J. Aquat. Plant Manage. 28: 55-64

Ecology of Eurasian Watermilfoil

CRAIG S. SMITH[1] AND J. W. BARKO[2]

ABSTRACT

We review recent literature describing the ecology of Eurasian watermilfoil. Biogeography, propagation and mineral nutrition of Eurasian watermilfoil are emphasized, as are effects of environmental factors on the distribution, productivity, and growth form of this species, its effect on other aquatic organisms, factors influencing milfoil invasions and declines, and other topics relevant to management.

Key words: macrophytes, *Myriophyllum spicatum*, management, disturbance, eutrophication, invasion, decline.

INTRODUCTION

Eurasian watermilfoil (*Myriophyllum spicatum* L.) is among the most troublesome submersed aquatic plants in North America. Nuisance growths of Eurasian watermilfoil have been reported from locations which include: Lake George (Madsen et al. 1989), Saratoga Lake (Mikol 1985) and Cayuga Lake (Miller and Trout 1985), New York; the Chesapeake Bay (Bayley et al. 1978); Currituck Sound, North Carolina (Davis and Brinson 1983); Tennessee Valley Authority (TVA) reservoirs (Smith et al. 1967); the Kawartha lakes, Ontario (Wile et al 1979); Devils Lake, Wisconsin (Lillie 1986); the Madison, Wisconsin lakes (Andrews 1986); and the Okanagan and nearby lakes in British Columbia (Newroth 1985). Excessive Eurasian watermilfoil growth primarily affects recreation, by interfering with swimming and boating, by reducing the quality of sport fisheries, and by reducing the aesthetic appeal of water bodies (see Newroth 1985). Other adverse effects of Eurasian watermilfoil growth include clogged industrial and power generation water intakes, lowered dissolved oxygen concentrations, and increased populations of permanent pool mosquitoes (Bates et al. 1985). In this article we review information on the ecology of Eurasian watermilfoil, the majority of which has been published since a review by Grace and Wetzel (1978). Factors influencing the distribution, productivity and growth form of this species are emphasized, as are effects on other aquatic organisms. This information is provided to facilitate management efforts by highlighting conditions that influence the severity of Eurasian watermilfoil problems and the resulting need for its control.

[1]Environmental Laboratory, Waterways Experiment Station, 3909 Halls Ferry Road, Vicksburg, MS 39180-6199 and Department of Plant Pathology, University of Wisconsin-Madison.

[2]Environmental Laboratory, Waterways Experiment Station, 3909 Halls Ferry Road, Vicksburg, MS 39180-6199.

Received for publication September 11, 1989 and in revised form April 23, 1990.

BIOGEOGRAPHY

Eurasian watermilfoil belongs to the Haloragaceae, a large and diverse family of dicotyledonous plants. The genus *Myriophyllum* is found on every continent except Antarctica, but most of the 39 recognized species have very limited geographic distributions (Cook 1985). Eurasian watermilfoil is native to Europe, Asia and northern Africa (Couch and Nelson 1985).

There is general agreement that Eurasian watermilfoil was introduced to North America, but the exact timing and location of its introduction or introductions are disputed (c.f., Reed 1977; Couch and Nelson 1985). Details of the introductions and expansion are particularly incomplete because *M. spicatum* was often confused with the native North American species *Myriophyllum sibiricum* Kom. (= *Myriophyllum exalbescens* Fern.). Herbarium records prior to 1950 show populations of Eurasian watermilfoil in several widely separated locations, including sites in the District of Columbia, Ohio, Arizona and California (Couch and Nelson 1985). By 1985, Eurasian watermilfoil had been found in 33 states, the District of Columbia and the Canadian provinces of British Columbia, Ontario and Quebec (Couch and Nelson 1985). Since 1985 it has been discovered in Minnesota (C. Smith, personal observation). Eurasian watermilfoil has also been reported from several locations in Northern Alaska (Holmquist 1971), but these plants may actually be *M. sibiricum.* At the edges of its present distribution, the species has probably not yet occupied all suitable habitats (Warrington 1985).

BIOLOGY

Eurasian watermilfoil is a submersed perennial with finely dissected leaves (see Aiken et al. 1979 for a detailed description). The species is typically most abundant in 1 to 4 m of water (Nichols and Shaw 1986), although it can be found in water 1 to 10 m deep (Aiken et al. 1979). Roots are adventitious and arise along lower, buried portions of the stem and, prior to fragmentation (see below), along upper portions of stems. Flowering occurs only when plants have reached the water surface. The inflorescence is a terminal spike and is borne above the water surface. Flowers are small and inconspicuous, and are probably wind-pollinated (Patten 1956).

Plants are essentially evergreen and form no specialized overwintering structures such as turions. Some shoots from the previous growing season persist through the winter and new shoots are initiated in the fall. These do not elongate until spring. Carbohydrate storage occurs throughout overwintering shoots and roots, without being concentrated in any particular plant part (Titus and Adams 1979b, Perkins and Sytsma 1987).

Eurasian watermilfoil exhibits a characteristic annual pattern of growth. In the spring shoots begin to grow rapidly as water temperatures approach about 15 C. As shoots grow, lower leaves drop off in response to shading (Adams et al. 1974). When they reach the surface, shoots branch profusely, forming a dense canopy above leafless vertical stems. Typically, plants flower upon reaching the surface, although some populations rarely flower (Madsen and Boylen 1989). After flowering, plant biomass declines as the result of fragmentation of stems. Where flowering occurs early, plant biomass may increase again later in the growing season, and reach a second biomass peak associated with additional flowering and fragmentation (Adams and McCracken 1974).

Variations in this annual pattern result from differences in climate, water clarity and rooting depth (see below). Plants growing in shallow water can reach the surface within a month or less of initiating growth, and are particularly likely to exhibit several biomass maxima and fragmentation periods. In deep clear water, plants typically grow continuously throughout the summer and reach the surface late in the growing season, if at all. Under such conditions, as in Lake George, New York, fragmentation does not occur until after the single, late-summer biomass peak (Madsen et al. 1988)

PROPAGATION/SPREAD

Eurasian watermilfoil can potentially spread by both sexual and vegetative means. However, vegetative spread of Eurasian watermilfoil by stem fragmentation and stolon formation is thought to be the major means of both intra- and interlake dispersal (Kimbel 1982, Nichols and Shaw 1986, Madsen et al. 1988). Stolons expand populations over distances of a few meters or less (Madsen et al. 1988). Fragments are the predominant means of dispersal over longer distances (Madsen et al. 1988) and are probably also the most important means by which Eurasian watermilfoil colonizes new habitats (Aiken et al. 1979). Within lakes and river systems, fragments are readily dispersed by water currents. The frequency of fragment transport between lakes by various mechanisms is not known but human activities, such as recreational boat traffic, are believed to be one of the most important means of dispersal (Johnstone et al. 1985). Other submersed plant species are known to have spread extensively by fragmentation (e.g. *Elodea canadensis* in Europe, Sculthorpe 1967). Vegetative reproduction alone probably accounts for the spread of Eurasian watermilfoil throughout North America.

Stem fragments are formed by mechanical damage and by autofragmentation; the latter occurs primarily after flowering (Gustafson and Adams 1973) and at the end of the growing season, just after maximum biomass is attained (Madsen et al. 1988). Human activities (e.g. harvesting) may increase the production of fragments or alter the timing of their production, but large numbers of fragments are produced without human intervention.

The importance of seeds as a means of dispersal has not been rigorously evaluated, but is generally considered to be minor. The relatively uniform appearance of North American Eurasian watermilfoil and the lack of any *in situ* observations of seedlings have been cited as evidence for the relative unimportance of seeds as a means of dispersal (Aiken et al. 1979). Many populations flower and produce seeds, particularly in the first few years after establishment. Seeds are often viable, as shown by high rates of germination in the laboratory (Patten 1955, Coble and Vance 1987, Madsen and Boylen 1988). The environmental tolerances of young seedlings are probably much narrower than those of established plants, and the requirements of seedlings are seldom met *in situ* (Patten 1956).

GROWTH AND MORPHOLOGY

Compared with other submersed plants of productive lakes, Eurasian watermilfoil is neither unusually productive nor does it attain unusually high levels of biomass (Grace and Wetzel 1978). Invasion of a lake by Eurasian watermilfoil does not necessarily lead to a major increase in aquatic plant productivity or biomass. In Lake Mendota, Wisconsin, for example, plant beds dominated by wild celery (*Vallisneria americana* Michx.) with a biomass of 289 g m^{-2} (dry weight) (Rickett 1921) were replaced by Eurasian watermilfoil which averaged 130 g m^{-2} (Lind and Cottam 1969). When Eurasian watermilfoil invades relatively unproductive lakes it may replace species which are less productive, but it does not usually become widespread in such lakes (see below).

Likewise, this species does not have unique photosynthetic characteristics, relative to other species. The similarity of photosynthetic responses reported by Van et al. (1976) for a variety of species, including Eurasian watermilfoil, has been documented. Submersed aquatic macrophytes in general possess extremely low rates of net photosynthesis compared to terrestrial vegetation, and their stature is related more to their ability to elongate and form a canopy at the water surface than to their production of biomass.

Table 1 summarizes the influence of environmental factors on the growth and morphology of Eurasian watermilfoil. Factors that influence morphology are particularly important because it is the morphology of Eurasian watermilfoil that imputes it as a nuisance species, rather than its productivity *per se*. Factors which affect growth are also important because of the influence of growth rate on propagation, spread, distribution, ecological impacts, etc.

Light intensity determines many aspects of the distribution and morphology of Eurasian watermilfoil. The species grows in lakes having a wide range in water clarity, but its morphology and depth distribution differ widely across the turbidity spectrum. Turbid water restricts Eurasian watermilfoil to shallow rooting depths and the plant forms a canopy of horizontal stems at the surface, considered to be a near-optimal growth form (Titus and Adams 1979a). In relatively clear water Eurasian watermilfoil grows at considerably greater rooting depths, from which it may not reach the surface (c.f., Madsen et al. 1989). The highly plastic growth form of Eurasian watermilfoil enables it to overtop and shade potential competitors over a wide range of water levels and turbidity. Dominance by this species is often established early in the growing season, owing to a combination of high overwintering biomass and rapid

TABLE 1. FACTORS INFLUENCING GROWTH AND MORPHOLOGY OF EURASIAN WATERMILFOIL

Factor	Influence of Factor on Watermilfoil Growth
Water Clarity	1. Low water clarity limits watermilfoil to shallow rooting depths and leads to canopy formation. 2. High water clarity allows milfoil growth at greater depths.
Temperature	1. Plants photosynthesize and grow over a broad temperature range (ca. 15 to 35 C). 2. Maximum growth rates occur at relatively high water temperatures (ca. 30-35 C). 3. Growth is initiated in the spring once the water temperature reaches approximately 15 C.
Inorganic Carbon	1. Plants grow best in relatively alkaline lakes. 2. Plants can grow in lakes of low alkalinity, but not as vigorously as elsewhere.
Mineral Nutrients	1. Nuisance growths of the plant are primarily restricted to moderately fertile lakes, or fertile locations in less fertile lakes. 2. Uptake of nutrients from sediments by roots is a very important source of mineral nutrients, particularly P and N. 3. Major cations and bicarbonate are taken predominately from the water.
Sediment Texture	1. Plants grow best on fine-textured inorganic sediments of intermediate density, because nutrient availability appears to be greatest there.
Water Movements	1. Vegetative spread of plant fragments is aided by water currents. 2. The plant does not usually occur in high energy environments.
Ice Scour	1. Ice scour may exclude the plant from shallow areas of lakes in cold climates.
Desiccation & Freezing	1. Desiccation during drawdown is a viable control measure particularly when accompanied by freezing during the wintertime.

spring growth (Nichols and Shaw 1986). Carbohydrate storage in overwintering tissues, by supporting shoot growth up to a depth where net photosynthesis is possible (Titus and Adams 1979b), contributes to the ability of Eurasian watermilfoil to persist at rooting depths where the light level at the sediment surface is below the compensation point.

Eurasian watermilfoil has a relatively high temperature optimum, but can photosynthesize and grow over a broad temperature range. Photosynthesis is maximal in the range of 30 to 35 C (Stanley and Naylor 1972; Van et al. 1976; Titus and Adams 1979a), and growth increases with increasing water temperature up to at least 32 C (Barko and Smart 1981a). High water temperatures promote multiple biomass peaks and multiple periods of flowering and fragmentation (Grace and Tilly 1976). In contrast, the plant is capable of appreciable photosynthesis at 10 C (Stanley and Naylor 1972), corresponding with the reported lower limit for rapid growth (British Columbia Ministry of the Environment 1981). The ability of this species to photosynthesize and grow at relatively low water temperatures contributes to its rapid growth to the surface in the spring and may increase its ability to compete with other species at relatively high latitudes (Barko et al. 1982). Eurasian watermilfoil is very susceptible to freezing temperatures (Stanley 1976), and short-term drawdown during freezing temperatures has been successfully used as a control technique in some TVA reservoirs (Bates et al. 1985).

Shoot elongation in this species is extremely sensitive to conditions of light and temperature (Barko and Smart 1981a). In general, conditions of low light and high water temperature, characteristics of many eutrophic environments, stimulate shoot elongation and canopy formation. Even though diminished light with depth in these systems ultimately limits depth distribution by negating net photosynthesis, low light conditions actually contribute to nuisance growth by promoting stem elongation and canopy formation at the surface.

Eurasian watermilfoil grows best on fine-textured, inorganic sediments with an intermediate density of about 0.8 to 1.0 g/ml (Barko and Smart, 1986). It grows relatively poorly on highly organic sediments (organic content > 20%), which have an intrinsically low sediment density, and on coarse substrates (sand and gravel), which have a high sediment density. The response to sediment texture and organic matter content is largely related to mineral nutrient availability, which is highest in sediments of intermediate density (Barko and Smart 1986).

Over the spectrum of infertile to enriched aquatic systems, Eurasian watermilfoil appears to prefer an approximate midpoint (Figure 1; c.f., Moss 1983). This species may not be able to compete with slower growing, nutritionally conservative species (e g., Isoetids) under infertile conditions, and it is potentially excluded due to shading by phytoplankton and attached algae under relatively enriched conditions (Jones et al. 1983). In less productive lakes, Eurasian watermilfoil typically does not dominate a large fraction of the littoral zone, but instead is restricted to locations with nutrient-rich sediments. For example, the most oligotrophic of the Okanagan Lakes, Kalamalka Lake (Stockner and Northcote 1974), supports only relatively sparse, scattered Eurasian watermilfoil, and the vast majority of plant growth is concentrated in a few areas which receive heavy public use (Wallis 1986). In the fundamentally oligotrophic Lake George, New York, the species is

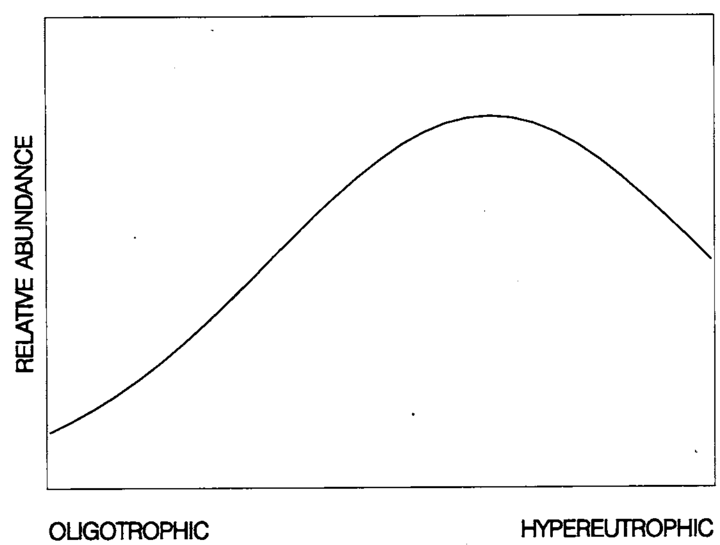

Figure 1. Influence of trophic status on Eurasian watermilfoil abundance.

abundant primarily in locations where sedimentation rates are high, such as near the mouths of creeks (Madsen et al. 1989). In Devil's Lake, Wisconsin, the species is restricted to three discrete areas (Lillie 1986), and there is evidence that nutrient-rich groundwater enters the lake at these locations (Lillie and Barko unpublished). Similar enhancement of submersed plant growth has been observed in areas of high groundwater flux in relatively unproductive Sparkling Lake, Wisconsin (Lodge et al. 1989).

Growth of Eurasian watermilfoil is poor in shallow water (less than 1 m deep), probably owing to a combination of such factors as: wave action, large temperature fluctuations, seasonal variations in water level, high light intensity, coarse substrate and enhanced epiphyte growth (British Columbia Ministry of the Environment 1981). In cold climates ice scour may also limit the long-term establishment of Eurasian watermilfoil in shallow areas.

MINERAL NUTRITION

The nutrition of a variety of submersed macrophytes has been an area of active interest and considerable investigative attention during the last 15 to 20 years (Denny 1980; Agami and Waisel 1986; Barko et al. 1986). The nutrition of Eurasian watermilfoil has been perhaps the best investigated among all submersed macrophyte species. Thus, rather than generalizing the results of studies involving other species, we consider below information obtained principally from studies of Eurasian watermilfoil.

It is generally agreed that uptake of phosphorus (P) from sediment by roots constitutes the primary mode of uptake for Eurasian watermilfoil in the majority of aquatic systems (Barko and Smart 1980; Carignan and Kalff 1980; Carignan 1982). Even in flowing water systems where uptake from surrounding water might be expected to exceed uptake from sediment, submersed macrophytes appear to obtain most of their P through root uptake (Chambers et al 1989). Fine-textured lake sediments contain large pools of available P. Thus, in most lakes it is unlikely that the availability of this element would often limit the growth of Eurasian watermilfoil. Indeed, an attempt experimentally to limit the growth of Eurasian watermilfoil in Lake Wingra, Wisconsin by reducing P availability through aluminum sulfate application was unsuccessful (Mesner and Narf 1987).

For nitrogen (N), no firm consensus currently exists concerning sources of uptake by Eurasian watermilfoil, in part because N has been less extensively investigated than P. Nitrogen can be absorbed by Eurasian watermilfoil either as ammonium from sediment or as ammonium and/or nitrate from the overlying water (Nichols and Keeney 1976). However, the concentration of ammonium in sediment is much greater than in the overlying water of most aquatic systems. Furthermore, ammonium is preferred over nitrate by Eurasian watermilfoil (Nichols and Keeney 1976). Investigations have indicated significant mobilization of N as ammonium from sediment (Best and Mantai 1978; Barko and Smart 1981b). Extensive reductions in sediment ammonium levels within Eurasian watermilfoil beds in conjunction with its seasonal growth (Carignan 1985) attest to the importance of roots in the N economy of this species. *In situ* fertilization of sediment by addition of ammonium-N has been demonstrated to significantly increase the growth of Eurasian watermilfoil (Anderson and Kalff 1986). Thus, unlike P, the availability of N may under some circumstances limit the growth of this species.

Other elements important to the growth of Eurasian watermilfoil include the cations Na, K, Ca and Mg. Their influence in solution on the growth of Eurasian watermilfoil has been examined extensively by Smart and Barko (1986). In general they concluded that these cations were unlikely to be growth limiting except under conditions of low inorganic carbon availability. Calcium in particular, as a component of the carbonate system, has been recognized to play an important role in inorganic carbon uptake during photosynthesis by Eurasian watermilfoil (Lowenhaupt 1956; Stanley 1970; Smart and Barko 1986).

Numerous studies of photosynthesis in relation to water chemistry emphasize the importance of bicarbonate as an inorganic carbon source to Eurasian watermilfoil, and suggest that carbon availability may often limit its growth (e.g., Stanley 1970; Adams et al. 1978; Titus and Stone 1982; Smart and Barko 1986). Optimal growth of this species occurs in alkaline (hardwater) systems, with concomitantly high concentrations of dissolved inorganic carbon (Spence 1967; Hutchinson 1970; Stanley 1970). Thus, the alkalinity of water provides a simple, but useful, measure of the growth potential of Eurasian watermilfoil. Like many plants that 'prefer' a hardwater situation, Eurasian watermilfoil can exist in softwater environments (Giesy and Tessier 1979), but it is not ideally suited to grow there.

Rooted aquatic macrophytes including Eurasian watermilfoil can satisfy their requirements for micronutrients by uptake from sediment (Smart and Barko 1985). Since these elements tend to precipitate in the presence of oxygen, they are usually available in low concentrations in lake surface waters. Their availability to Eurasian watermilfoil growing in anaerobic sediments is much greater than in the overlying water. However, the relationship between growth and micronutrient supply for this and other macrophyte species has not been well investigated. In any event, it is unlikely that the growth of Eurasian watermilfoil would be limited by supply of micronutrients under most circumstances, because of relatively minor requirements for these elements in tissues.

MOBILIZATION OF SEDIMENT NUTRIENTS

Substantial quantities of nutrients can be transferred from the sediments into the water as Eurasian watermilfoil takes up minerals from the sediment, translocates them to shoots, and releases them upon senescence and decomposition (Prentki et al. 1979; Barko and Smart 1980; Carpenter 1980b; Landers 1982; Smith and Adams 1986). However, this species, and in fact a variety of other freshwater macrophyte species investigated to date, do not actively 'pump', i.e., excrete nutrients directly into the water column (Denny 1980; Barko and Smart 1981b; Barko et al. 1986). The ability to mobilize sediment nutrients, then release these nutrients to the water column upon tissue senescence is certainly not unique to Eurasian watermilfoil.

As in other species, biomass turnover in Eurasian watermilfoil is affected by environmental conditions. Westlake (1982), based on information provided in Carpenter (1980b), indicated high biomass turnover in Eurasian watermilfoil. Nutrient release from this species during the growing season may be more prolonged than from other species, due to the relatively continuous sloughing of leaves and stems (Smith and Adams 1986). However, Carpenter (1980b) actually showed similar or somewhat higher tissue turnover (net production/peak biomass) in two native species than in Eurasian watermilfoil. Thus, there is no firm basis for suggesting that nutrient leaching or decay will be any faster in this species than in other species. Westlake (1982) stresses that environmental variables weigh heavily on tissue turnover (and associated nutrient release) in aquatic macrophytes. Turnover in eutrophic systems, regardless of species composition, is usually greater than in oligotrophic systems because of greater productivity in the former.

HABITAT RELATIONSHIPS

Both invertebrates and fish tend to be more abundant and diverse in macrophyte beds than in adjacent open water regions, presumably owing to the shelter and substrate provided by plants (Wiley et al. 1984; Kilgore et al. 1989). Populations of benthic invertebrates beneath submersed vegetation can be more than 100 times larger than those in non-vegetated openings within plant beds (Miller et al. 1989). Eurasian watermilfoil has been shown to provide a better habitat for invertebrates (Pardue and Webb 1985) and for fish (Kilgore et al. 1989) than the open water of the littoral zone. Production of forage fish and invertebrates appears to increase directly with increasing macrophyte biomass, while bass (*Micropterus salmoides* L.) production and their condition have been shown to be maximal at intermediate levels of macrophyte biomass (Figure 2) (Colle and Shireman 1980; Wiley et al. 1984). Small fish hide in vegetation, while adult fish remain along edges of vegetation or in open channels within plant beds (Engel 1988). Reduced predation success by largemouth bass in dense macrophyte beds contributes to diminished bass production (Savino and Stein 1982; Engel 1987).

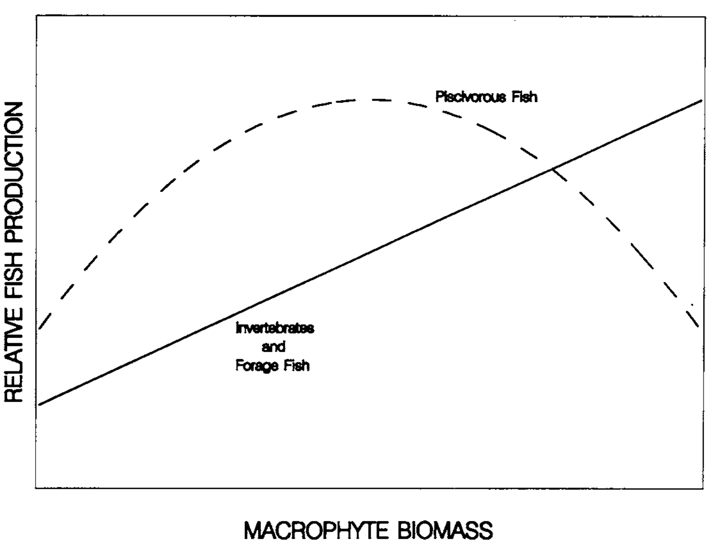

Figure 2. Influence of submersed plant biomass on production of invertebrates, forage fish and piscivores (largemouth bass) (Wiley et al. 1984).

Invertebrate and fish communities in Eurasian watermilfoil beds differ from those associated with other submersed macrophytes, but these differences are not particularly great. Dvorak and Best (1982) found that of 8 morphologically distinct species, Eurasian watermilfoil had the poorest invertebrate fauna, although all plant species had a high number of macroinvertebrate species in common. In Lake Opinicon, Ontario, Eurasian watermilfoil beds supported significantly fewer benthic and foliar invertebrates per square meter than did mixed beds of pondweeds (*Potamogeton* spp.) and wild celery (Keast 1984), but much of the difference can be attributed to the three-fold higher biomass of the pondweed-wild celery community. Likewise, fish abundance in the pondweed-wild celery community during daytime feeding periods was 3 to 4 times greater than in Eurasian watermilfoil beds. The effect of Eurasian watermilfoil on salmonids is potentially much greater than for other fish species, because the plant reduces spawning success by covering spawning gravels (Newroth 1985). Thus, the greatest effects can be expected when invasion is associated with a large change in total plant biomass or when particularly sensitive species (e g., salmonids) are affected. Except in these cases, invasion of native macrophyte communities by Eurasian watermilfoil will probably not prompt major changes in fish or invertebrate populations.

INVASIONS/DECLINES

Eurasian watermilfoil is often described as an invasive species, and it is loosely accepted that invasions are followed by rapid growth and concomitant displacement of native species. Certainly this species has a history of rapidly obtaining dominance in many eutrophic systems, but this pattern is by no means universal. In the Great Lakes for example, this species, although present for some time, has not been reported to be a common or a nuisance component of the submersed macrophyte community (Schloesser and Manny 1984). At present, this species does not appear to be significantly expanding its distribution in Lake George, New York (Madsen et al. 1989).

The extent to which Eurasian watermilfoil replaces native species differs from location to location. Native species were nearly completely displaced in Lakes Mendota (Lind and Cottam 1969) and Wingra (Nichols and Mori 1971), Wisconsin, while in TVA systems the plant almost exclusively invaded new habitat (L. Bates, personal communication). In Devil's Lake, Wisconsin, Eurasian watermilfoil took over areas formerly dominated by Elodea (*Elodea canadensis*), but appears to have had little effect on the distribution of other species (Lillie 1986). In Lake Opinicon, Ontario, Eurasian watermilfoil invaded areas which had for the most part been unvegetated (Keast 1984).

Specific factors contributing to successful invasion by Eurasian watermilfoil are unknown, and there is equally little information available to explain its explosive growth in some systems, but not in others, following invasion. In a unique review of information on plant invasions, Johnstone (1986) suggests that invasions are caused by the removal of barriers that previously excluded a plant species from a particular area. Barriers appear to be removed in association with disturbance (change). Indeed, the near complete dominance of Eurasian watermilfoil in Lake Wingra, Wisconsin for about a decade (Carpenter 1980a) followed a long history of disturbance for this system (Baumann et al. 1974). For invasion to be successful, the timing of barrier relief by disturbance or directional change (succession) must coincide with incursion by the invading species. Thus, invasions appear to be rather stochastic events.

Several characteristics of Eurasian watermilfoil enable it to rapidly colonize disturbed areas and to remain in place once established. The ability to spread rapidly by fragmentation allows Eurasian watermilfoil to quickly colonize new habitat whenever it is made available, such as by sediment deposition, water level changes, or declines/removal of populations of other species. Characteristics of Eurasian watermilfoil which make it an effective competitor for light are probably extremely important in its ability to replace other species and to persist once established, as light is probably the most critical factor for submersed macrophyte growth in the aquatic environment.

The kinds of disurbances that can lead to invasion by Eurasian watermilfoil are probably the same as those influencing macrophyte succession (Sheldon 1986). These may include, for example: sedimentation; ice scouring; wave action; bioturbation; herbivory; changes in water level, water clarity, temperature, nutrient loading, or climate; and a variety of possible anthropogenic factors. Disturbance resulting from Tropical Storm Agnes led to an increase in Eurasian watermilfoil abundance that nearly excluded other, previously abundant species at the south end of Cayuga Lake, New York (Oglesby and Vogel 1976). Eutrophication or reversal of eutrophication, both constituting disturbances, can effect pronounced changes in macrophyte community composition (Moss 1983; Osborne and Polunin 1986). Invasion windows for this species apparently open in close association with marked changes (either an increase or decrease) in trophic state.

Composite environmental changes simultaneously alter several facets of the environment. In drought years, for example, lowered runoff typically results in reduced sediment and nutrient loading, temperatures are higher than normal, turbidity is reduced and water levels may drop. The resulting conditions are ideal for expansion of Eurasian watermilfoil populations. Lowered nutrient inputs reduce phytoplankton growth, thereby further increasing water clarity. Increased water clarity and lower water levels mean that areas that were formerly too poorly illuminated to sustain the growth of rooted plants are now accessible. High light intensities and warm water temperatures promote abundant growth of Eurasian watermilfoil. Nutrient availability for the growth of rooted plants is relatively unaffected, since Eurasian watermilfoil plants obtain mineral nutrients primarily from the sediments. Thus, Eurasian watermilfoil problems are likely to be worse in (and following) drought years than in non-drought years. Some evidence for this is provided by the observation that Eurasian watermilfoil problems were particularly severe in the Madison, WI lakes (C. Smith, personal observation), and in TVA reservoirs (L. Bates, personal communication) during the summer of 1988, when eastern and midwestern North America was experiencing a drought.

Major declines in populations of Eurasian watermilfoil have been reported and evaluated (Carpenter 1980a; Nichols and Shaw 1986; Painter and McCabe 1988). Hypotheses tendered as to the cause of these declines include nutrient depletion, shading by phytoplankton and attached algae, attack by parasites or pathogens, long-term effects of harvesting and/or herbicides, accumulation of a toxin, climatic fluctuations, competition from other macrophytes (Carpenter 1980a), and insect herbivory (Painter and McCabe 1988), but none of the declines has been adequately explained. In many locations Eurasian watermilfoil populations increased to a high level of dominance, maintained dominance for a few years, and then declined. To date, Eurasian watermilfoil has declined in the Chesapeake Bay area (Bayley et al. 1968); in the Madison, Wisconsin, area lakes (Carpenter 1980a); in several southern Ontario lakes (Wile et al. 1979; Painter and McCabe 1988); in Devil's Lake, Wisconsin (R.A. Lillie, personal communication) and in a few localized areas within the Okanagan Valley lakes of British Columbia (British Columbia Ministry of the Environment 1981). In these locations the period of peak milfoil abundance ranged from approximately 5 to 10 years, with 10 years being typical (Carpenter 1980a). When milfoil declined, the rate and amount of decline varied from location to location. Typically, post-decline populations of Eurasian watermilfoil are less likely than pre-decline populations to reach the water surface or to flower. Recovery of native species has not been studied, but in Lake Wingra, Wisconsin, wild celery and several pondweeds (*Potamogeton* spp.) increased following the milfoil decline (C. S. Smith, personal observation). As pointed out by Carpenter (1980a), the potential transience of Eurasian watermilfoil abundance needs to be considered in the development of aquatic plant management programs. In view of the apparent relationship between disturbance and invasion (see above), it would be useful to have better information than at present on effects of specific control measures on the longevity of Eurasian watermilfoil abundance.

MANAGEMENT

Most Eurasian watermilfoil control efforts have been directed towards maintenance, since eradication of this particular species, with a demonstrated ability to reproduce from fragments, is rarely if ever, likely to succeed (c.f., Newroth 1988a). Efforts to limit the spread of Eurasian watermilfoil have met with only marginal success, slowing the expansion of Eurasian watermilfoil but rarely preventing its dispersion. For example, despite two years of intensive control operations (diver dredging, bottom barrier placement and derooting) in Shuswap Lake, British Columbia, Eurasian watermilfoil increased in density and extent, and spread to other lakes in the drainage system (Einarson 1987). After several years of a major public education and quarantine program in British Columbia, boaters continued to transport Eurasian watermilfoil fragments, and the spread of the plant into previously uncolonized lakes continued unabated (Newroth 1985).

Existing control techniques for Eurasian watermilfoil are short-lived and expensive (see Nichols and Shaw 1983; Andrews 1986; Nichols et al. 1988 for discussions of specific control techniques). Since nuisance populations of Eurasian watermilfoil frequently cover large areas, treatment of the entire affected area is seldom economical. Management plans must therefore define specific goals in order to concentrate treatment efforts where they will produce greatest benefits. Goals might include, for example, keeping beaches free of plant growth, opening boat lanes from the shore to open water, maintaining optimal plant cover for fish production, or restoring the diversity of submersed plant communities for aesthetic purposes. The nature of the goals selected will determine how much control is desirable and which techniques are appropriate. Goals which are unstated or unrealistic will never be met, leading to a continuous need for management.

Factors that influenc the vigor of Eurasian watermilfoil growth will determine the extent of the nuisance and the appropriateness of particular management approaches. Shallow, moderately turbid bodies of water with widespread areas of nutrient-rich sediments will experience the most severe problems because these conditions support luxuriant milfoil growth and encourage canopy formation. Multiple biomass peaks will often necessitate repeated control. When there is concern about fragment production in such systems, management will need to begin early in the year before fragmentation has begun. In oligotrophic lakes, management of Eurasian watermilfoil may only be required in those areas having sediments sufficiently rich to support dense plant growth. Populations growing in deep clear water typically will not form a dense canopy at the surface and thus should not require management.

The growth of Eurasian watermilfoil varies considerably from year to year in most lakes. Declines in Eurasian watermilfoil, when they occur, should reduce the demand for control. However, post-decline populations of Eurasian watermilfoil in the Madison, Wisconsin lakes were still considered undesirable (Andrews 1986). Thus, the decline in nuisance populations of this species may not eliminate the perceived need for management. The selected management approach should be flexible in design in order to deal with declines, and conversely increases, in the population density of this species. Such flexibility will guarantee economic savings by increasing the overall treatment efficiency.

Since Eurasian watermilfoil appears to respond positively to disturbance, some control techniques may actually promote expansion of plant populations or delay declines. For example, Carpenter (1980a) reported that frequently harvested areas in Lake Wingra continued to support robust plant growth after the species had declined in other parts of the lake. Techniques such as derooting, shallow dredging and drawdown, and others which create favorable habitat may perpetuate high Eurasian watermilfoil populations. The two locations where robust Eurasian watermilfoil populations are reported to have persisted for more than 10 to 15 years, Guntersville Reservoir and the Okanagan area lakes, are more intensely managed than locations where the plant has declined (Table 2). Evaluation of the possibility that control techniques may prolong Eurasian watermilfoil problems awaits studies of the long-term effects of management practices on Eurasian watermilfoil persistance.

ACKNOWLEDGMENTS

Support for the preparation of this article was provided by the US Army Engineer St. Paul District and by the US Army Engineer Aquatic Plant Control Research Program. Mr. Herbert Nelson served as a point of contact with the CE St. Paul District. Conversations with Drs. Leon Bates and Peter Newroth were instrumental in the formulation of some of the opinions expressed herein. These two individuals; Drs. Douglas Gunnison, Nancy McCreary and William Taylor; and Mr. Stevin Colvin are gratefully acknowledged for providing critical reviews of an early draft of this text. Permission was granted by the Chief of Engineers to publish this document

TABLE 2. APPARENT RELATIONSHIP BETWEEN MANAGEMENT AND EURASIAN WATERMILFOIL PERSISTENCE

Lake	Technique	Approximate Percentage of Milfoil Affected	Decline
Chesapeake Bay	None	~0%	Yes[1]
Lake Wingra, WI	Harvesting	< 5%[2]	Yes[3]
Devils Lake, WI	None	0%[4]	Yes[4]
Guntersville Reservoir, AL	Herbicides	7%[5]	No[5]
	Drawdown	100%[6]	
Okanagan Valley Lakes, B.C.	Harvesting, rototilling, cultivation, bottom barriers	18%[7]	Locally[7]
Cultus Lake, B. C.	Rototilling	33%[7]	No[7]
Shuswap Lake, B. C.	Rototilling, cultivation, dredging, bottom barriers	44%[7]	No[7]

[1]Bayley et al. 1968.
[2]C. S. Smith, personal observation.
[3]Carpenter 1980a.
[4]R. A. Lillie, personal communication.
[5]D. Webb, personal communication.
[6]We assume that fluctuating water levels disturb the entire shallow water plant community.
[7]Newroth 1988b.

LITERATURE CITED

Adams, M. S. and M. D. McCracken. 1974. Seasonal production of the *Myriophyllum* component of Lake Wingra, Wisconsin. J. Ecol. 62:457-467.

Adams, M. S., J. Titus and M. McCracken. 1974. Depth distribution of photosynthetic activity in a *Myriophyllum spicatum* community in Lake Wingra. Limnol. Oceanogr. 19:377-389.

Adams, M. S., P. Guilizzoni and S. Adams. 1978. Relationship of dissolved inorganic carbon to macrophyte photosynthesis in some Italian lakes. Limnol. Oceanogr. 23:912-913.

Agami, Y. and Y. Waisel. 1986. The ecophysiology of roots of submerged vascular plants. Physiol. Veg. 24:607-624.

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

Anderson, M. R. and J. Kalff. 1986. Nutrient limitation of *Myriophyllum spicatum* growth *in situ*. Freshwater Biol. 16:735-743.

Andrews, J. H. (editor). 1986. Nuisance vegetation in the Madison lakes: Current status and options for control. University of Wisconsin, Madison, WI. 196 pp.

Barko, J. W. and R. M. Smart. 1980. Mobilization of sediment phosphorus by submersed freshwater macrophytes. Freshwater Biol. 10:229-238.

Barko, J. W. and R. M. Smart. 1981a. Comparative influences of light and temperature on the growth and metabolism of selected submersed freshwater macrophytes. Ecol. Monographs 51:219-235.

Barko, J. W. and R. M. Smart. 1981b. Sediment-based nutrition of submersed macrophytes. Aquat. Bot. 10:339-352.

Barko, J. W. and R. M. Smart. 1986. Sediment-related mechanisms of growth limitation in submersed macrophytes. Ecol. 67:1328-1340.

Barko, J. W., D. G. Hardin and M. S. Matthews. 1982. Growth and morphology of submersed freshwater macrophytes in relation to light and temperature. Can. J. Bot. 60:877-887.

Barko, J. W., M. S. Adams and N. L. Clesceri. 1986. Environmental factors and their consideration in the management of submersed aquatic vegetation: A review. J. Aquat. Plant Manage. 24:1-10.

Bates, A. L., E. R. Burns and D. H. Webb. 1985. Eurasian watermilfoil (*Myriophyllum spicatum* L.) in the Tennessee-valley: An update on biology and control. *In*: L. W. J. Anderson (ed), Proceedings of the First International Symposium on watermilfoil (*Myriophyllum spicatum*) and related Haloragaceae species. Aquat. Plant Manage. Soc., Washington, D.C. pp. 104-115.

Baumann, P. C., J. F. Kitchell, J. J. Magnuson and R. B. Kayes. 1974. Lake Wingra, 1837-1973: A case history of human impact. Wisconsin Academy of Science, Arts and Letters 62:57-94.

Bayley, S., H. Rabin and C. H. Southwick. 1968. Recent decline in the distribution and abundance of Eurasian milfoil in the Chesapeake Bay. Chesapeake Sci. 9:173-181.

Bayley, S., V. D. Stotts, P. F. Springer and J. Steenis. 1978. Changes in the submerged aquatic macrophyte populations at the head of the Chesapeake Bay, 1958-1975. Estuaries 1:73-84.

Best, M. D. and K. E. Mantai. 1978. Growth of *Myriophyllum*: sediment or lake water as the source of nitrogen and phosphorus? Ecol. 59:1075-1080.

British Columbia Ministry of the Environment. 1981. A summary of biological research on Eurasian water milfoil in British Columbia. Aquatic Plant Management Program. Information Bulletin, Vol. IX. British Columbia Ministry of the Environment, Water Resource Branch, Victoria, B.C. 18 p.

Carignan, R. 1982. An empirical model to estimate the relative importance of roots in phosphorus uptake by aquatic macrophytes. Can J. Fish. Aquat. Sci. 39:243-247.

Carignan, R. 1985. Nutrient dynamics in a littoral sediment colonized by the submersed macrophyte *Myriophyllum spicatum*. Can J. Fish. Aquat. Sci. 42:1303-1311.

Carignan, R. and J. Kalff. 1980. Phosphorus sources for aquatic weeds: water or sediment. Sci. 207:987-989.

Carpenter, S. R. 1980a. The decline of *Myriophyllum spicatum* in a eutrophic Wisconsin lake. Can. J. Bot. 58:527-535.

Carpenter, S. R. 1980b. Enrichment of Lake Wingra, Wisconsin, by submersed macrophyte decay. Ecol. 61:1145-1155.

Chambers, P. A., E. E. Prepas, M. L. Bothwell and H. R. Hamilton. 1989. Roots versus shoots in nutrient uptake by aquatic macrophytes in flowing waters. Can J. Fish. Aquat. Sci. 46:435-439.

Coble, T. A. and B. D. Vance. 1987. Seed Germination in *Myriophyllum spicatum* L. J. Aquat. Plant Manage. 25:8-10.

Colle, D. E. and J. W. Shireman. 1980. Coefficients of condition for largemouth bass, bluegill, and radar sunfish in hydrilla-infested lakes. Trans. Amer. Fish. Soc. 109:521-531.

Cook, C. D. K. 1985. Worldwide distribution and taxonomy of *Myriophyllum* species. *In*: L. W. J. Anderson (ed), Proceedings of the First International Symposium on the watermilfoil (*Myriophyllum spicatum*) and related Haloragaceae species. Aquat. Plant Manage. Soc., Washington, D.C. pp. 1-7.

Couch, R. and E. Nelson. 1985. *Myriophyllum spicatum* in North America. *In*: L. W. J. Anderson (ed), Proceedings of the First International Symposium on watermilfoil (*Myriophyllum spicatum*) and related Haloragaceae species. Aquat. Plant Manage. Soc., Washington, D.C. pp. 8-18.

Davis, G. J. and M. M. Brinson. 1983. Trends in submersed communities of the Currituck Sound: 1909-1979. J. Aquat. Plant Manage. 21:83-87.

Denny, P . 1980. Solute movement in submerged angiosperms. Biol. Rev. 55:65-92.

Dvorak, J. and E. P. Best. 1982. Macro-invertebrate communities associated with the macrophytes of Lake Vechten: structural and functional relationships. Hydrobiologia 95:115-126.

Einarson, E. D. 1987. The 1986 Eurasian water milfoil surveillance and control program in the Shuswap drainage basin. British Columbia Ministry of the Environment, Water Management Branch, Victoria, B.C. 36 p.

Engel, S. 1987. Impact of submerged macrophytes on largemouth bass and bluegills. Lake and Reservoir Manage. 3:227-234.

Engel, S. 1988. The role and interactions of submersed macrophytes in a shallow Wisconsin lake. J. Freshwat. Ecol. 4:329-341.

Giesy, Jr. J. P. and L. E. Tessier. 1979. Distribution potential of *Myriophyllum spicatum* (Angiospermae, Haloragidaceae) in softwater systems. Arch. Hydrobiol. 85:437-447.

Grace, J. B. and L. J. Tilly. 1976. Distribution and abundance of submersed macrophytes, including *Myriophyllum spicatum* L. (Angiospermae), in a reactor cooling reservoir. Archiv. Hydrobiol. 77:475-487.

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

Gustafson, T. D. and M. S. Adams. 1973. The remote sensing of aquatic macrophytes. University of Wisconsin-Madison, Institute for Environmental Studies Remote Sensing Program, Madison, WI. Report No. 24. 26 pp.

Holmquist, C. 1971. Northerly localities for three aquatic plants, *Lemna trisulca* L., *Ceratophyllum demersum* L., and *Myriophyllum spicatum* L. Botaniska Notiser 124:335-342.

Hutchinson, G. E. 1970. The chemical ecology of three species of *Myriophyllum* (Angiospermae, Haloragaceae). Limnol. Oceanogr. 15:1-5.

Johnstone, I. M. 1986. Plant invasion windows: a time-based classification of invasion potential. Biol. Rev. 61:369-394.

Johnstone, I. M., B. T. Coffey and C. Howard-Williams. 1985. The role of recreational boat traffic in interlake dispersal of macrophytes: a New Zealand case study. J. Environmental Manage. 20:263-279.

Jones, R. C., K. Walti and M. S. Adams. 1983. Phytoplankton as a factor in the decline of the submersed macrophyte *Myriophyllum spicatum* L. in Lake Wingra Wisconsin, U.S.A. Hydrobiologia 107:213-219.

Keast, A. 1984. The introduced aquatic macrophyte, *Myriophyllum spicatum*, as habitat for fish and their invertebrate prey. Can. J. Zool. 62:1289-1303.

Kilgore, K. J., R. P. Morgan II and N. B. Rybicki. 1989. Seasonal and temporal distribution and abundance of fishes association with submersed aquatic plants. North Amer. J. Fish Manage. 9:101-111.

Kimbel, J. C. 1982. Factors influencing potential intralake colonization by *Myriophyllum spicatum* L. Aquat. Bot. 14:295-307.

Landers, D. H. 1982. Effects of naturally senescing aquatic macrophytes on nutrient chemistry and chlorophyll *a* of surrounding waters. Limnol. Oceanogr. 27:428-439.

Lillie, R. A. 1986. The spread of Eurasian watermilfoil *Myriophyllum spicatum* in Davis Lake, Sauk County, Wisconsin. Lake and Reservoir Manage. 2:64-68.

Lind, C. T. and G. Cottam. 1969. The submerged aquatics of University Bay: A study in eutrophication. Amer. Midl. Natur. 81:353-369.

Lodge, D. M., D. P. Krabbenhoft and R. G. Striegl. 1989. A positive relationship between groundwater velocity and submersed macrophyte biomass in Sparkling Lake, Wisconsin. Limnol. Oceanogr. 34:235-239.

Lowenhaupt, B. 1956. The transport of calcium and other cations in submerged aquatic plants. Biol. Rev. 31:371-395.

Madsen, J. D. and C. W. Boylen. 1988. Seed ecology of Eurasian watermilfoil (*Myriophyllum spicatum* L.). Rensselaer Fresh Water Institute Report 88-7, Rensselaer Polytechnic Institute, Troy, New York. November 1988.

Madsen, J. D. and C. W. Boylen. 1989. Eurasian watermilfoil seed ecology from an oligotrophic and eutrophic lake. J. Aquat. Plant Manage. 27:119-121.

Madsen, J. D., L. W. Eichler and C. W. Boylen. 1988. Vegetative spread of Eurasian watermilfoil in Lake George, New York. J. Aquat. Plant Manage. 26:47-50.

Madsen, J. D., J. W. Sutherland, J. A. Bloomfield and K. Roy. 1989. The Lake George aquatic plant survey. Lake George Park Commission. Final Report. New York State Department of Environmental Conservation, Albany, NY.

Mesner, N. and R. Narf. 1987. Alum injection into sediments for phosphorus inactivation and macrophyte control. Lake and Reservoir Manage. 3:256-265.

Mikol, G. F. 1985. Effects of harvesting on aquatic vegetation and juvenile fish populations at Saratoga Lake, New York. J. Aquat. Plant Manage. 23:59-63.

Miller, A. C., D. C. Beckett and E. J. Bacon. 1989. The habitat value of aquatic macrophytes for macroinvertebrates: Benthic Studies in Eau Galle Reservoir, Wisconsin. Proceedings, 23rd Annual Meeting, Aquatic Plant Control Research Program. Misc. Paper A-89-1, Environmental Laboratory, U.S. Army Engineers Waterways Experiment Station, Vicksburg, MS. pp. 190-201.

Miller, G. L. and M. A. Trout. 1985. Changes in the aquatic plant community following treatment with the herbicide 2,4-D in Cayuga Lake, New York. *In*: L. W. J. Anderson (ed), Proceedings of the First International Symposium on watermilfoil (*Myriophyllum spicatum*) and related Haloragaceae species. Aquat. Plant Manage. Soc., Washington, D.C. pp. 126-138.

Moss, B. 1983. The Norfolk Broadland: experiments in the restoration of a complex wetland. Biol. Rev. 58:521-561.

Newroth, P. R. 1985. A review of Eurasian water milfoil impacts and management in British Columbia. *In*: L. W. J. Anderson (ed), Proceedings of the First International Symposium on the watermilfoil (*Myriophyllum spicatum*) and related Haloragaceae species. Aquat. Plant Manage. Soc., Washington, D.C. pp. 139-153.

Newroth, P. R. 1988a. A five year plan for aquatic plant management in British Columbia. British Columbia Ministry of the Environment, Water Resources Branch, Victoria, B.C. 14 p.

Newroth, P. R. 1988b. Review of current aquatic plant management activities in British Columbia. Proceedings of 22nd Annual Meeting, Aquatic Plant Control Program. Misc. Paper A-88-5, Environmental Laboratory, Waterways Experiment Station, Vicksburg, MS. pp. 66-71.

Nichols, S. A., S. Engel and T. McNabb. 1988. Developing a plan to manage lake vegetation. Aquatics 10:10-19.

Nichols, S. A. and D. R. Keeney, 1976. Nitrogen nutrition of *Myriophyllum spicatum* uptake and translocation of ^{15}N by shoots and roots. Freshwater Biol. 6:145-154.

Nichols, S. A. and S. Mori. 1971. The littoral macrophyte vegatation of Lake Wingra. Trans. Wis. Acad. Sci. Arts Lett. 59:107-119.

Nichols, S. A. and B. H. Shaw. 1983. Physical, chemical, and biological control of aquatic macrophytes. Lake Restoration, Protection and Management. Proc. 2nd Ann. Conf. N. Amer. Lk. Manage. Soc., Oct. 1982, Vancouver, British Columbia. EPA 404/5-83-001. U.S. Environmental Protection Agency, Washington, D.C. pp. 181-192.

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

Oglesby, R. T. and A. Vogel. 1976. Changes in submerged plants at the south end of Cayuga Lake following Tropical Storm Agnes. Hydrobiologia 48:251-255.

Osborne, P. L. and V. C. Polunin. 1986. From swamp to lake: recent changes in a lowland trophical swamp. J. Ecol. 74:197-210.

Painter, D. S. and K. J. McCabe. 1988. Investigation into the disappearance of Eurasian watermilfoil from Kawartha Lakes. J. Aquat. Plant Manage. 26:3-12.

Pardue, W. J. and D. H. Webb. 1985. A comparison of aquatic macroinvertebrates occurring in association with Eurasian watermilfoil (*Myriophyllum spicatum* L.) with those found in the open littoral zone. J. Fresh. Ecol. 3:69-79.

Patten, B. C. 1955. Germination of the seed of *Myriophyllum spicatum* L. Bull. Torrey Bot. Club 82:50-56.

Patten, B. C. 1956. Notes on the biology of *Myriophyllum spicatum* L. in a New Jersey lake. Bull. Torrey Bot. Club 83:5-18.

Perkins, M. A. and Mark D. Systsma. 1987. Harvesting and carbohydrate accumulation in Eurasian watermilfoil. J. Aquat. Plant Manage. 25:57-62.

Prentki, R. T., M. S. Adams, S. R. Carpenter, A. Gasith, C. S. Smith and P. R. Weiler. 1979. The role of submersed weedbeds in internal loading and interception of allochthonous materials in Lake Wingra, Wisconsin, USA. Arch. Hydrol. Suppl. 57:221-250.

Reed, C. F. 1977. History and distribution of Eurasian watermilfoil in United States and Canada. Phytologia 36:417-436.

Rickett, W. H. 1921. A quantitative study of the large aquatic plants of Lake Mendota. Trans. Wis. Acad. Sci. Arts Lett. 20:501-527.

Savino, J. F. and R. A. Stein. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated submersed vegetation. Trans. Amer. Fish Soc. 111:255-266.

Schloesser, D. W. and B. A. Manny. 1984. Distribution of Eurasian watermilfoil, *Myriophyllum spicatum*, in the St. Clair-Detroit river system in 1978. J. Great Lakes Res. 10:322-326.

Sculthorpe, C. D. 1967. The biology of aquatic vascular plants. Edward Arnold, London. 610 pp.

Sheldon, S. P. 1986. The effects of short-term disturbance on a freshwater macrophyte community. J. Fresh. Ecol. 3:309-317.

Smart, R. M. and J. W. Barko. 1985. Laboratory culture of submersed freshwater macrophytes on natural sediments. Aquat. Bot. 21:251-263.

Smart, R. M. and J. W. Barko. 1986. Effects of water chemistry on aquatic plants: growth and photosynthesis of *Myriophyllum spicatum* L. Technical Report A-86-2, Environmental Laboratory, US Army Engineer Waterways Experiment Station, Vicksburg, MS, 34 pp.

Smith, C. S. and M. S. Adams. 1986. Phosphorus transfer from sediments by *Myrophyllum spicatum*. Limnol. Oceanogr. 31:1312-1321.

Smith, G. E., T. F. Hall and R. A. Stanley. 1967. Eurasian watermilfoil in the Tennessee Valley. Weeds 15:95-98.

Spence, D. H. N. 1967. Factors controlling the distribution of freshwater macrophytes, with particular reference to Scottish lochs. J. Ecol. 55:147-170.

Stanley, R. A. 1970. Studies on nutrition, photosynthesis and respiration in *Myriophyllum spicatum* L. Ph.D. dissertation. Duke University, Durham, North Carolina, USA.

Stanley, R. A. 1976. Response of Eurasian watermilfoil to subfreezing temperature. J. Aquat. Plant Manage. 14:36-39.

Stanley, R. A. and A. W. Naylor. 1972. Photosynthesis in Eurasian watermilfoil (*Myriophyllum spicatum* L.). Plant Physiol. 50:149-151.

Stockner, J. G. and T. G. Northcote. 1974. Recent limnological studies of Okanagan Basin lakes and their contribution to comprehensive water resource planning. J. Fish. Res. Board Can. 31:955-976.

Titus, J. E. and M. S. Adams. 1979a. Coexistence and the comparative light relations of the submersed macrophytes *Myriophyllum spicatum* L. and *Vallisneria americana* Michx. Oecologia 40:273-286.

Titus, J. E. and M. S. Adams. 1979b. Comparative carbohydrate storage and utilization patterns in the submersed macrophytes (*Myriophyllum spicatum* L. and *Vallisneria americana* Michx. Amer. Midland Nat. 102:263-272.

Titus, J. E. and W. H. Stone. 1982. Photosynthetic response of two submersed macrophytes to dissolved inorganic carbon concentration and pH. Limnol. Oceanogr. 27:151-160.

Van, T. K., W. T. Haller and G. Bowes. 1976. Comparison of the photosynthetic characteristics of three submersed aquatic plants. Plant Physiol. 58:761-768.

Wallis, M. 1986. 1984-1985 Okanagan Valley Eurasian water milfoil control program. British Columbia Ministry of the Environment, Water Management Branch, Victoria, B.C. 54 p.

Warrington, P. D. 1985. Factors associated with the distribution of

Myriophyllum in British Columbia. *In*: L. W. J. Anderson (ed), Proceedings of the First International Symposium on watermilfoil (*Myriophyllum spicatum*) and related Haloragaceae species. Aquat. Plant Manage. Soc., Washington, D.C. pp. 79-94.

Westlake, D. F. 1982. Ecology-community metabolism and production: the primary productivity of water plants. *In*: J. J. Symoens, S. S. Hooper and P. Compere, (ed), Studies on Aquatic Vascular Plants. Royal Botanical Society of Belgium, Brussels, pp. 165-180.

Wile, I., G. Hitchin and G. Beggs. 1979. Impact of mechanical harvesting on Chemung Lake. *In*: J. E. Breck et al. (ed), Aquatic Plants, Lake Management, and Ecosystem Consequences of Lake Harvesting. Proc. Conf. Madison, WI, Feb. 1979. Institute for Environmental Studies, Univ. Wisconsin-Madison, Madison, WI. pp. 145-159.

Wiley, M. J., R. W. Gordon, S. W. Waite and T. Powless. 1984. The relationship between aquatic macrophytes and sport fish production in Illinois ponds: a simple model. North Am. J. Fish. Manage. 4:111-119.