$; $P<0.0001$).

Site	s^2	N
Au Gres	0.36	50
Pinconning	1.11	71
Bay City	1.38	36
Quanicassee	9.24	51
Sand Point	0.42	52

Quanicassee and Bay City relative to Au Gres, Pinconning, and Sand Point.

Multiple comparisons were made between data collected at sites where a significant year effect was detectable using Tukey's studentized range test for main effects (Table 11). At Au Gres and Pinconning zone 2, k was greater in 1991 than 1992 and 1993.

A significant month by year interaction was detected in k data, as it was in turbidity data (Tables 3 and 9). The similarity in two data sets suggests that the same monthly pattern found in each year of the turbidity data was also present in k data. However, missing data from unsampled sites and small sample size prevented a comparison between sites, years, and months with the k data as was made between these variables with the turbidity data. A second ANOVA for site effects was attempted, but interpretations were confounded by these problems, as well.

A zone effect was evident only at Quanicassee and Bay City, but not at Au Gres (Table 9). Sand Point only had one zone. Zone effects could not be tested with Pinconning data, due to significant zone by year interactions.

Multiple comparisons were made between zones where a significant zone effect was present in k data using Tukey's studentized range test for main effects (Table 12). At Bay City and Quanicassee the deeper zone (zone 1) was less transparent than the shallower zone (zone 2; Table 12).

Table 11. Tukey's Studentized Range test for year effects in $\log(k)$ data at five sites in littoral Saginaw Bay, 1991-1993. $P < 0.10$ was considered significant for all multiple comparisons. Years marked with the same symbol were not different. Means are reported as actual values in m^{-1} , and 1 SE is in parentheses.

Site	Mean		
	1991	1992	1993
Au Gres	1.43 (0.22) [†]	0.82 (0.16) [‡]	0.77 (0.06) [‡]
Pinconning			
zone 1		No effect	
zone 2	2.85 (0.58) [†]	1.02 (0.39) [‡]	0.78 (0.06) [‡]
Bay City		No effect	
Quanicassee		No effect	
Sand Point		No effect	

Table 12. Tukey's Studentized Range tests for zone effects in $\log(k)$ data at four sites in littoral Saginaw Bay, 1991-1993. $P < 0.10$ was considered significant for all multiple comparisons. Zones marked with the same symbol were not different. Means are reported as actual values in m^{-1} , and 1 SE is in parentheses.

Site	Mean	
	Zone 1	Zone 2
Au Gres	No effect	
Pinconning	NA	
Bay City	1.83 (0.17) [†]	3.09 (0.54) [‡]
Quanicassee	1.79 (0.20) [†]	3.13 (0.83) [‡]

Significant site by month (within year) interactions also were present in Secchi depth data, therefore it was necessary to test each site separately for a year effect (Table 13). Secchi depth associated with the littoral regions of Saginaw Bay increased from 1991 to 1993 at Au Gres and Sand Point, but did not change significantly at Pinconning, Bay City, and Quanicassee (Table 13; Figure 6). High variance and small sample size probably limited the ability of the statistical tests to detect a year effect at the latter sites. The sample size for Secchi depth data was approximately one-fourth as large as turbidity data (Tables 3 and 13).

Moreover, although Secchi depth measures were taken at the deepest end of each transect, the means were slightly biased by water depths that were too shallow on several occasions. At all sites, the proportion of Secchi depth measures that were equal to water depth measures increased from 5.6% in 1991 to 42.9% in 1992 and 32.4% in 1993 (Pearson χ^2 Contingency Analysis, $N=110$, d.f.=2, $\chi^2=6.905$, $P=0.032$). The variance of Secchi depths was also not homogeneous, and Pinconning had the greatest variability (Table 14).

Multiple comparisons were made between years where significant year effects were present in Secchi depth data using Tukey's studentized range test for main effects (Table

Table 13. Analysis of Variance for year effects in log(Secchi depth) data at five sites in littoral Saginaw Bay, 1991-1993. Probabilities marked with symbols were considered significant.

Site	Main Effects	N	Degrees of Freedom	F	Probability
All Sites	Month*Year	106	6,16	4.62	P=0.0008 [†]
	Site*Month(Year)	106	32,32	1.93	P=0.0173 [†]
Au Gres	Year	23	2,9	5.20	P=0.0316 [†]
Pinconning	Year	20	1,8	1.30	P=0.2874
Bay City	Year	19	1,8	0.41	P=0.5386
Quanicassee	Year	19	1,8	1.54	P=0.2497
Sand Point	Year	25	2,9	3.24	P=0.0873 [†]

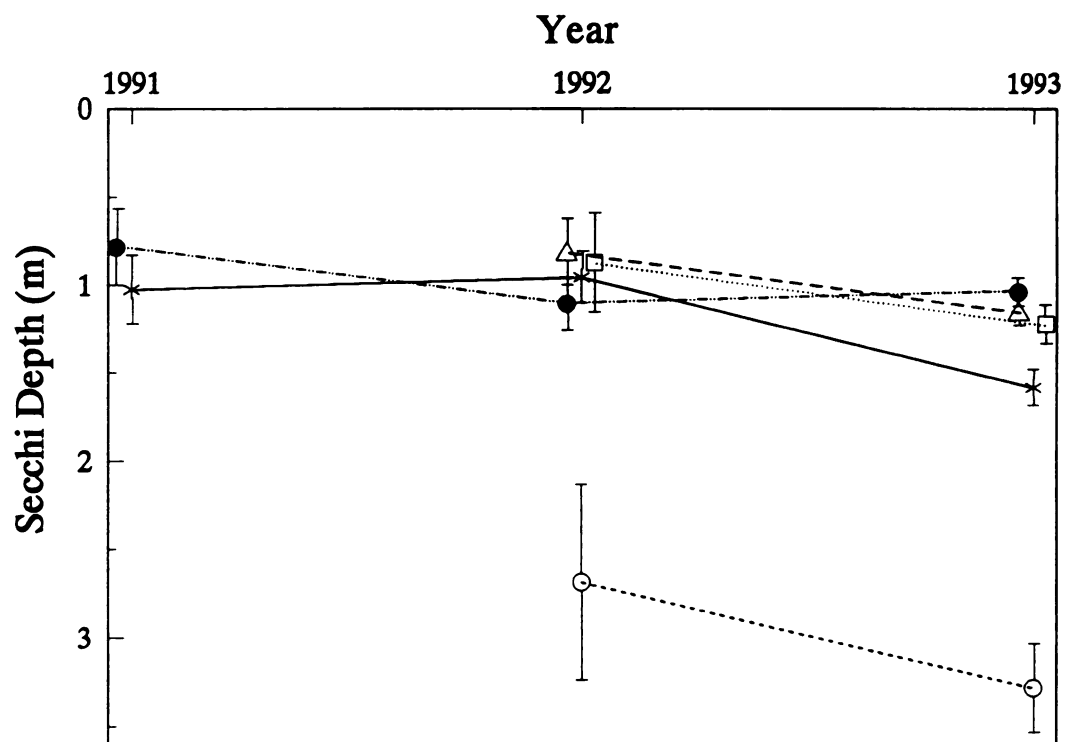


Figure 6. Mean annual Secchi depths (1991-1993) for five sites in littoral Saginaw Bay. Error bars represent ± 1 SE. Lines represent Au Gres (*), Pinconning (○), Bay City (□), Quanicassee (Δ), and Sand Point (●). Pinconning, Bay City, and Quanicassee were not sampled in 1991.

Table 14. Variance estimates (s^2) for non-transformed Secchi depth measurements at five sites in littoral Saginaw Bay. Variance was not homogeneous among sites (Levene's test for homogeneity; $F=12.43$; $df=4,101$; $P<0.0001$).

Site	s^2	N
Au Gres	2,104	23
Pinconning	10,558	20
Bay City	2,661	19
Quanicassee	1,334	19
Sand Point	935	25

15). Secchi depth was deeper in 1993 than 1991 and 1992 at Au Gres, but not at Sand Point (Table 15; Figure 6).

Site effects within the Secchi depth data were not tested, because missing data from unsampled sites and small sample size confounded analysis. Secchi data also had no zone variables, therefore zone effects were not tested.

Water Depth, Temperature, and Wind. Water depth increased from 1991 to 1993 in all zones at Au Gres, Pinconning, and in zones 1 and 2 at Quanicassee (Table 16; Figure 7). No change in water depth was evident at Bay City, zones 1 and 2, Sand Point, and zone 3 at Quanicassee.

Saginaw Bay water elevation data collected by NOAA at Essexville confirmed a net increase in water depth from 1991 to 1993 (Figure 8). However, these data showed a decrease in water elevation from 1991 to 1992 that our analysis did not.

No significant change in water temperatures was detected at any site in data collect for this study (Table 17; Figure 9). Water temperature data collected by the BMWTP at their water intake, however, began to increase earlier in April 1991 than April 1992 and 1993, and was higher in June-August 1991 (Figure 10). Degree days above 6°C began to accumulate earlier in 1991, and continued to accumulate at a greater rate than 1992 and 1993 from June-August due to warmer temperatures (Figure 10).

Table 15. Tukey's Studentized Range test for year effects in log(Secchi depth) data at five sites in littoral Saginaw Bay, 1991-1993. $P < 0.10$ was considered significant for all multiple comparisons. Years marked with the same symbol were not different. Means are reported as actual values in m, and 1 SE is in parentheses.

Site	Mean		
	1991	1992	1993
Au Gres	1.03 (0.20) [†]	0.96 (0.16) [†]	1.58 (0.10) [‡]
Pinconning		No effect	
Bay City		No effect	
Quanicassee		No effect	
Sand Point	0.79 (0.17) [†]	1.11 (0.14) [†]	1.05 (0.07) [†]

Table 16. Analysis of Variance for year effects in log(water depth) data at five sites in littoral Saginaw Bay, 1991-1993. Probabilities marked with symbols were considered significant.

Site	Main Effects	N	Degrees of Freedom	F	Probability
All Sites	Month*Year	307	7,38	5.73	P<0.0001 [†]
Au Gres	Year				NA
	Zone*Year	70	4,16	13.23	P<0.0001 [†]
zone 1	Year	25	2,9	12.46	P=0.0026 [†]
zone 2	Year	25	2,9	40.91	P<0.0001 [†]
zone 3	Year	20	2,7	30.60	P=0.0003 [†]
Pinconning	Year	89	2,9	6.42	P=0.0185 [†]
Bay City	Year	49	2,10	1.45	P=0.2790
Quanicassee	Year				NA
	Zone*Month(Year)	72	20,20	3.69	P=0.0005 [†]
zone 1	Year	26	2,11	4.14	P=0.0457 [†]
zone 2	Year	24	2,10	11.64	P=0.0024 [†]
zone 3	Year	22	2,10	1.76	P=0.2209
Sand Point	Year	27	2,10	2.68	P=0.1170

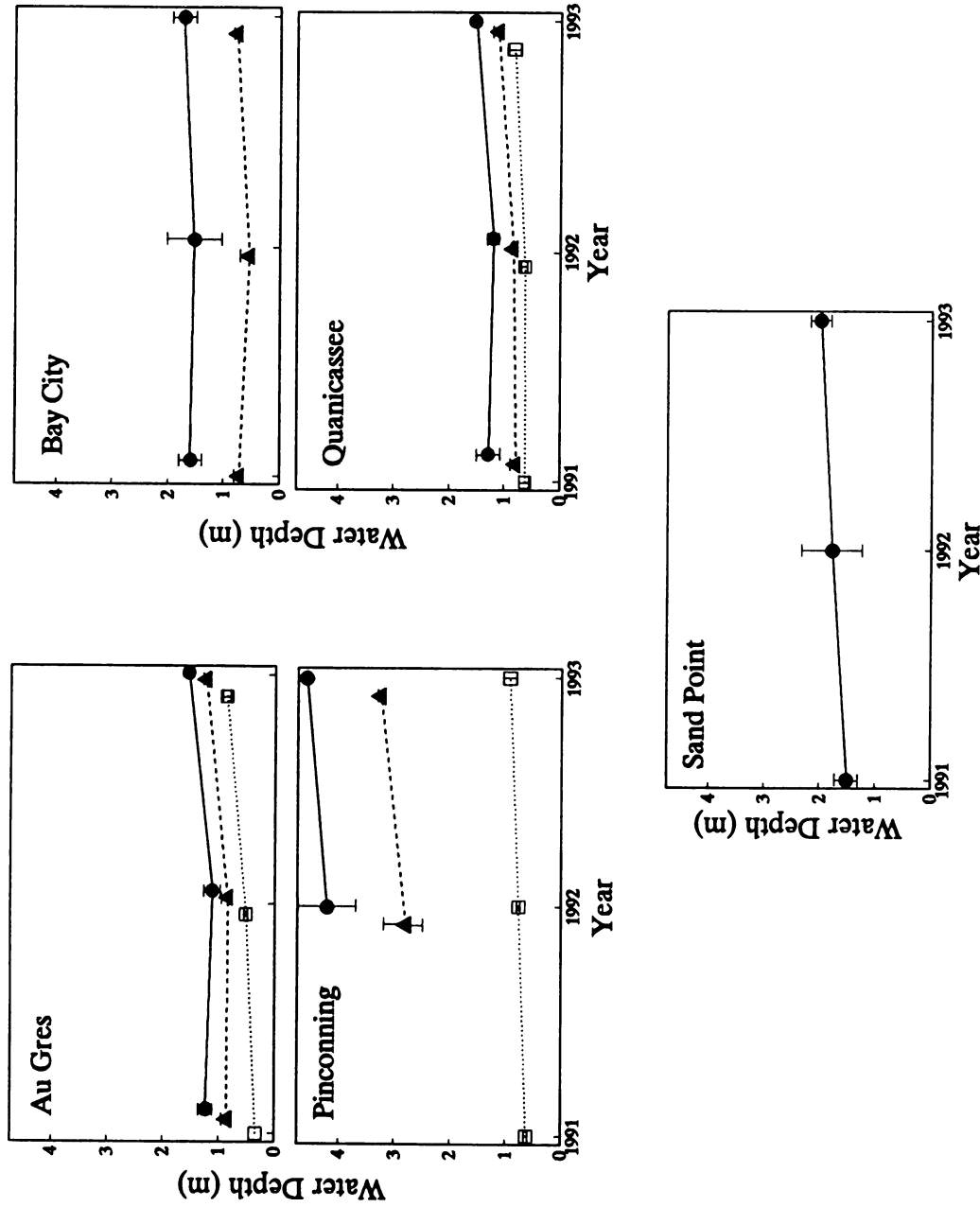


Figure 7. Mean annual water depth from 1991-1993 at five sites in littoral Saginaw Bay. Error bars represent ± 1 SE. Lines represent zone 1 (●), zone 2 (▲), and zone 3 (□). Bay City had no zone 3, and Sand Point only had zone 1. Zone 1 and 2 were not sampled at Pinconning in 1991.

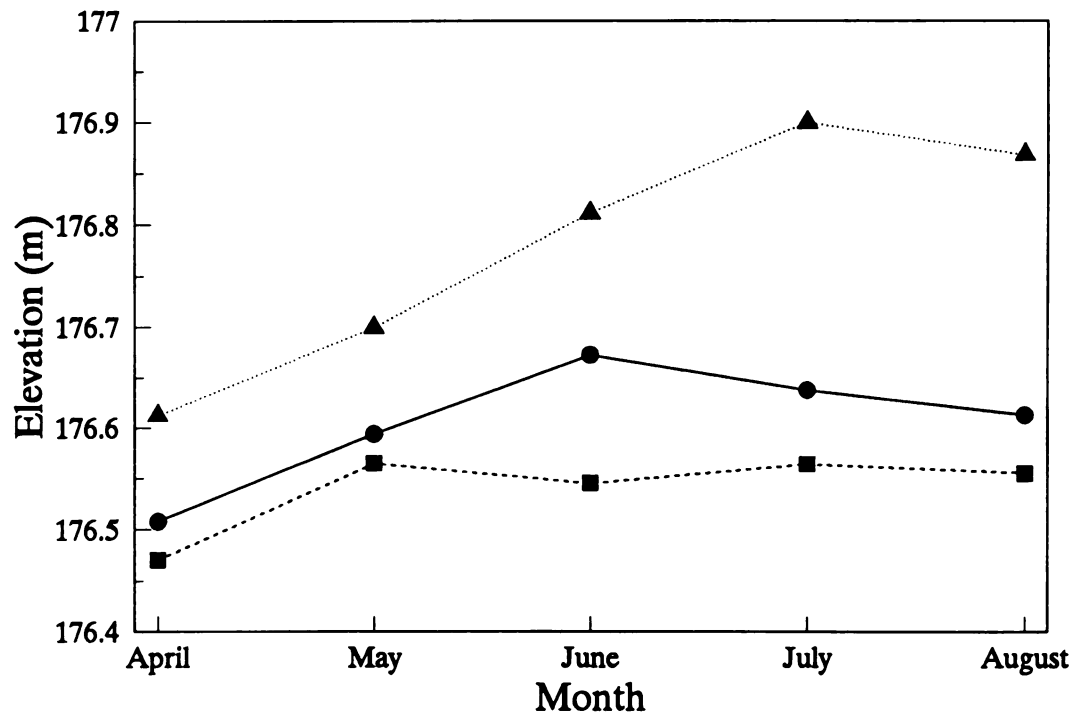


Figure 8. Mean monthly water elevation collected by NOAA at Essexville, MI 1991-1993. All standard errors were ≤ 0.0007 m. Lines represent 1991 ($\bullet$), 1992 ($\blacksquare$), and 1993 ($\blacktriangle$).

Table 17. Analysis of Variance for year effects in temperature data at five sites in littoral Saginaw Bay, 1991-1993. Probabilities marked with symbols were considered significant.

Site	Main Effects	N	Degrees of Freedom	F	Probability
All Sites	Month*Year	416	7,20	9.43	P<0.0001 [†]
Au Gres	Year	74	2,9	0.09	P=0.9119
Pinconning	Year	88	2,8	0.54	P=0.6013
Bay City	Year	75	2,10	0.90	P=0.4387
Quanicassee	Year	81	2,11	0.25	P=0.7809
Sand Point	Year	98	2,10	0.24	P=0.7887

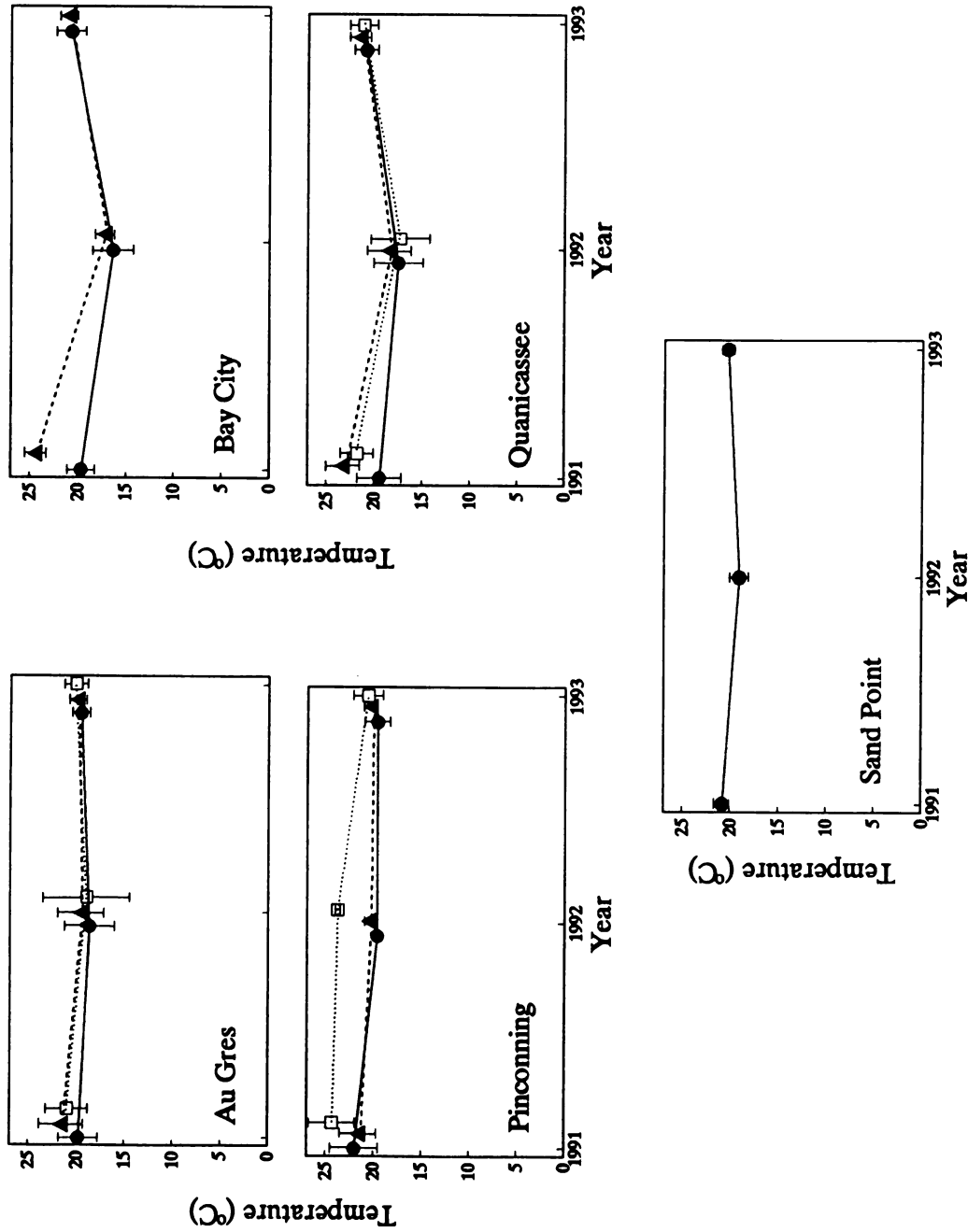


Figure 9. Mean annual temperature collected from 1991-1993 at five sites in littoral Saginaw Bay. Error bars represent ± 1 SE. Lines represent zone 1 (●), zone 2 (▲), and zone 3 (□). Bay City had no zone 3, and Sand Point had only zone 1.

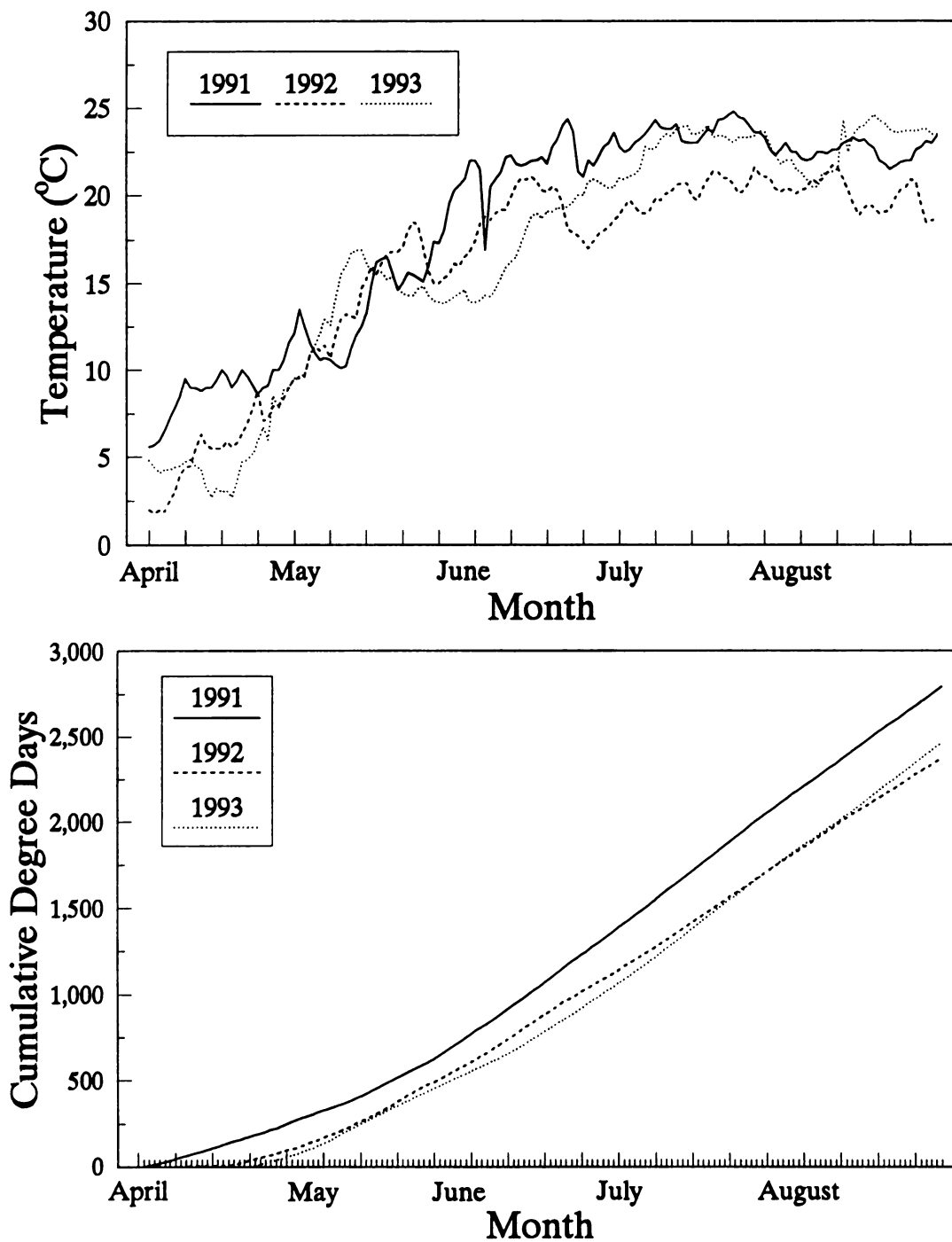


Figure 10. Water temperature and cumulative degree days above 6°C calculated from water temperature collected at the intake station of the Bay Metropolitan Water Treatment Plant near Bay City, MI.

No change in wind direction was evident in data collected at the BMWTP from 1991 to 1993 (Figure 11). Wind was from either quadrant 1 (NNE to E) or 3 (SSW to W) approximately 65% of the days in each growing season. Wind from quadrant 1 blows into the inner bay, and wind from quadrant 3 blows out of the inner bay, both of which follow the long fetch of the bay.

Macrophyte and Species Abundance. Macrophyte relative abundance in June data was divided by site and tested with separate CMH tests, because both negative and positive patterns of association were present among the sites. Data collected at Pinconning in June also were tested separately with CMH tests by zone, because both negative and positive patterns of association were present among the zones.

In June, macrophyte RA decreased from 1992 to 1993 in all zones at Au Gres, zone 2 at Pinconning, and Sand Point (Table 18; Figure 12). Macrophyte RA increased from June 1992 to June 1993 in all zones at Quanicassee and Bay City, and Pinconning zone 1. RA at Pinconning zone 3 did not change (Table 18).

In July, macrophyte relative abundance increased from 1991-1993 at all sites (Table 18; Figure 13). In all zones, except zone 3 at Au Gres, the change in macrophyte RA from 1991 to 1993 was positive (Table 19; Figure 13).

The net change in macrophyte RA in July was least in zone 3 at every site (Table 19). At Au Gres and Pinconning

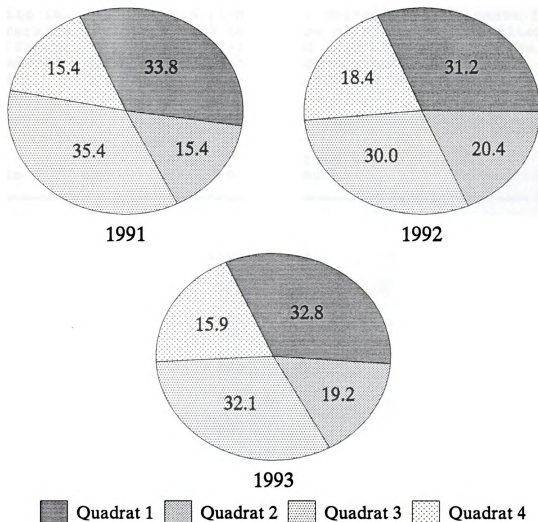


Figure 11. The proportion of days with the wind out of quadrant 1, 2, 3, or 4 at BMWTP, Bay City, MI, April to August 1991-1993. Wind blowing out of quadrant 1 was from NNE to E and blew into Saginaw Bay. Wind blowing out of quadrant 2 was from ESE to S and blew across Saginaw Bay. Wind blowing out of quadrant 3 was from SSW to W and blew out of Saginaw Bay. Wind blowing out of quadrant 4 was from WNW to N and blew across Saginaw Bay. The frequency of days with the wind blowing out one of the four quadrants was not different among 1991, 1992, and 1993 (Pearson χ^2 Contingency Analysis, $N=917$, d.f.=6, $\chi^2=4.923$, $P=0.554$).

Table 18. Cochran-Mantel-Haenszel chi-square (X^2) tests for general association used to compare plant RA at five sites in Saginaw Bay, June 1992-1993 and July 1991-1993. Tests compared presence and absence frequency patterns between years. Probabilities marked with symbols were considered significant.

Site	Net change in relative abundance	N	Degrees of freedom	X^2	Probability
<i>June</i>					
All sites	-0.06	1800	1	4.706	$P=0.03^\dagger$
Au Gres	-0.24	400	1	27.595	$P<0.0001^\dagger$
Pinconning	0.0	500	1	0.0	$P=1.0$
zone 1	0.40	100	1	17.647	$P<0.0001^\dagger$
zone 2	-0.13	200	1	9.779	$P=0.002^\dagger$
zone 3	-0.07	200	1	0.992	$P=0.319$
Bay City	0.22	200	1	3.805	$P=0.051^\dagger$
Quanicassee	0.06	400	1	3.145	$P=0.076^\dagger$
Sand Point	-0.03	300	1	5.594	$P=0.018^\dagger$
<i>July</i>					
All sites	0.31	2685	2	204.89	$P<0.0001^\dagger$

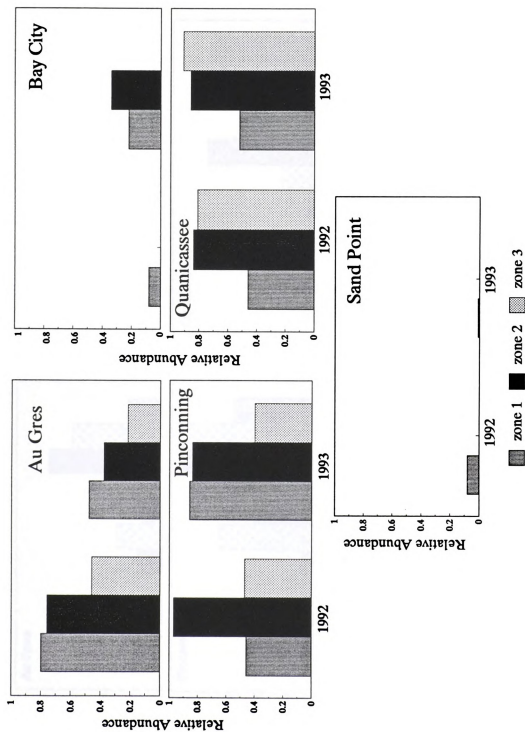


Figure 12. Macrophyte relative abundance at five sites in Saginaw Bay collected in June 1992-1993.

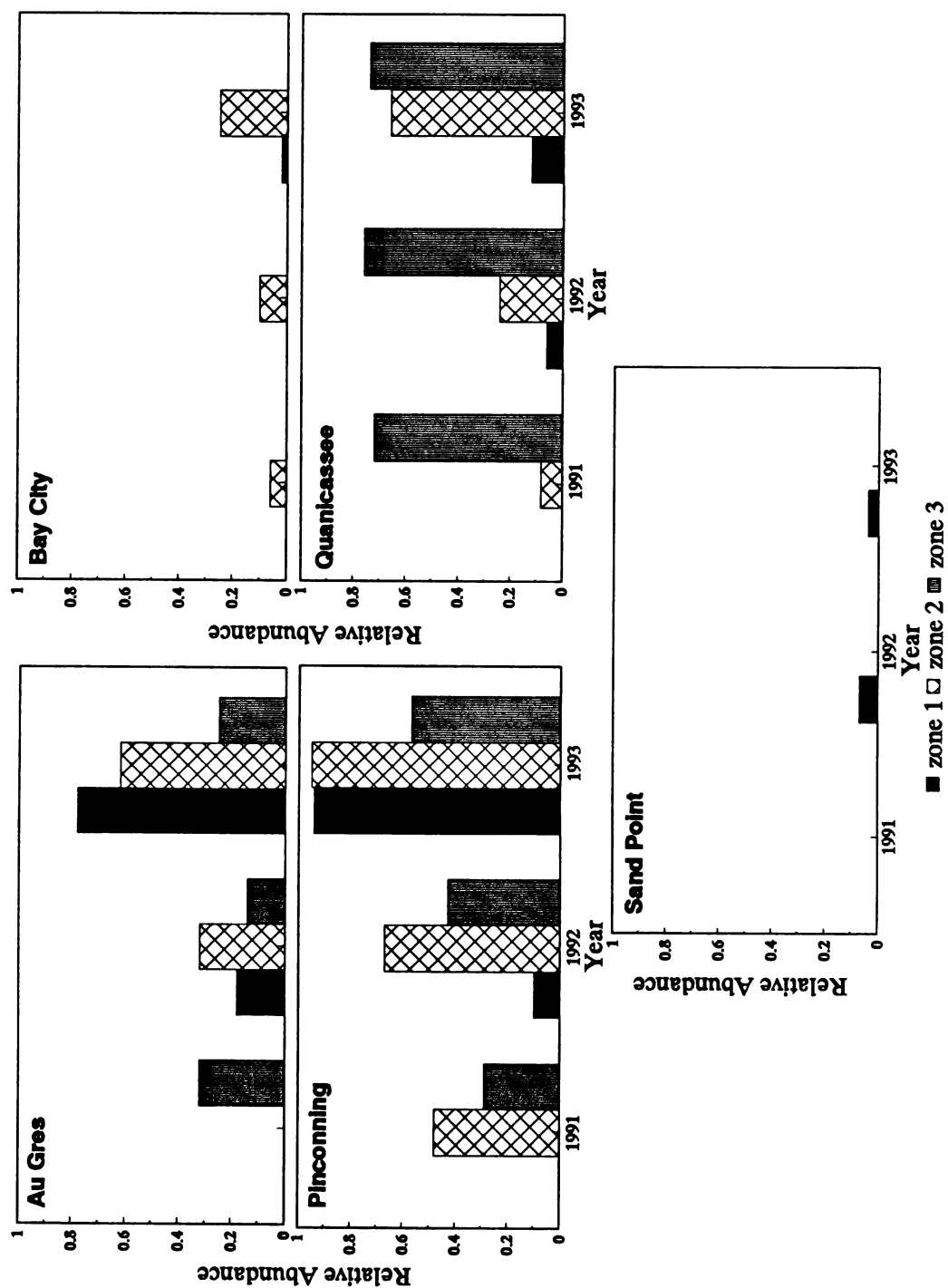


Figure 13. Macrophyte relative abundance at five sites in Saginaw Bay collected in July 1991-1993.

Table 19. Changes in macrophyte RA, the most abundant species, and species RA along five transects in Saginaw Bay, 1991-1993.

Zone	Month	Year	Net change in relative abundance	Most abundant Species	Species relative abundance
<i>Au Gres</i>					
1	June	1992		Filamentous algae	0.64
		1993	-0.32	Charophytes	0.42
	July	1991			0
		1992		Charophytes	0.18
		1993		Filamentous algae	0.70
			0.78		
2	June	1992		Filamentous algae	0.68
		1993	-0.38	Charophytes	0.18
	July	1991			0
		1992		Filamentous algae	0.18
		1993		Filamentous algae	0.50
			0.68		
3	June	1992		Filamentous algae	0.43
		1993	-0.24	Charophytes	0.11
	July	1991		<i>Potamogeton</i> <i>pectinatus</i>	0.19
		1992		<i>Potamogeton</i> <i>alpinus</i>	0.08
		1993	-0.07	Charophytes	0.13

Table 19 (cont'd).

Zone	Month	Year	Net change in relative abundance	Most abundant Species	Species relative abundance
<i>Pinconning</i>					
1	June	1992		Charophytes	0.40
		1993		Filamentous	
			0.40	algae	0.68
	July	1991			0
		1992		Charophytes	0.10
		1993		Filamentous	
			0.94	algae	0.94
2	June	1992		Filamentous	
				algae	0.66
		1993	-0.13	Charophytes	0.80
	July	1991		Charophytes	0.44
		1992		Charophytes	0.63
		1993	0.50	Charophytes	0.91
3	June	1992		Filamentous	
				algae	0.43
		1993	-0.07	Charophytes	0.19
	July	1991		Filamentous	
				algae	0.15
		1992		Charophytes	0.17
		1993	0.28	Charophytes	0.45
<i>Bay City</i>					
1	June	1992		Filamentous	
				algae	0.04
		1993		Filamentous	
			0.14	algae	0.22
	July	1991			0
		1992			0
		1993	0.02	Charophytes	0.02
2	June	1993		Filamentous	
			NA	algae	0.27
	July	1991		<i>Potamogeton</i>	
				<i>pectinatus</i>	0.12
		1992		<i>Potamogeton</i>	
				<i>pectinatus</i>	0.10
		1993		<i>Potamogeton</i>	
			0.21	<i>pectinatus</i>	0.25

Table 19 (cont'd).

Zone	Month	Year	Net change in relative abundance	Most abundant Species	Species relative abundance
<i>Quanicassee</i>					
1	June	1992		Filamentous algae	0.42
		1993		Filamentous algae	0.52
	July	1991	0.06		0
		1992		<i>Potamogeton</i> <i>pectinatus</i>	0.06
		1993		Filamentous algae	0.12
2	June	1992	0.12	Filamentous algae	0.64
		1993		Filamentous algae	0.76
	July	1991	0.02	<i>Potamogeton</i> <i>illinoensis</i>	0.04
				<i>Vallisneria</i> <i>americana</i>	0.04
		1992		<i>Potamogeton</i> <i>pectinatus</i>	0.20
		1993		Filamentous algae	0.62
3	June	1992	0.58	Charophytes	0.31
		1993		Filamentous algae	0.82
	July	1991	0.10	<i>Utricularia</i> <i>vulgaris</i>	0.28
		1992		<i>Potamogeton</i> <i>illinoensis</i>	0.17
		1993	0.02	<i>Najas spp.</i>	0.25
<i>Sand Point</i>					
1	June	1992		Filamentous algae	0.04
		1993		Filamentous algae	0.01
	July	1991	-0.03		0
		1992		<i>Potamogeton</i> <i>pectinatus</i>	0.02
		1993	0.02	Filamentous algae	0.01

the increase in RA was greater in zone 1 than zone 2. At Quanicassee and Bay City, zone 2 increased more than zone 1. With the exception of Quanicassee zone 2, the six largest increases in RA were in zones at sites in northwestern littoral regions, i.e. Au Gres and Pinconning. Of the remaining seven increases in RA, six were in zones at sites in the southern or eastern littoral regions, i.e. Quanicassee, Bay City and Sand Point (Table 19).

The only species to increase in RA between June 1992 and June 1993 was the charophyte, *Nitella flexilis* (Table 20; Figure 14). All other taxa did not change.

Between July 1991, 1992, and 1993, *V. americana*, *Najas* spp., *C. globularis*, *N. flexilis*, and filamentous algae increased in RA (Table 20; Figure 14). *P. pectinatus* and *E. canadensis* did not change. *P. richardsonii* and *P. illinoensis* decreased in samples.

Filamentous algae was ubiquitous in Saginaw Bay. It was the most abundant taxon in the most zones, and at the most sites, each month and each year sampled (Table 19). This group reached the highest RA in June in 1992 and 1993 (Figure 14). In 1992, the RA of filamentous algae decreased from 0.36 in June to 0.04 in July. In 1993, however, RA remained high (June 0.36; July 0.35).

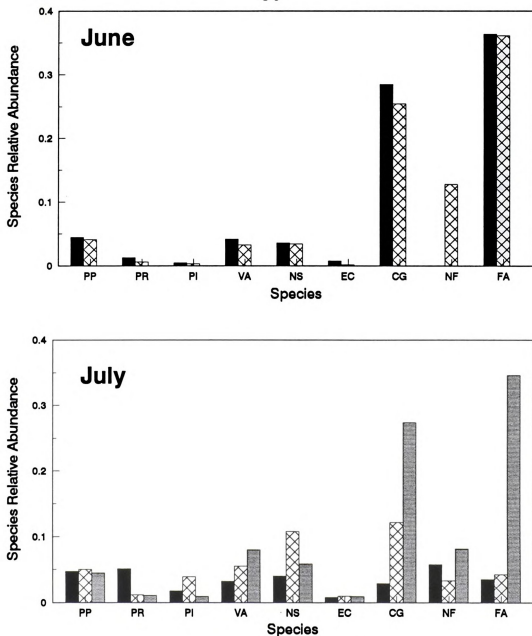
Filamentous algae had the greatest RA more often in zones 1 and 2 than within the emergent wetlands (zone 3; Table 19). The small increases in RA between June 1992-1993

Table 20. Pearson chi-square (X^2) tests for association used to compare plant species RA in Saginaw Bay, June 1992-1993 and July 1991-1993. Tests compared presence and absence frequency patterns between years. Probabilities marked with symbols were considered significant.

Species	Net change in relative abundance	N	Degrees of freedom	X^2	Probability
<i>June</i>					
Filamentous algae	0.0	1800	1	0.012	P=0.913
<i>Nitella</i> <i>flexilis</i> (L.) Ag.	0.13	1300	1	85.511	P<0.0001 [†]
<i>Chara</i> <i>globularis</i> Thuill.	-0.03	1300	1	1.563	P=0.211
<i>Potamogeton</i> <i>pectinatus</i> (L.)	0.0	1550	1	0.091	P=0.763
<i>Potamogeton</i> <i>richardsonii</i> (Benn.) Rydb.	-0.01	1300	1	1.345	P=0.246
<i>Potamogeton</i> <i>illinoensis</i> Morong	0.0	1300	1	0.201	P=0.654
<i>Vallisneria</i> <i>americana</i> Michx.	-0.01	1300	1	0.778	P=0.378
<i>Najas</i> spp.	0.0	1300	1	0.023	P=0.879
<i>Elodea</i> <i>canadensis</i> Michx.	-0.01	1300	1	2.677	P=0.102

Table 20 (cont'd).

Species	Net change in relative abundance	N	Degrees of freedom	X ²	Probability
<i>July</i>					
Filamentous algae	0.33	2685	2	506.7	P<0.0001 [†]
<i>Nitella</i> <i>flexilis</i> (L.) Ag.	0.02	1785	2	11.943	P=0.003 [†]
<i>Chara</i> <i>globularis</i> Thuill.	0.24	1785	2	157.077	P<0.0001 [†]
<i>Potamogeton</i> <i>pectinatus</i> (L.)	0.0	2265	2	0.198	P=0.906
<i>Potamogeton</i> <i>richardsonii</i> (Benn.) Rydb.	-0.04	1785	2	26.447	P<0.0001 [†]
<i>Potamogeton</i> <i>illinoensis</i> Morong	-0.01	1785	2	13.122	P=0.001 [†]
<i>Vallisneria</i> <i>americana</i> Michx.	0.05	1785	2	13.899	P=0.001 [†]
<i>Najas</i> spp.	0.04	1785	2	21.905	P<0.0001 [†]
<i>Elodea</i> <i>canadensis</i> Michx.	0.0	1785	2	0.111	P=0.946



■ 1991 ▨ 1992 ▩ 1993

Figure 14. Relative abundance (RA) of the most abundant species in Saginaw Bay collected in June 1992 and 1993, and July 1991-1993. Species RA is equal to the number of samples with the designated species present divided by the total number of samples taken. Zone and site RAs were grouped over each zone and site of the primary transects. PP=*Potamogeton pectinatus* (L.); PR=*Potamogeton richardsonii* (Benn.) Rydb.; PI=*Potamogeton illinoensis* Morong; VA=*Vallisneria americana* Michx.; NS=*Najas* sp.; EC=*Elodea canadensis* Michx.; CG=*Chara globularis* Thuill.; NF=*Nitella flexilis* (L.) Ag.; FA=filamentous algae.

in all zones at Quanicassee and Bay City were due almost exclusively to increases in filamentous algae. Decreases between June 1992-1993 in all zones at Au Gres, and Pinconning zone 2 were due primarily to reductions in filamentous algae RA. In July, the small increase between 1991 and 1993 in macrophyte RA in the deepest two zones at Quanicassee and Au Gres were due, in part, to the increased RA of filamentous algae.

Charophytes, primarily *N. flexilis* and *C. globularis*, were the second most abundant macrophyte taxon in Saginaw Bay (Figure 14). As was true with the filamentous algae, the charophytes were more abundant during June 1992 than July 1992. In 1993, charophyte RA were similar in June and July (Figure 14).

Charophytes were common throughout Saginaw Bay, but were the most abundant taxa most often in zones 1 and 2 at Pinconning (Table 19). The large increases in RA between years in zone 1 during June and July in all zones at Pinconning were due to increases in both charophytes and filamentous algae. The increases in RA between years at Au Gres in July were also due to increases in charophytes and filamentous algae.

The remaining macrophytes analyzed (Figure 14) had greater RA values in July than June during 1992 and 1993. All of these taxa were vascular hydrophytes.

P. pectinatus was common in the deepest zones, 1 and 2, at Quanicassee in July 1992. It was the most abundant taxon only in zone 2 in July 1992 (Table 19). It was rare in June 1992, and in June and July in 1991 and 1993. Zone 2 at Bay City consisted of *P. pectinatus* almost exclusively all three summers during July. This was the only site where *P. pectinatus* was solely responsible for an increase in macrophyte RA.

V. americana was common in the deepest zones, 1 and 2, at Au Gres, Quanicassee, and Pinconning. It contributed to increases in RA at all three sites. However, it was only dominant at Quanicassee in July 1991 (Table 19).

Najas spp. were common in all emergent wetlands, and was the most abundant taxon in July 1993 in zone 3 at Quanicassee (Table 19). These species contributed to increases between July 1991 and 1993 in the emergent wetlands at Quanicassee and Pinconning.

P. illinoensis and *P. richardsonii* were most common during July in the emergent wetlands also, but declined from 1991 to 1993 (Table 20). *E. canadensis* never had high abundances anywhere (Table 19), but was most common during July in the emergent wetlands.

A complete list of species occurrence by month, year, site, and zone is included in Appendix B, and a list of accession numbers for voucher specimens located at the Beal-

Darlington Herbarium, Department of Botany and Plant Pathology, is included in Appendix C.

Maximum Depth of Colonization and Area of Macrophyte Coverage. The proportion of successful rake samples (y) was comparable to the proportion of successful grab samples (x) by:

$$y=0.19+1.5x \quad (3)$$

The maximum depth of 0.20 and 0.40 successful rake samples corresponded with the depths at which <0.01 and 0.14 of grab samples were successful, respectively (Figure 15). Therefore, the depths which I recorded during rake sampling are referred to henceforth as the maximum depth of 0.14 RA ($ZMAX_{14}$) and the maximum depth of <0.01 RA ($ZMAX_0$).

$ZMAX_{14}$ and $ZMAX_0$ increased in Saginaw Bay from 1992 to 1993 (Figure 16, 17, and 18; Paired comparison; $t=3.395$; d.f.=60; $P=0.007$). The mean increase of $ZMAX_{14}$ and $ZMAX_0$ were 38 cm and 32 cm, respectively. The area of macrophyte coverage estimated by both maximum depth measures increased from 1992 and 1993, as well (13.4 km² and 12.8 km², respectively). This was an increase of approximately 15% and 13%, respectively.

However, the increases in maximum depths could be grouped in several regions in Saginaw Bay (Figure 16, 17, and 18). $ZMAX_{14}$ and $ZMAX_0$ increased the most at transects 0-13 on the northwestern shoreline (Figure 16). $ZMAX_{14}$ increased by a mean of 79 cm, and $ZMAX_0$ increased by a mean

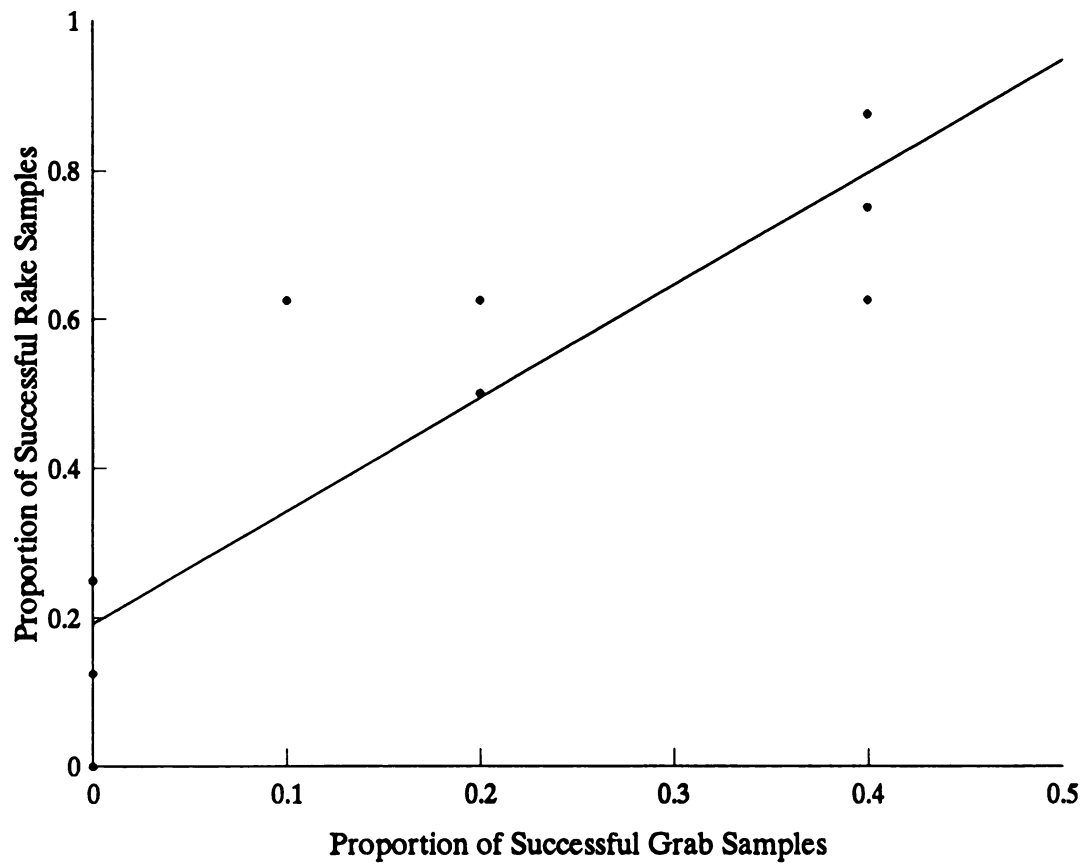


Figure 15. The proportion of successful double-headed rake samples (y) to the proportion of successful petite Ponar or Ekman grab samples (x) ($y=0.19+1.5x$; $r^2=0.77$; $N=12$; $F=33.69$; $df=1,10$; $P<0.0001$).

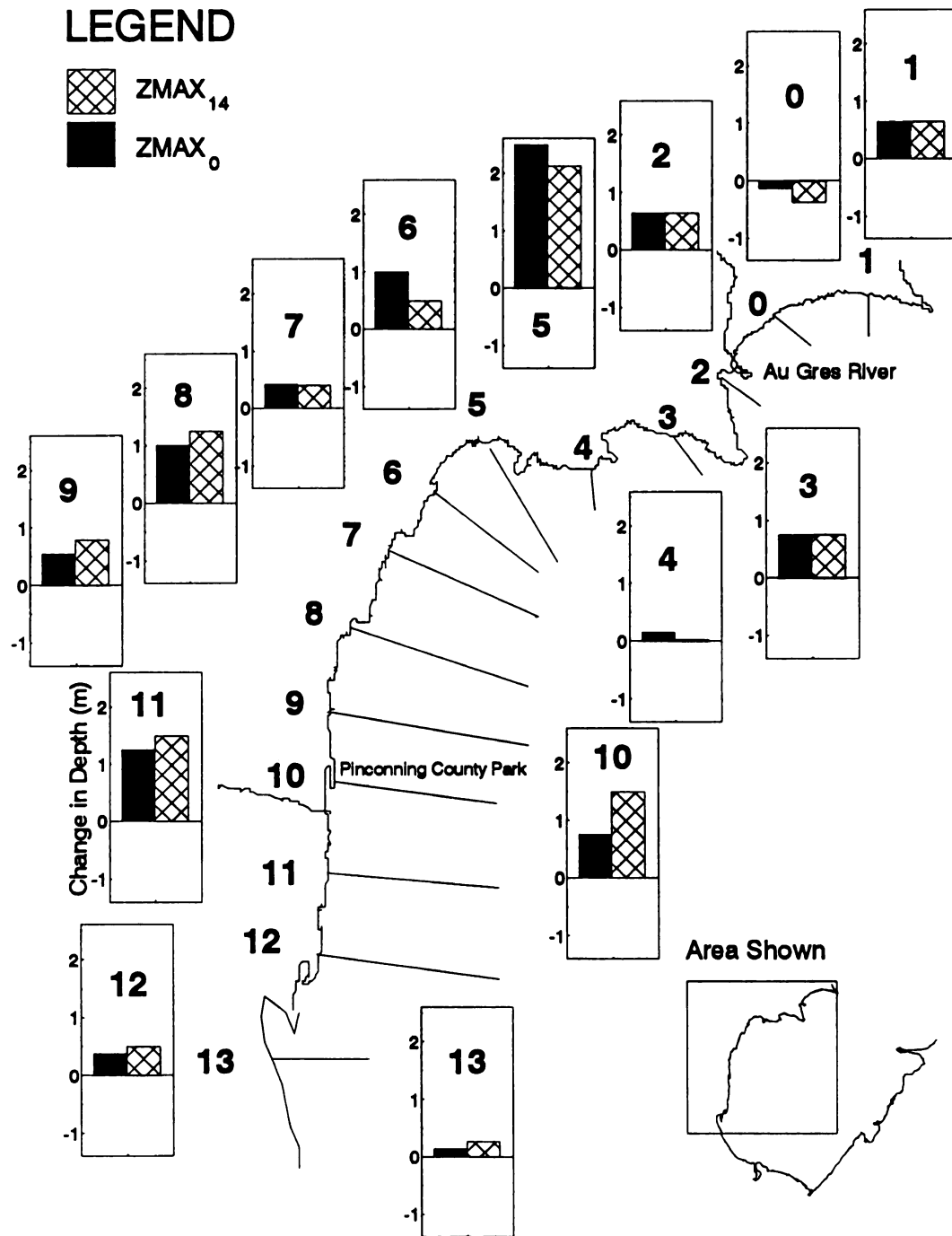


Figure 16. The magnitude of change between 1992-1993 of the maximum depth of <0.01 macrophyte RA ($ZMAX_0$), and 0.14 macrophyte RA ($ZMAX_{14}$) at secondary sites 0-13 in Saginaw Bay. Bars above zero indicate an increase in maximum depth, and bars below zero indicate a decrease in maximum depth.

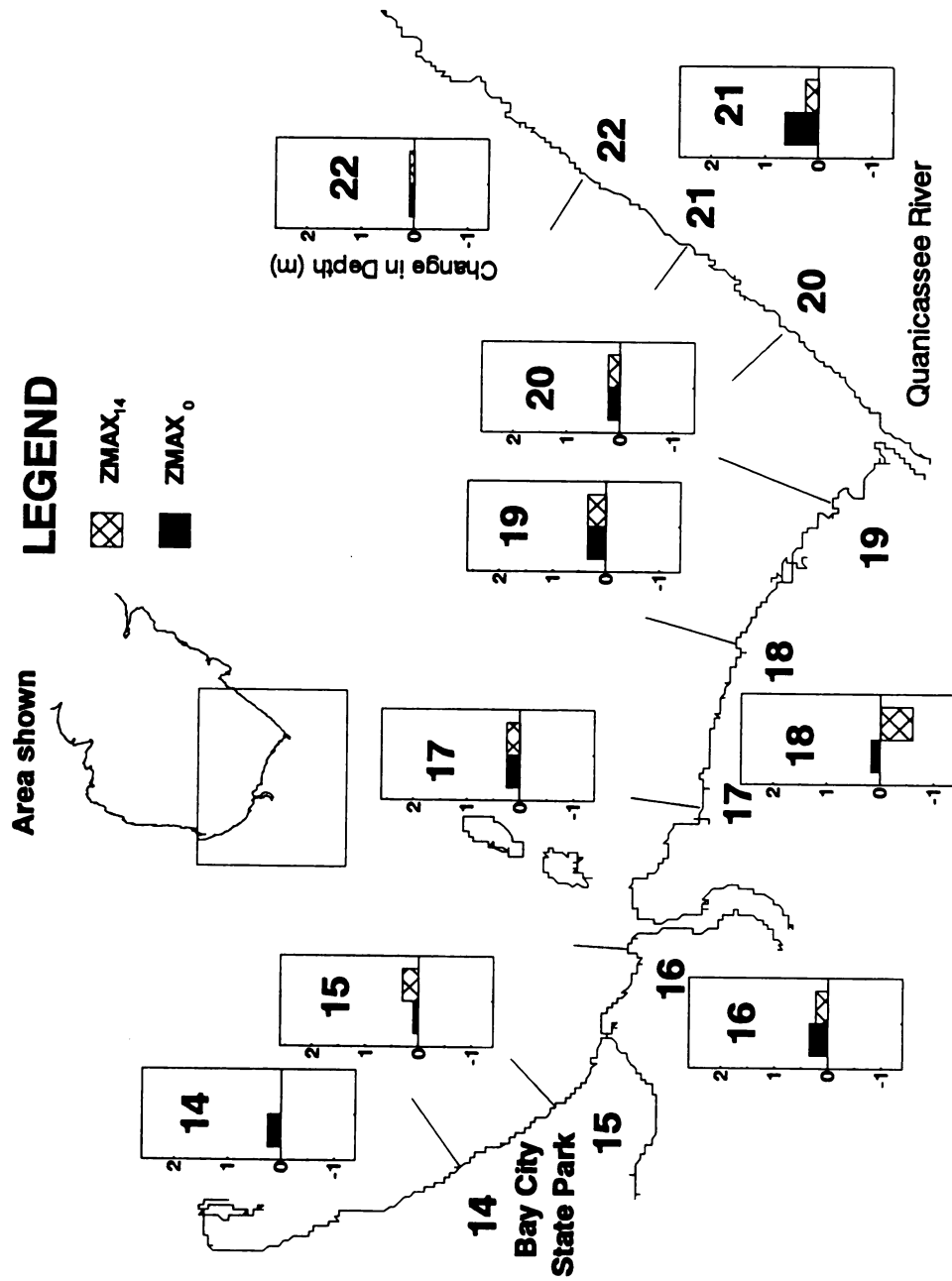


Figure 17. The magnitude of change between 1992-1993 of the maximum depth of <0.01 macrophyte RA ($ZMAX_0$), and 0.14 macrophyte RA ($ZMAX_{14}$) at secondary sites 14-22 in Saginaw Bay. Bars above zero indicate an increase in maximum depth, and bars below zero indicate a decrease in maximum depth.

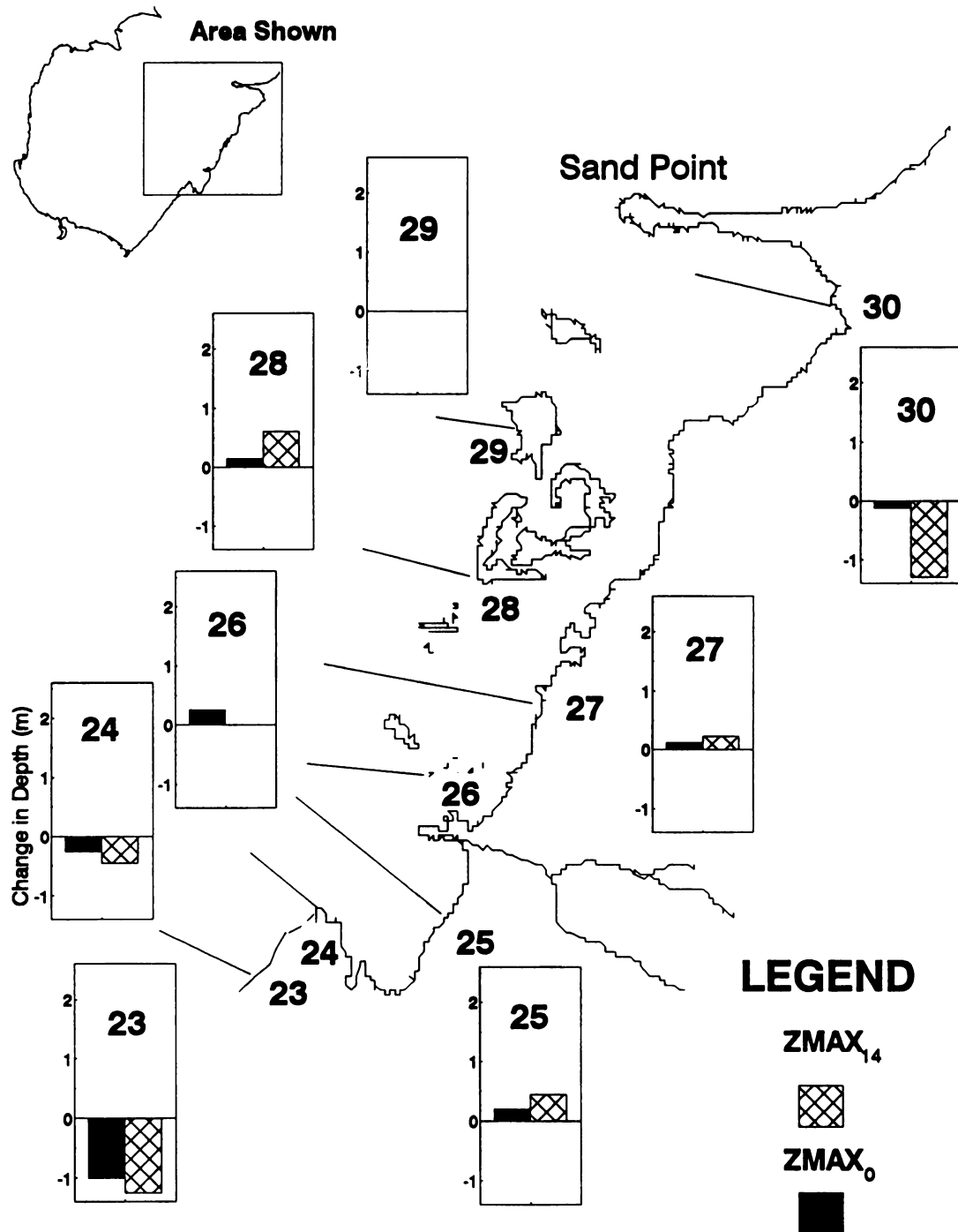


Figure 18. The magnitude of change between 1992-1993 of the maximum depth of <0.01 macrophyte RA ($ZMAX_0$), and 0.14 macrophyte RA ($ZMAX_{14}$) at secondary sites 23-30 in Saginaw Bay. Bars above zero indicate an increase in maximum depth, and bars below zero indicate a decrease in maximum depth.

of 72 cm. At transects 20-22, along the southeastern shoreline between the Quanicassee River and Fish Point, $ZMAX_{14}$ and $ZMAX_0$ increased by a mean of 19 cm and 25 cm, respectively (Figure 17). At transects 25-29, which includes the Sebewaing River area and the island complex along the eastern shoreline, $ZMAX_{14}$ and $ZMAX_0$ increased by a mean of 26 cm and 15 cm, respectively (Figure 18). Along the southwestern shoreline between the Tobico Marsh area and the Quanicassee River, transects 14-19, $ZMAX_{14}$ and $ZMAX_0$ increased by a mean of 9 cm and 25 cm, respectively (Figure 17). At the remaining three transects, 23 and 24 at Fish Point, and 30 in Wildfowl Bay, $ZMAX_{14}$ and $ZMAX_0$ decreased by a mean of 100 cm and 46 cm, respectively (Figure 18).

At transects 0-13, charophytes were the taxa found most often in rake samples taken at the deepest colonization. *Myriophyllum spicatum* appeared in rake samples more often than any other taxa at sites 2, 4, and 5 in 1992. At these sites, and other sites where *M. spicatum* was common at the maximum depths, e.g. sites 19, 25, and 30, *M. spicatum* disappeared in 1993. At each of these sites except site 30, *V. americana*, *P. pectinatus*, or charophytes replaced *M. spicatum*. Site 30 was not re-colonized by any taxa at the deepest colonization. Rake samples at transects 14-19 contained *P. pectinatus* almost exclusively at the maximum depths. Increases in $ZMAX_{14}$ and $ZMAX_0$ at transects 20-22 were due to increases in the depth of colonization of

emergent species, primarily of the genus *Scirpus*. Very few submersed species were present at these sites. At the Fish Point transects, 23 and 24, and all the transects in the island complex along the eastern shoreline, charophytes were the most common taxa found in rake samples at the maximum depths.

DISCUSSION

Zebra Mussel Densities. Zebra mussels were first discovered in Saginaw Bay in 1990. The staff of the Great Lakes Environmental Research Laboratory, NOAA, have monitored zebra mussel densities since 1991 (Nalepa in press; Appendix D). The first year of this study, 1991, was the first year zebra mussel densities were high in Saginaw Bay. However, they were not present in high densities until late summer 1991, after the majority of the growing season had passed (Nalepa in press). Although zebra mussels persisted throughout the study period, densities were highly variable and demonstrated no consistent pattern across years and sampling sites from 1991-1993. It cannot be concluded whether zebra mussels were the primary agent of water clarity change in Saginaw Bay. However, none of the physical parameters monitored in this study can explain the changes observed. A discussion of the zebra mussel density data is included in Appendix D.

Although it has been shown that zebra mussels can attach to macrophytes and directly inhibit their growth by weighing them down (e.g. Buchan and Padilla 1994), mussels were rarely observed on macrophytes in Saginaw Bay during

this study. Occasionally small mussels (<10 mm long) were discovered on mats of charophytes, but their densities were very low. Zebra mussels were never observed on vascular hydrophytes in Saginaw Bay during this study.

Light Environment. Although zebra mussel densities varied greatly, turbidity, k , and Secchi depth changed from 1991 to 1993 at the northern group of sites, i.e. Au Gres, Pinconning, and Sand Point. This result was consistent with the prediction that water clarity would increase from 1991 to 1993. Significant increases in water clarity, i.e. decreased turbidity, decreased k , and increased Secchi depth, occurred at no less than two of the sites in the northern group from 1991-1993 (Tables 3, 9, and 13). Wherever a year effect was present, with the exception of Secchi depth data collected at Sand Point, water clarity was always greater in 1992 and/or 1993 than 1991 (Tables 5, 11, and 15). Moreover, the frequency of Secchi depth samples that were equal to the water depth increased bay wide from 1991 to 1992 and 1993.

No change in water clarity was evident from 1991 through 1993 at the southern two sites, i.e. Bay City and Quanicassee (Tables 3, 9, and 13). Two factors probably contributed to this result. First, water clarity was usually greater at the northern sites than the southern sites. Greater concentrations of suspended solids and solutes may have overwhelmed the agent of water clarity

change, e.g. the zebra mussels' filtration ability. Second, greater variability in water clarity variables at the southern sites probably reduced the power of statistical tests to detect subtle changes.

A significant site effect was evident in turbidity data in 11 of the 13 months that it was sampled (Table 6). The linear comparisons which best explained these site effects tested the northern sites against the southern sites. In 10 of the 13 months (77%) sampled the southern sites were more turbid than the northern sites (Table 7). The prevalence of this pattern of turbidity in Saginaw Bay was consistent with known current and suspended solid patterns in Saginaw Bay.

Currents in Saginaw Bay are episodic and driven by weather patterns (Johnson 1958; Ayers 1959; Beeton et al. 1967). Weather systems which produce northerly, northeasterly, or northwesterly winds cause water to move into the bay past Point Lookout and along the northwestern side of the bay until it reaches the southeastern shoreline near the Saginaw River. Water moves in a counterclockwise direction and out of the bay along the southeastern side of the bay past Sand Point driven partially by currents from the Saginaw River (Johnson 1958; Ayers 1959; Beeton et al. 1967).

When currents move in this manner, warmer water with greater solute content is concentrated in the shallow regions, i.e. ≤ 4 m depth, along the southern shoreline

(Beeton et al. 1967; Robbins 1986). Schelske and Roth (1973) and Beeton et al. (1967) have reported that phosphorus concentration, temperature, and productivity were greater in the southern littoral regions than in the northern littoral regions. The region with the warmest temperatures during the growing season and the highest solute concentrations is an eddy region in the southern most corner of Saginaw Bay near the Quanicassee River (Beeton et al. 1967; Robbins 1986).

However, current patterns cannot completely explain the pattern of turbidity we observed in Saginaw Bay. Wind direction data collected by BMWTP demonstrated that during the summers of 1991-1993 wind direction was out of the quadrants which include winds from the northeast, northwest, or north a combined 49.2% in 1991, 51.6% in 1992, and 52.0% of the days in 1993 (Figure 11). Winds were out of the remaining two quadrants a combined 50.8% in 1991, 48.4% in 1992, and 48.0% of the days in 1993. This pattern of wind would have caused the counterclockwise current pattern and the subsequent increase in turbidity at Bay City and Quanicassee to occur about 50% of the time, and inconsistent water movement about 50% of the time.

Surface water inputs, and a long fetch probably combined with the counterclockwise current pattern to increase the occurrence of high turbidity in the southern littoral regions from 50% to 77%. Beeton et al. (1967) and

the International Joint Commission (IJC 1979) have reported that >92% of the surface water input into Saginaw Bay comes from the Saginaw and Kawkawlin Rivers. Suspended solid and solute loads entering the bay from these sources may have been major contributors to the lower water clarity along the southern shoreline.

The force of waves acting on sediments is related to fetch, wind speed, and duration (Gross 1987). When counterclockwise current patterns were not present, the higher turbidity in the southern regions may have been maintained by strong winds and large waves. The force of the waves and their ability to suspend sediments is potentially greater along the southern shoreline. The waves with the largest fetch in Saginaw Bay would originate in the outer bay and Lake Huron from winds blowing out of quadrant 1 (Figure 11), move in a southwesterly direction, and break along the southern shorelines (Figure 2).

In the shallow near-shore regions of Saginaw Bay, the importance of wind and waves in controlling water clarity was evident. A significant zone effect in the turbidity data, at all sites with multiple zones, and at the southern sites in k data suggested that the sheer force at the sediment surface increased as water depth decreased (Tables 3, 8, 9, and 12). Turbidity at Au Gres, Pinconning, and Bay City, and k at Bay City increased in zones closer to the shore (Tables 8 and 12).

The failure of multiple comparisons to detect higher turbidity in zones closer to the shoreline at Quanicassee may have been caused by low turbidity occurring periodically in July and August within the dense emergent wetland (pers. observ.). Emergent vegetation can buffer the forces of wind and waves, reduce the turbulence and water movement in the wetland, and allow particulates to settle (Wetzel 1983). Wetzel (1983) and Hutchinson (1975) explained how flexible, elongated stem cells in the genus *Scirpus*, the predominant emergent species at Quanicassee, can absorb the energy of wind and waves, and thereby facilitate the settling of suspended solids.

These factors probably combined to decrease water clarity and decrease the ability of any agent of water clarity change to affect change in the light environment of the southern littoral regions. For example, phytoplankton productivity may have exceeded the capacity of the zebra mussels to reduce phytoplankton biomass in the southern littoral regions, or the rates of particle input and suspension in the southern littoral regions may have masked significant reductions in phytoplankton biomass.

Greater variability in water clarity also may have reduced the power of statistical tests to detect changes in water clarity in the southern littoral regions. The variances in turbidity and k at the southern sites were greater than at the northern sites (Tables 4 and 10).

Turbidity and k were about twice as variable at Quanicassee as at any other site (Tables 4 and 10). Apparently, the higher suspended solid and solute loads along the southern shoreline of the bay associated with the counterclockwise currents, greater productivity, surface water inputs, and a long fetch were concentrated and diluted such that a greater range of turbidity and k values were evident in data collected in these regions, particularly at Quanicassee.

Secchi depth variances did not follow the same pattern as turbidity and k variances, however, it was biased by the maximum Secchi depth possible, particularly at Pinconning, and small sample size (Table 14).

Although statistical tests failed to detect increased water clarity over the study period at the southern sites, turbidity data provided some evidence that water clarity did change at these sites as well. The seasonal turbidity pattern was not consistent each year, i.e. a significant year by month interaction was detected (Table 3; Figure 4). Turbidity was relatively high, especially at Quanicassee for five months in 1991, in 1992 turbidity was high for three months, i.e. April, July, and August, and in 1993 turbidity remained high for only one month, i.e. April (Figure 4). This change in the seasonal pattern of turbidity was consistent with the prediction that water clarity would increase from 1991 to 1993. Furthermore, this trend in the

seasonal pattern in turbidity was most evident in turbidity data collected at Quanicassee and Bay City (Figure 4).

Water Depth, Temperature, and Wind. Water depth data collected at the five primary sites (Table 16; Figure 7), and water elevation data collected by NOAA at Essexville (Figure 8) showed that water depth in Saginaw Bay decreased from 1991 to 1992, and increased from 1992 to 1993, when depth was also greater than in 1991.

Batterson et al. (1991) demonstrated that the distribution of emergent macrophytes covaried with changes in water level in Saginaw Bay. They showed that when water depth increased, emergent macrophyte abundance decreased. If changes in water depth were responsible for the changes in the macrophyte community from 1991-1993, then a decrease in macrophyte RA and the maximum depth of colonization would be predicted. The opposite trend was evident in macrophyte abundance and maximum depth of colonization data (Tables 18 and 19; Figures 13, 16, 17, and 18). Therefore, these data suggested that changes in water depth were not responsible for changes in the submersed macrophyte communities of Saginaw Bay. Instead, the macrophyte community expanded despite a rise in water level.

No significant year effect was evident at any site in temperature data (Table 17). However, water temperature data collected at the BMWTP water intake suggested there were small temperature differences between 1991, 1992, and

1993. Colder temperatures were evident in April, 1992 and 1993, and from mid-June-August, 1992, compared to 1991. Although water temperature from mid-June to August 1993 were not consistently lower than 1991, cumulative degree days were greater in 1991 than 1992 or 1993.

Most temperate macrophytes, such as those found in Saginaw Bay, are more productive in warmer temperatures, up to 30°C, as long as no other factor is limiting (e.g. Barko and Smart 1981; Pip 1989; Spencer and Ksander 1991). Temperature increases of 4°C over a 4 week period can significantly increase macrophyte production (Barko and Smart 1981; Spencer and Ksander 1991). If water temperature differences were the primary cause of changes in the aquatic plant communities from 1991 to 1993, the plant response at the ecosystem level would favor the growing season of 1991 over 1992, because temperature tended to be warmer in 1991 (Figure 10). However, if water clarity changes were more important, 1992 and 1993 would have been more productive years than 1991, because water clarity was greater in 1992 and 1993, especially during the early growing season (Table 5; Figures 3 and 4). Macrophyte RA was greater in July 1992 than in July 1991 (Table 18; Figure 13), which suggests that the variable with the greatest influence on macrophyte RA was water clarity, and not temperature.

Moreover, the increases in macrophyte RA continued into the 1993 growing season (Tables 5 and 18; Figures 3, 4, and

13). Cumulative degree days between 1992 and 1993 were similar throughout the respective summers (Figure 10). Between 1992 and 1993, as well, the patterns of macrophyte RA change and temperature do not correspond, but the changes in water clarity and macrophyte RA do.

Wind was important to water movement patterns and water clarity patterns in Saginaw Bay (Beeton et al. 1967). Wind data collected by the staff of BMWTP confirmed that the distribution of wind directions was not significantly different among 1991, 1992, and 1993 (Figure 11). Therefore, changes in water clarity and the macrophyte response could not be attributed to changes in wind and current patterns. The persistence of the northern versus southern site turbidity pattern over all three years suggested that no change occurred during 1991-1993 in wind and current patterns (Table 7).

Macrophyte and Species Abundance. From June 1992 to 1993 macrophyte RA decreased at Au Gres, Sand Point, and Pinconning zone 2, but increased at Bay City, Quanicassee, and Pinconning zone 1 (Table 18; Figure 12). The increases in macrophyte RA at Bay City and Quanicassee suggested that biologically significant increases may have occurred at these sites even though no statistically significant year effects were evident in water clarity data. The decreases in macrophyte RA at Au Gres, Sand Point, and Pinconning zone 2 do not correspond with changes in water clarity. It is

not clear why these changes occurred. However, all changes in the macrophyte RA from June 1992-1993 were primarily a result of changes in abundance of charophytes and/or filamentous algae.

No differences were evident in species RA for any taxa between 1992-1993, except in the relative abundance of *Nitella flexilis* (Table 20; Figure 14). *N. flexilis* was the only taxon that increased in RA enough during the early growing season to be evident in June. However, the increase in macrophyte RA at Pinconning zone 1 was the only increase upon which *N. flexilis* had a major influence (Tables 18 and 20; Figures 12 and 14).

Changes in filamentous algae RA were concordant with changes in macrophyte RA, i.e. they decreased at Au Gres, Sand Point, and Pinconning zone 2, and increased at Bay City, Quanicassee, and Pinconning zone 1 from June 1992-1993. The failure to detect any bay wide change across years in filamentous algae RA was a result of the opposite trends found at different sites. Species RA data were pooled across sites to perform Pearson χ^2 tests for general association across years, and this masked any evidence of year effects. The failure to detect any changes in species RA of the remaining taxa was a result of no significant changes in relative abundance. There were no opposite trends in the data of the remaining taxa.

The relative abundances of filamentous algae and *Chara globularis* were about 6-7 times larger than that of the vascular hydrophytes in June. The charophytes, including *C. globularis* and *N. flexilis*, are often found at the deepest extent of the distribution of plants in aquatic systems, because they are adapted to low light conditions (Hutchinson 1975; Darley 1982), have lower temperature tolerances (Darley 1982), and take up limiting nutrients more efficiently than most vascular hydrophytes (Engel and Nichols 1984). The filamentous algae that were common in Saginaw Bay, such as *Cladophora*, *Spirogyra*, and *Hydrodictyon*, are known to have lower temperature tolerances for photosynthesis, nutrient absorption, and growth than many vascular hydrophytes as well (Weise et al. 1986; Gumbricht 1993). Furthermore, these genera of filamentous algae are known to have faster growth rates early in the growing season when temperature is low than many vascular hydrophytes (Simpson and Eaton 1986).

Although some of the changes in macrophyte RA from June 1992-1993 do not correspond with yearly water clarity changes, the changes in the abundance of filamentous algae from June to July do correspond with changes in water clarity (Figures 4 and 14). Charophyte RA, filamentous algae RA, and water clarity were greater in June than July 1992 and 1993 (Figure 14). Filamentous algae decreased in relative abundance simultaneously with water clarity, i.e.

from June 1992 to July 1992 (Figure 4). We observed large quantities of decaying algae along the shorelines of Saginaw Bay in July 1992. The following year, filamentous algae RA did not change from June to July (Figure 14), and turbidity remained low throughout the summer (Figure 4).

Changes in macrophyte RA among July samples from 1991 through 1993 were consistent with the hypothesis that macrophyte RA would increase in Saginaw Bay, if water clarity increased. Changes in macrophyte RA from July 1991 through 1993, the month with the greatest relative abundance for most of the species, mirrored the interannual changes in water clarity.

All zones at all sites increased in macrophyte RA from July 1991 through 1993, except Au Gres zone 3 (Table 18; Figure 13). In addition, the magnitude of the increases corresponded with water clarity changes. The zones with the largest increases in abundance were zones at sites in the northwestern littoral regions, i.e. Au Gres and Pinconning, where water clarity increased significantly over the study period (Table 19; Figure 13). The zones with the smallest increases were located at sites in the southern littoral regions, i.e. Bay City and Quanicassee, where changes in water clarity were not statistically significant.

Sand Point did not show large increases in macrophyte RA in July even though increases in water clarity were evident. However, a large increase in macrophyte RA was not

expected at this site, because factors other than water clarity appeared to control macrophyte abundance. Sandy, mobile sediments and currents apparently prevented vegetation from colonizing this site abundantly in any year (pers. observ.).

Increases in macrophyte RA not only mirrored changes in water clarity across years and by site, they also followed the pattern of water clarity by zone at Pinconning and Au Gres (Table 19; Figure 13). At these two sites, the magnitude of the increase in macrophyte RA was greater in the deeper zones than the shallow zones. At Bay City and Quanicassee, the maximum depths of colonization did not increase as much as they did at the northern sites (Figures 16, 17, and 18), and relative abundance in zone 1 did not increase as much as in zone 2 (Table 19; Figure 13).

In July 1991, the species RA of each of the taxa analyzed were very similar (Figure 14). By 1993, the charophytes and filamentous algae were the most abundant taxa. The rapid growth rates, high nutrient absorption efficiency, and low light adaptations of these taxa are known to predispose these taxa to opportunistic colonization strategies (Hutchinson 1975; Darley 1982; Wetzel 1983). Engel and Nichols (1984) have suggested that these taxa are evolutionarily equipped to be pioneer species, and they have demonstrated that these taxa can assume this role in other aquatic systems, as they appear to have done in Saginaw Bay.

The zebra mussels may also have enhanced the response of the filamentous algae and charophytes by releasing them from competition for nutrients and light from the smaller palatable planktonic algae. Particles $>200\text{ }\mu\text{m}$ are unpalatable to zebra mussels (Stanczykowska 1977). However, this hypothesis has not been tested.

Only two taxa of vascular hydrophytes increased in abundance over the study period, *Vallisneria americana* and *Najas* spp. (Figure 14). *V. americana* was common in samples collected in deep zones, i.e. zones 1 and 2, at Au Gres, Pinconning, and Quanicassee. This was the only vascular hydrophyte that was common in deep zones where water clarity increases were greatest, especially at the sites in the northern littoral regions. *Potamogeton pectinatus* was common in deep zones at Bay City and Quanicassee, but there was no significant change in the abundance of this species (Figure 14). The difference in the responses of these two species, and the increase in charophyte RA, most common at the northern sites, appear to be related to the differences in water clarity change between sites. The magnitude of the increase in relative abundance of the species abundant in the northern littoral regions was greater than those common at southern littoral sites.

There was some overlap between species, however, as was the case in the distribution of *V. americana* and *P. pectinatus* in the deepest two zones at Quanicassee (Table

19). In this case, the change in the relative abundance of these species from 1991-1993 suggested that the control of abundance of individual species may not have been simply a response to increased water clarity. The responses of these two taxa were probably due to two different sprouting and growth strategies, and the timing of temperature increase and light increase in April and May, as previously explained.

The mixed responses of the taxa most common in the emergent wetlands also indicated that some responses were not related to changes in water clarity. *Najas spp.*, which increased from July 1991 through 1993 (Table 20), were most abundant in the emergent wetlands, i.e. zone 3, at Quanicassee and Pinconning (Figure 14). However, the remaining taxa, *P. richardsonii*, *P. illinoensis*, and *E. canadensis* decreased or did not change (Table 20: Figure 14).

Water clarity increases were least in zone 3, which may have contributed to a mixed response. *E. canadensis* has a narrow range of optimal light intensities to which it can physiologically acclimate compared to most other vascular hydrophytes (Spencer 1986; Wolff and Senger 1991). Although little is known about the range of light intensities that *Najas spp.* acclimate to, they probably are broader than *E. canadensis* (Kirk 1983). Increases in light intensity, to which *Najas spp.* could acclimate, but not *E. canadensis*, may

have been present in 1992 and 1993, especially in the variable light environment at Quanicassee. Therefore, in part, some of the changes in macrophyte RA do correspond with water clarity changes.

However, the mixed responses probably occurred because the submersed macrophytes in the emergent wetlands were not limited by light. *P. richardsonii* and *P. illinoensis*, for example, decreased in relative abundance, a change that did not correspond with water clarity changes (Figure 14). Specific ranges of light to which *P. richardsonii* and *P. illinoensis* can acclimate are not known. However, if the changes that occurred in the emergent wetlands were strictly light related, the changes in the abundance of these taxa, e.g. *Najas spp.*, would be greater than that of *E. canadensis*. This did not occur.

Maximum Depths of Colonization and Area of Macrophyte Coverage. Both maximum depth of colonization parameters were monitored in Saginaw Bay in anticipation that the persistent domain ($ZMAX_{14}$) would have less variability and show larger increases than the transient domain ($ZMAX_0$) of the macrophytes (Rorslett 1987). However, both $ZMAX_{14}$ and $ZMAX_0$ increased significantly in Saginaw Bay from 1992 to 1993 (Figures 16, 17, and 18). Significant increases in the area of macrophyte coverage in Saginaw Bay also occurred.

Although lake elevation increased approximately 30 cm between 1992 and 1993, all increases in maximum depth also

represented a movement of latitude and longitude coordinates further from the shoreline along each transect. The mean increase at transects 0-13, i.e. 79 cm, at least, were significant, because they exceeded 30 cm. Furthermore, the increase in the area of macrophyte coverage was a conservative estimate of increased macrophyte distribution in Saginaw Bay, because a fixed shoreline was used in 1992 and 1993 to determine the area of coverage. An increase of 30 cm in water elevation presumably increased the surface area of Saginaw Bay around the perimeter that was not accounted for in 1993.

Increases in $ZMAX_{14}$ and $ZMAX_0$ were also consistent with changes in water clarity. Both parameters increased more at transects 0-13 located in northern littoral regions than at any other group of transects (Figure 16). Moreover, maximum depth parameters decreased only at 1 of 13 (8%) transects in the northern littoral regions, and at 4 of 17 (24%) transects in the southern and eastern regions.

Biologically significant increases in water clarity in the southern regions were also apparent from these data. At 76% of the southern and eastern transects, both maximum depth parameters increased from 1992 to 1993.

CONCLUSIONS

Water clarity in littoral Saginaw Bay did increase from 1991-1993 (Table 3). These changes were statistically significant in the northern littoral regions of the bay where water clarity was generally high. However, water clarity did not increase from 1991 to 1993 was not true in the southern littoral regions.

Macrophyte abundance, depth of colonization, and area of coverage increased throughout the bay with each successive year of water clarity increase (Table 18; Figures 16, 17, and 18). Changes in these parameters mirrored changes in water clarity across sites, months, and zones.

This suggests that water clarity is important in determining the distribution of macrophytes throughout Saginaw Bay. Increases in macrophyte abundance, depth of colonization, and area of coverage were greatest in the deepest zones of the northwestern littoral regions (Table 19; Figures 16, 17, and 18). However, macrophyte RA did increase in the southern littoral regions despite the lack of detectable changes in water clarity. Water depth, wind direction, and temperature differences do not correspond with the changes in macrophyte distribution as well as the

small, statistically insignificant increases in water clarity in the southern littoral regions. This suggests that small biologically significant changes in water clarity did occur in the southern littoral regions, and that macrophyte distribution was sensitive to small changes in light availability in Saginaw Bay. The most common taxon to be sampled, i.e. filamentous algae, was especially sensitive to changes in water clarity. This taxon was able to respond to monthly changes in water clarity, evident from June 1992 to July 1992 (Figure 14), as well as responding the most from 1991-1993.

Moreover, the taxa responding the most to increased light availability were primarily the opportunistic taxa, i.e. filamentous algae and charophytes. These taxa are adapted to pioneer colonization strategies, and can disperse and respond to changes in their environment quickly.

In contrast, the vascular hydrophytes were not as sensitive to changes in water clarity. The vascular hydrophytes did not increase in abundance as much as filamentous algae and charophytes. Only *Najas spp.* and *V. americana* increased significantly in abundance, but these taxa increased about seven times less than the pioneer taxa.

The responses of the vascular hydrophytes did mirror the changes in water clarity over the study period. Of the vascular hydrophytes which increased in bay wide abundance, the taxon with the greatest response, *V. americana*, was

common in the deep zones of the northern transects. In contrast, *P. pectinatus*, a vascular hydrophyte which was common in the deep zones of the southern transects, did not change in bay wide abundance (Table 19; Figure 14). This suggests that the vascular hydrophytes were sensitive to changes in water clarity, just not as sensitive as the non-vascular taxa.

Changes in macrophyte RA appeared to be related to changes in parameters other than measures of water clarity only in one case. The bay wide response of *P. illinoensis* and *P. richardsonii* suggested that changes in water clarity were not strictly responsible for changes in plant abundance within the emergent wetlands (Figure 14). Macrophyte abundance did increase in the emergent wetlands, as well (Figure 13), but these changes probably were not strictly related to changes in water clarity.

No direct detrimental impacts were observed by zebra mussels, known to attach and weigh down aquatic plants in other aquatic systems, to the macrophytes in Saginaw Bay. Macrophytes may not increase in abundance if zebra mussels show significant attachment. However, this hypothesis has not been tested.

In Saginaw Bay, water clarity, and macrophyte abundance did increase with the establishment of zebra mussels, and it is likely that similar changes can be expected in systems limnologically similar to Saginaw Bay. These findings do

not elucidate, however, the causal relationships between zebra mussels and changes in water clarity or plant abundance, and warrant further study into the mechanisms by which zebra mussels influence productivity in the benthic, pelagic, and littoral regions of the systems they invade. Such information will be vital to managers who wish to mitigate the ecological impacts of zebra mussels.



APPENDIX A

APPENDIX A

Table 21. LORAN C coordinates for primary and secondary transects. Transects lay along a line extended from location 1 to the shoreline through location 2.

Site	Location 1	Location 2
<i>Primary Transects</i>		
Au Gres	44°02.10N 83°39.64W	44°02.22N 83°39.74W
Pinconning	43°50.74N 83°51.52W	43°51.17N 83°53.29W
Bay City	43°39.87N 83°53.61W	43°39.79N 83°53.67W
Quanicassee	43°36.58N 83°39.14W	43°36.58N 83°39.14W
Sand Point	43°53.94N 83°24.25W	43°54.14N 83°24.19W
<i>Secondary Transects</i>		
0	44°02.19N 83°39.70W	44°02.38N 83°39.82W
1	44°03.42N 83°36.88W	44°03.52N 83°36.80W
2	44°01.10N 83°40.74W	44°01.17N 83°40.93W
3	43°58.92N 83°42.08W	43°59.04N 83°42.15W
4	43°58.68N 83°45.74W	43°58.72N 83°45.72W

Table 21 (cont'd).

Site	Location 1	Location 2
<i>Secondary Transects cont'd.</i>		
5	43°57.11N 83°46.83W	43°57.24N 83°47.05W
6	43°56.24N 83°47.78W	43°57.02N 83°47.87W
7	43°55.49N 83°49.35W	43°55.51N 83°49.36W
8	43°53.03N 83°50.02W	43°53.61N 83°52.11W
9	43°51.83N 83°50.68W	43°52.00N 83°51.68W
10	43°50.82N 83°51.68W	43°50.89N 83°52.41W
11	43°49.98N 83°51.74W	43°49.48N 83°52.93W
12	43°47.66N 83°53.97W	43°47.67N 83°54.10W
13	43°44.26N 83°55.03W	43°44.31N 83°55.09W
14	43°42.30N 83°55.48W	43°42.27N 83°55.59W
15	43°39.86N 83°53.55W	43°39.82N 83°53.51W
16	43°38.86N 83°51.94W	43°38.87N 83°52.09W
17	43°38.40N 83°48.48W	43°38.79N 83°48.42W
18	43°38.03N 83°45.17W	43°37.68N 83°45.52W

Table 21 (cont'd).

Site	Location 1	Location 2
<i>Secondary Transects cont'd.</i>		
19	43°36.65N 83°40.68W	43°35.95N 83°41.01W
20	43°36.58N 83°39.14W	43°36.45N 83°38.94W
21	43°38.90N 83°36.05W	43°38.87N 83°35.96W
22	43°40.28N 83°35.04W	43°40.24N 83°34.46W
23	43°42.23N 83°33.06W	43°42.17N 83°33.02W
24	43°43.93N 83°31.59W	43°43.72N 83°31.52W
25	43°44.66N 83°30.83W	43°44.43N 83°29.87W
26	43°45.51N 83°29.92W	43°45.46N 83°29.68W
27	43°46.92N 83°29.27W	43°46.77N 83°28.64W
28	43°48.71N 83°27.95W	43°48.62N 83°27.50W
29	43°51.33N 83°27.37W	43°51.34N 83°27.18W
30	43°53.07N 83°22.33W	43°53.31N 83°20.18W

APPENDIX B

APPENDIX B

Table 22. List of all macrophyte and taxon relative abundance for taxa found at five sites in Saginaw Bay.

Zone	Total Macrophyte Relative Abundance	Plant Taxa	Species Relative Abundance
AU GRES			
July 1991			
1	0		0
2	0		0
3	0.32	<i>Elodea canadensis</i> Michx.	0.01
		<i>Potamogeton pectinatus</i> L.	0.19
		<i>Vallisneria americana</i> Michx.	0.01
PINCONNING			
July 1991			
1	0		0
2	0.48	<i>Nitella flexilis</i> (L.) Ag.	0.44
		<i>Vallisneria americana</i>	0.04
3	0.29	Filamentous algae ¹	0.15
		<i>Myriophyllum spicatum</i> L.	0.03
		<i>Najas flexilis</i> (Willd.) Rostk. & Sch.	0.03
		<i>Nitella flexilis</i>	0.09
		<i>Potamogeton alpinus</i> Balbis	0.04
		<i>Potamogeton illinoensis</i> Morong	0.03
		<i>Potamogeton richardsonii</i> (Benn.) Rydb.	0.07
		<i>Vallisneria americana</i>	0.07
BAY CITY			
July 1991			
1	0		0
2	0.06	<i>Potamogeton pectinatus</i>	0.06

¹Includes several genera of Chlorophyta, e.g. *Cladophora glomerata* L. Kuetzing, *Hydrodictyon* sp., *Oedogonium* sp., *Spirogyra* sp., and *Zygnema* sp.

Table 22 (cont'd).

Zone	Total Macrophyte Relative Abundance	Plant Taxa	Species Relative Abundance
QUANICASSEE			
July 1991			
1	0		0
2	0.08	<i>Vallisneria americana</i>	0.04
		<i>Potamogeton illinoensis</i>	0.04
3	0.72	<i>Alisma plantago-aquatica</i> L.	0.02
		<i>Ceratophyllum demersum</i> L.	0.27
		Filamentous algae	0.23
		Charophytes ²	0.27
		<i>Elodea canadensis</i>	0.05
		<i>Najas flexilis</i>	0.17
		<i>Najas minor</i> All.	0.12
		<i>Potamogeton illinoensis</i>	0.07
		<i>Potamogeton pectinatus</i>	0.03
		<i>Sagittaria</i> sp. ³	0.02
		<i>Utricularia vulgaris</i> L.	0.28
		<i>Vallisneria americana</i>	0.08
SAND POINT			
July 1991			
1	0		0
AU GRES			
October 1991			
1	0.04	<i>Potamogeton illinoensis</i>	0.04
2	0.04	<i>Potamogeton illinoensis</i>	0.04
		<i>Vallisneria americana</i>	0.02
3	0.25	<i>Potamogeton illinoensis</i>	0.13
		<i>Potamogeton pectinatus</i>	0.07
		<i>Vallisneria americana</i>	0.05

²Includes three Characeae genera; *Chara*, *Nitella*, and *Tolypella*.

³Includes *Sagittaria* sp. vegetation which was floating or submersed only.

Table 22 (cont'd).

Zone	Total Macrophyte Relative Abundance	Plant Taxa	Species Relative Abundance
PINCONNING			
October 1991			
1	0.20	<i>Nitella flexilis</i>	0.20
2	0.58	<i>Myriophyllum spicatum</i>	0.06
		<i>Nitella flexilis</i>	0.56
3	0.70	<i>Chara globularis</i> Thuill.	0.40
		Filamentous algae	0.16
		<i>Myriophyllum spicatum</i>	0.25
		<i>Potamogeton illinoensis</i>	0.06
		<i>Potamogeton pectinatus</i>	0.01
		<i>Potamogeton richardsonii</i>	0.07
		<i>Utricularia vulgaris</i>	0.20
QUANICASSEE			
October 1991			
1	0		0
2	0.18	<i>Potamogeton illinoensis</i>	0.04
		<i>Potamogeton richardsonii</i>	0.02
		<i>Vallisneria americana</i>	0.12
3	0.51	<i>Chara globularis</i>	0.28
		<i>Najas flexilis</i>	0.10
		<i>Nymphaea tuberosa</i> Paine	0.05
		<i>Potamogeton illinoensis</i>	0.23
		<i>Potamogeton nodosus</i> Poiret	0.03
		<i>Potamogeton pectinatus</i>	0.11
		<i>Tolypella</i> sp.	0.01
		<i>Utricularia vulgaris</i>	0.01

Table 22 (cont'd).

Zone	Total Macrophyte Relative Abundance	Plant Taxa	Species Relative Abundance
AU GRES			
June 1992			
1	0.80	<i>Chara</i> sp. ⁴	0.30
		Filamentous algae	0.64
		<i>Potamogeton richardsonii</i>	0.06
		<i>Vallisneria americana</i>	0.12
2	0.76	<i>Chara</i> sp.	0.02
		Filamentous algae	0.68
		<i>Potamogeton pectinatus</i>	0.04
		<i>Vallisneria americana</i>	0.02
3	0.46	Filamentous algae	0.43
		<i>Potamogeton alpinus</i>	0.01
		<i>Potamogeton pectinatus</i>	0.02
		<i>Vallisneria americana</i>	0.01
PINCONNING			
June 1992			
1	0.46	<i>Chara</i> sp.	0.40
		Filamentous algae	0.08
2	0.97	<i>Chara</i> sp.	0.58
		Filamentous algae	0.66
		<i>Myriophyllum spicatum</i>	0.04
		<i>Vallisneria americana</i>	0.02
3	0.47	<i>Ceratophyllum demersum</i>	0.01
		<i>Chara</i> sp.	0.36
		Filamentous algae	0.43
		<i>Myriophyllum spicatum</i>	0.16
		<i>Potamogeton illinoensis</i>	0.02
		<i>Potamogeton richardsonii</i>	0.05
		<i>Potamogeton pectinatus</i>	0.01
		<i>Vallisneria americana</i>	0.06
BAY CITY			
June 1992			
1	0.08	Filamentous algae	0.04
		<i>Myriophyllum spicatum</i>	0.02
		<i>Potamogeton pectinatus</i>	0.02
2	NA		

⁴Includes unidentified species of the genus *Chara*, but is primarily *Chara globularis*.

Table 22 (cont'd).

Zone	Total Macrophyte Relative Abundance	Plant Taxa	Species Relative Abundance
QUANICASSEE			
June 1992			
1	0.46	<i>Chara sp.</i>	0.18
		Filamentous algae	0.42
		<i>Potamogeton pectinatus</i>	0.06
2	0.84	<i>Chara sp.</i>	0.30
		Filamentous algae	0.64
		<i>Potamogeton pectinatus</i>	0.10
		<i>Vallisneria americana</i>	0.06
3	0.81	<i>Ceratophyllum demersum</i>	0.03
		<i>Chara sp.</i>	0.31
		Filamentous algae	0.25
		<i>Elodea canadensis</i>	0.05
		<i>Myriophyllum spicatum</i>	0.01
		<i>Najas sp.</i> ⁵	0.23
		<i>Nymphaea tuberosa</i>	0.09
		<i>Potamogeton filiformis</i> Pers.	0.21
		<i>Potamogeton illinoensis</i>	0.01
		<i>Potamogeton pectinatus</i>	0.17
		<i>Utricularia vulgaris</i>	0.14
		<i>Vallisneria americana</i>	0.08
		<i>Zanichellia palustris</i> L.	0.01
SAND POINT			
June 1992			
1	0.08	<i>Ceratophyllum demersum</i>	0.01
		<i>Chara sp.</i>	0.01
		Filamentous algae	0.05
		<i>Potamogeton pectinatus</i>	0.01

⁵Includes *Najas flexilis* and *Najas minor*.

Table 22 (cont'd).

Zone	Total Macrophyte Relative Abundance	Plant Taxa	Species Relative Abundance
AU GRES			
July 1992			
1	0.18	<i>Chara sp.</i>	0.18
		Filamentous algae	0.06
		<i>Vallisneria americana</i>	0.06
2	0.32	<i>Chara sp.</i>	0.08
		Filamentous algae	0.18
		<i>Potamogeton alpinus</i>	0.08
		<i>Potamogeton richardsonii</i>	0.02
		<i>Vallisneria americana</i>	0.14
3	0.14	<i>Chara sp.</i>	0.02
		<i>Potamogeton alpinus</i>	0.08
		<i>Potamogeton pectinatus</i>	0.02
		<i>Potamogeton richardsonii</i>	0.02
		<i>Vallisneria americana</i>	0.02
PINCONNING			
July 1992			
1	0.10	<i>Nitella flexilis</i>	0.10
2	0.67	<i>Chara sp.</i>	0.63
		<i>Myriophyllum spicatum</i>	0.04
3	0.43	<i>Chara sp.</i>	0.17
		Filamentous algae	0.09
		<i>Myriophyllum spicatum</i>	0.15
		<i>Najas sp.</i>	0.08
		<i>Potamogeton alpinus</i>	0.06
		<i>Potamogeton illinoensis</i>	0.03
		<i>Potamogeton pectinatus</i>	0.02
		<i>Potamogeton richardsonii</i>	0.02
		<i>Vallisneria americana</i>	0.07
BAY CITY			
July 1992			
1	0		0
2	0.10	<i>Potamogeton pectinatus</i>	0.10

Table 22 (cont'd).

Zone	Total Macrophyte Relative Abundance	Plant Taxa	Species Relative Abundance
QUANICASSEE			
July 1992			
1	0.06	<i>Potamogeton pectinatus</i>	0.06
2	0.24	<i>Chara</i> sp.	0.02
		Filamentous algae	0.02
		<i>Potamogeton pectinatus</i>	0.20
		<i>Vallisneria americana</i>	0.02
3	0.76	<i>Chara</i> sp.	0.11
		Filamentous algae	0.11
		<i>Elodea canadensis</i>	0.05
		<i>Lemna minor</i> L.	0.12
		<i>Myriophyllum spicatum</i>	0.05
		<i>Najas</i> sp.	0.47
		<i>Nitella flexilis</i>	0.14
		<i>Nymphaea tuberosa</i>	0.08
		<i>Potamogeton alpinus</i>	0.02
		<i>Potamogeton filiformis</i>	0.06
		<i>Potamogeton illinoensis</i>	0.17
		<i>Potamogeton pectinatus</i>	0.06
		<i>Potamogeton richardsonii</i>	0.02
		<i>Sagittaria</i> sp.	0.04
		<i>Utricularia vulgaris</i>	0.02
		<i>Vallisneria americana</i>	0.09
SAND POINT			
July 1992			
1	0.04	<i>Chara</i> sp.	0.01
		<i>Potamogeton pectinatus</i>	0.03
AU GRES			
September 1992			
1	0.28	Filamentous algae	0.06
		<i>Nitella flexilis</i>	0.18
		<i>Potamogeton pectinatus</i>	0.16
		<i>Vallisneria americana</i>	0.20
2	0.14	<i>Chara</i> sp.	0.04
		<i>Nitella flexilis</i>	0.06
		<i>Potamogeton alpinus</i>	0.08
		<i>Vallisneria americana</i>	0.02
3	0.06	<i>Potamogeton pectinatus</i>	0.06

Table 22 (cont'd).

Zone	Total Macrophyte Relative Abundance	Plant Taxa	Species Relative Abundance
PINCONNING			
September 1992			
1	0.42	Filamentous algae	0.06
		<i>Nitella flexilis</i>	0.40
		<i>Vallisneria americana</i>	0.02
2	0.77	<i>Chara</i> sp.	0.61
		Filamentous algae	0.08
		<i>Nitella flexilis</i>	0.39
		<i>Myriophyllum spicatum</i>	0.02
		<i>Potamogeton richardsonii</i>	0.01
3	0.46	<i>Chara</i> sp.	0.06
		Filamentous algae	0.07
		<i>Elodea canadensis</i>	0.02
		<i>Myriophyllum spicatum</i>	0.18
		<i>Najas</i> sp.	0.08
		<i>Nitella flexilis</i>	0.07
		<i>Potamogeton alpinus</i>	0.01
		<i>Potamogeton illinoensis</i>	0.03
		<i>Potamogeton richardsonii</i>	0.02
		<i>Vallisneria americana</i>	0.10
BAY CITY			
September 1992			
1	0		0
2	0.01	<i>Chara</i> sp.	0.01
		<i>Potamogeton pectinatus</i>	0.01

Table 22 (cont'd).

Zone	Total Macrophyte Relative Abundance	Plant Taxa	Species Relative Abundance
QUANICASSEE			
September 1992			
1	0.06	<i>Potamogeton pectinatus</i>	0.06
2	0.16	<i>Potamogeton pectinatus</i>	0.16
3	0.71	<i>Ceratophyllum demersum</i>	0.02
		<i>Chara sp.</i>	0.25
		Filamentous algae	0.06
		<i>Elodea canadensis</i>	0.12
		<i>Lemna minor</i>	0.05
		<i>Myriophyllum spicatum</i>	0.04
		<i>Najas sp.</i>	0.43
		<i>Nitella flexilis</i>	0.01
		<i>Nymphaea tuberosa</i>	0.10
		<i>Potamogeton illinoensis</i>	0.09
		<i>Potamogeton pectinatus</i>	0.08
		<i>Potamogeton richardsonii</i>	0.01
		<i>Sagittaria sp.</i>	0.02
		<i>Tolypella sp.</i>	0.06
		<i>Utricularia vulgaris</i>	0.07
		<i>Vallisneria americana</i>	0.08
SAND POINT			
September 1992			
1	0		0

Table 22 (cont'd).

Zone	Total Macrophyte Relative Abundance	Plant Taxa	Species Relative Abundance
AU GRES			
<i>June 1993</i>			
1	0.48	<i>Chara sp.</i>	0.42
		Filamentous algae	0.36
		<i>Vallisneria americana</i>	0.06
2	0.38	<i>Chara sp.</i>	0.32
		Filamentous algae	0.18
		<i>Potamogeton pectinatus</i>	0.02
3	0.22	<i>Chara sp.</i>	0.11
		Filamentous algae	0.05
		<i>Najas sp.</i>	0.01
		<i>Potamogeton pectinatus</i>	0.09
		<i>Potamogeton richardsonii</i>	0.04
PINCONNING			
<i>June 1993</i>			
1	0.86	Filamentous algae	0.68
		<i>Myriophyllum spicatum</i>	0.04
		<i>Nitella flexilis</i>	0.58
2	0.84	<i>Chara sp.</i>	0.48
		Filamentous algae	0.58
		<i>Myriophyllum spicatum</i>	0.04
		<i>Nitella flexilis</i>	0.54
		<i>Vallisneria americana</i>	0.01
3	0.40	<i>Chara sp.</i>	0.19
		<i>Elodea canadensis</i>	0.01
		Filamentous algae	0.14
		<i>Myriophyllum spicatum</i>	0.02
		<i>Najas sp.</i>	0.09
		<i>Potamogeton illinoensis</i>	0.02
		<i>Vallisneria americana</i>	0.08
BAY CITY			
<i>June 1993</i>			
1	0.22	Filamentous algae	0.22
2	0.34	Filamentous algae	0.27
		<i>Myriophyllum spicatum</i>	0.01
		<i>Potamogeton pectinatus</i>	0.15



Table 22 (cont'd).

Zone	Total Macrophyte Relative Abundance	Plant Taxa	Species Relative Abundance
QUANICASSEE			
June 1993			
1	0.52	Filamentous algae	0.52
2	0.86	Filamentous algae	0.76
		<i>Potamogeton pectinatus</i>	0.04
		<i>Vallisneria americana</i>	0.12
3	0.91	<i>Chara sp.</i>	0.13
		Filamentous algae	0.82
		<i>Myriophyllum spicatum</i>	0.01
		<i>Najas sp.</i>	0.12
		<i>Nymphaea tuberosa</i>	0.01
		<i>Potamogeton nodosus</i>	0.01
		<i>Potamogeton pectinatus</i>	0.08
		<i>Sagittaria sp.</i>	0.02
		<i>Utricularia vulgaris</i>	0.05
		<i>Vallisneria americana</i>	0.03
SAND POINT			
June 1993			
1	0.01	Filamentous algae	0.01
AU GRES			
July 1993			
1	0.78	<i>Chara sp.</i>	0.14
		Filamentous algae	0.70
		<i>Vallisneria americana</i>	0.08
2	0.62	<i>Chara sp.</i>	0.32
		Filamentous algae	0.50
		<i>Potamogeton pectinatus</i>	0.02
3	0.25	<i>Chara sp.</i>	0.13
		Filamentous algae	0.09
		<i>Potamogeton pectinatus</i>	0.03
		<i>Potamogeton richardsonii</i>	0.03
		<i>Vallisneria americana</i>	0.04

Table 22 (cont'd).

Zone	Total Macrophyte Relative Abundance	Plant Taxa	Species Relative Abundance
PINCONNING			
July 1993			
1	0.94	<i>Chara sp.</i>	0.08
		Filamentous algae	0.94
		<i>Myriophyllum spicatum</i>	0.02
		<i>Nitella flexilis</i>	0.76
2	0.95	<i>Chara sp.</i>	0.82
		Filamentous algae	0.70
		<i>Myriophyllum spicatum</i>	0.04
		<i>Najas sp.</i>	0.01
		<i>Nitella flexilis</i>	0.14
3	0.57	<i>Chara sp.</i>	0.45
		<i>Elodea canadensis</i>	0.03
		Filamentous algae	0.20
		<i>Myriophyllum spicatum</i>	0.14
		<i>Najas sp.</i>	0.12
		<i>Nitella flexilis</i>	0.01
		<i>Potamogeton illinoensis</i>	0.01
		<i>Potamogeton richardsonii</i>	0.03
		<i>Vallisneria americana</i>	0.16
BAY CITY			
July 1993			
1	0.02	<i>Nitella flexilis</i>	0.02
2	0.25	Filamentous algae	0.08
		<i>Potamogeton pectinatus</i>	0.25

Table 22 (cont'd).

Zone	Total Macrophyte Relative Abundance	Plant Taxa	Species Relative Abundance
QUANICASSEE			
July 1993			
1	0.12	Filamentous algae	0.12
2	0.66	Filamentous algae	0.62
		<i>Vallisneria americana</i>	0.14
3	0.74	<i>Chara</i> sp.	0.09
		<i>Elodea canadensis</i>	0.03
		Filamentous algae	0.07
		<i>Myriophyllum spicatum</i>	0.03
		<i>Najas</i> sp.	0.25
		<i>Nymphaea tuberosa</i>	0.11
		<i>Potamogeton filiformis</i>	0.06
		<i>Potamogeton illinoensis</i>	0.05
		<i>Potamogeton pectinatus</i>	0.07
		<i>Potamogeton richardsonii</i>	0.01
		<i>Sagittaria</i> sp.	0.06
		<i>Tolypella</i> sp.	0.08
		<i>Utricularia vulgaris</i>	0.17
		<i>Vallisneria americana</i>	0.21
SAND POINT			
July 1993			
1	0.02	Filamentous algae	0.01
		<i>Potamogeton pectinatus</i>	0.01



APPENDIX C

APPENDIX C

Table 23. A list of accession numbers for voucher specimens located in the Beal-Darlington Herbarium, Department of Botany and Plant Pathology, Michigan State University.

Species	Identification Number	Accession Number
<i>Chara globularis</i> Thuill.	934	338659
<i>Elodea canadensis</i> Michx.	939	338663
<i>Myriophyllum spicatum</i> L.	937	338657
<i>Najas flexilis</i> (Willd.) Rostk. & Schmidt	932	338661
<i>Nitella flexilis</i> (L.) Ag.	933	338666
<i>Nymphaea tuberosa</i> Paine	936	338664
<i>Potamogeton illinoensis</i> Morong	931	338660
<i>Potamogeton pectinatus</i> L.	922	338667
<i>Potamogeton richardsonii</i> (Benn.) Rydb.	935	338658
<i>Sagittaria latifolia</i> Willd. Wapato.	923	338662
<i>Utricularia vulgaris</i> L.	938	338665
<i>Vallisneria americana</i> Michx.	921	338668

APPENDIX D

APPENDIX D

Table 24. Mean zebra mussel density (individuals/m²) at six stations in the inner portion of Saginaw Bay 1991-1993 (Tom Nalepa, GLERL, pers. com.). One SE is in parentheses.

Site	Year		
	1991	1992	1993
5	28,240 (2,460)	75,300 (29,280)	240 (50)
6	4,450 (1,390)	3,620 (2,440)	3,560 (1,620)
13	NA	8,960 (6,720)	380 (60)
14	210 (120)	63,240 (19,000)	7,510 (3,460)
15	43,120 (1,050)	5,560 (2,490)	7,340 (2,830)
16	30 (30)	46,360 (7,730)	4,270 (1,770)

Zebra mussel sampling sites were selected by random selection of a sub-group of previously established long-term water quality monitoring sites in Saginaw Bay. Samples were collected by divers with 1 m² quadrats.

Site densities are reported as the mean density of three replicate samples of zebra mussels collected in randomly placed 1 m² quadrats.

Zebra mussels were first found in Saginaw Bay in 1990, but densities were relatively low compared to 1991-1993.

These data represent the first three years of high densities of zebra mussels in Saginaw Bay.

There was no consistent pattern of zebra mussel distribution in Saginaw Bay that persisted from 1991-1993. In addition, there was no consistent trend of increasing or decreasing densities across the three years (Tom Nalepa pers. com.). The apparent differences in means from 1992 to 1993, as explained by Tom Nalepa (NOAA), was not a statistically significant decrease. He offered two hypotheses: 1) Zebra mussel densities did not decrease in Saginaw Bay, but their distribution changed from very patchy in 1991 and 1992 to less patchy in 1993. A sampler that was too small and inadequate sampling size may have biased density means and variances when zebra mussel distribution was patchy. 2) Zebra mussels present in 1991 and 1992 increased in size and biomass, and fewer zebra mussels could occupy a specific substrate in 1993. Neither explanation was tested.

If either hypothesis was correct, the impact of zebra mussels on water clarity would not be expected to decrease. However, if mussel densities did decrease, their impact would be expected to decrease if zebra mussels can affect water clarity directly through their filter feeding activity. If the impact on water clarity is indirect, e.g. through the regulation of available P or N, then a significant decrease in zebra mussel densities may be

expected to have little effect on water clarity until P or N, for example, were released from the accumulated biomass of the dead mussels. In this case, a lag time may be expected that persisted for a time dependent on the rate of decomposition and resuspension of the P or N pooled in the dead zebra mussels.

None of these hypotheses have been tested. Therefore, it is inconclusive whether zebra mussels had an impact on the water clarity of Saginaw Bay from 1991 to 1993.

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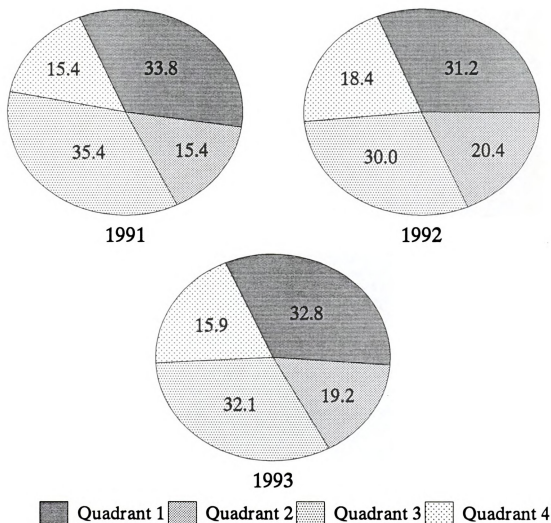


Figure 11. The proportion of days with the wind out of quadrant 1, 2, 3, or 4 at BMWTP, Bay City, MI, April to August 1991-1993. Wind blowing out of quadrant 1 was from NNE to E and blew into Saginaw Bay. Wind blowing out of quadrant 2 was from ESE to S and blew across Saginaw Bay. Wind blowing out of quadrant 3 was from SSW to W and blew out of Saginaw Bay. Wind blowing out of quadrant 4 was from WNW to N and blew across Saginaw Bay. The frequency of days with the wind blowing out one of the four quadrants was not different among 1991, 1992, and 1993 (Pearson χ^2 Contingency Analysis, $N=917$, $d.f.=6$, $\chi^2=4.923$, $P=0.554$).



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