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Vegetative Spread of Eurasian Watermilfoil Colonies

JOHN D. MADSEN[1] AND DIAN H. SMITH[2]

ABSTRACT

Colonies of Eurasian watermilfoil (*Myriophyllum spicatum* L.) expand via stolon and fragment production. Clonal expansion primarily by stolons provides Eurasian watermilfoil with a means of localized spread, while intermediate distance expansion is provided by fragment production. These mechanisms of spread were studied in outdoor ponds at Lewisville, Texas, and the results were compared to a 1987 Lake George, New York study. In both studies, the predominant mechanism of vegetative propagation was stolon production. In the southern study, stolon production accounted for 74% of areal expansion while fragments accounted for 26%. Although plant establishment in new quadrats by fragments was not as successful an expansion strategy as stolons, this study determined that 46% of the fragments which settled onto the substrate successfully established and thus provided the species with a significant mechanism for a more rapid rate of population expansion.

Key words: autofragmentation, fragmentation, stolon, vegetative reproduction, clonal reproduction, *Myriophyllum spicatum.*

[1]U.S. Army Engineer Waterways Experiment Station, CEWES-ES-P 3909 Halls Ferry Road, Vicksburg, MS 39180-6199.

[2]U.S. Army Engineer Waterways Experiment Station, Lewisville Aquatic Ecosystem Research Facility R.R. #3, Box 446, Lewisville, Texas 75056-9720.
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INTRODUCTION

Eurasian watermilfoil is a submersed aquatic macrophyte which has three mechanisms of propagation: seed production, stolon production, and fragmentation (Smith and Barko 1990). Seeds serve as a long-term mechanism of reproduction (Madsen and Boylen 1989) which enables the species to survive protracted periods of dormancy (Madsen 1991). Seeds may sink in the immediate area of production or be transported long distances as fruit-containing spikes float (Nichols 1975).

Vegetative propagation is regarded as a more important mechanism of population expansion than seed dispersal, as indicated from previous studies (Kimbel 1982, Madsen and Boylen 1989, Madsen et al. 1988). Asexual propagules of Eurasian watermilfoil provide a mechanism for short-term clonal reproduction with contiguous to intermediate distance dispersal (Madsen 1991). Localized expansion is provided by stolon growth. Stems which form adventitious roots may establish new plants in the immediate area of the parent. Stolons, located in the upper few centimeters of the sediment, extend outward from the parent plant and produce new plants in the immediate area.

Fragmentation is another type of vegetative clonal propagation which provide intermediate to long distance dispersal (Aiken et al. 1979). Eurasian watermilfoil exhibits two types of fragmentation: autofragmentation and allofragmentation. Autofragmentation is the self-induced abscission of shoot apices, which generally occurs after peak biomass has been attained (Madsen et al. 1988, Madsen 1997, Kimbel 1982). Typically, one or more of the internodes located on the upper 15 cm to 20 cm of the apical tip develops roots and separation occurs shortly thereafter (Aiken et al. 1979). Allofragments are formed by the mechanical breakage of the plant stem by disturbances in the water, such as those generated by boats, swimmers, animals, and wave action. After separation from the parent plant, fragments usually descend to the sediment where they produce roots, anchor and establish new plants, depending on the suitability of *in situ* conditions. Autofragments, which have higher total nonstructural carbohydrate content, have been shown to grow and overwinter better than allofragments (Kimbel 1982).

The relative importance of the various methods of reproduction to expansion of Eurasian watermilfoil from an established population was studied previously in a four month investigation in Lake George, New York (Madsen et al. 1988). The Lake George study indicated that local spread was largely dependent on stolons. Stoloniferous expansion was prominent during mid-summer followed by a decline later in the season. This decline was correlated with plant mortality. Similarly, fragmentation demonstrated a strong seasonal trend with its prominence in September. The relative frequencies of newly-vegetated quadrats established by stolons and fragments were 74% and 26%, respectively. However, 50% of the quadrats into which autofragments settled early in the season did not contain Eurasian watermilfoil by the end of the study (Madsen et al.1988). Therefore, by the end of the northern investigation, the relative frequency of successful expansion by stolons accounted for 87%, while successful expansion by fragments accounted for only 13% of the total expansion.

The objectives of the current study in a southern climate were to determine the prominence of two modes of vegetative population expansion (stolons and autofragments) from a new, small colony of Eurasian watermilfoil; to determine the rate of spread over two growing seasons; and to analyze seasonal dispersal patterns of the two modes of propagation.

MATERIAL AND METHODS

The study was conducted in two 0.26 ha man-made ponds, approximately 30 m by 85 m each, at the U.S. Army Corps of Engineers Lewisville Aquatic Ecosystem Research Facility in Lewisville, Texas (Latitude 33°04’45”N, Longitude 96°57’33”W). Each of the two ponds were divided in half by an impervious barrier to provide a total of four separate study areas. The sampling regions in each pond contained one shallower region, which ranged in depth from 70 cm to 126 cm, and one deeper region, with depths ranging from 89 cm to 148 cm (Figure 1). Water was supplied by Lake Lewisville and constant water levels were maintained by screened standpipes.

Each sampling region was delineated by a 324 m^2 grid. The grid was formed by eighteen contiguous PVC frames with dimensions of 6 m by 3 m. Within each of the PVC frames, eighteen 1 m^2 quadrats were formed by nylon cord attached to the PVC perimeter. Therefore, each sampling region contained contiguous 1 m^2 quadrats forming an 18 m by 18 m grid. The grid systems were suspended in the water

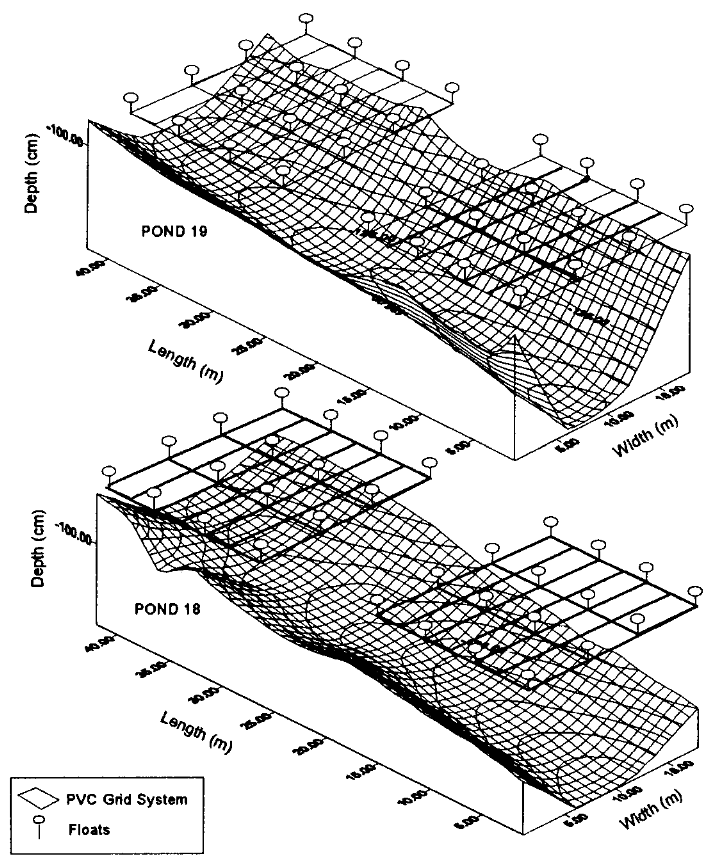

Figure 1. Schematic of the arrangement of grid system within the ponds.

via floats attached to the PVC perimeters and held stationary by attachment to metal posts driven into the sediment (Figure 1). The frame did not interfere with fragment dispersal.

Water temperature data was measured with an Omnidata EasyLogger™ (Logan, Utah) underwater thermistor affixed to a float and held at a depth of 15 cm below the surface of the water. Data were logged at 5 minute intervals and daily average water temperatures for the study period were calculated from logged hourly averages.

The study examined the local spread of Eurasian watermilfoil by planting, directly into the sediment, four shoot apices (each cutting was 10 cm in length) in the center four quadrats of each grid. From April 1992 to December 1993, observers recorded the presence or absence of rooted plants and fragments within the quadrats of the grid in each of the study regions approximately every other week.

Enumeration of the presence of rooted plants or fragments within the quadrats, which were recorded during each observation period, revealed the percent coverage by the two types of vegetative propagules and the overall growth of the colony. The transition from presence or absence of the type of vegetative propagule observed within a quadrat from one sampling period to the next was used to calculate daily rates of expansion (Madsen et al. 1988).

Stoloniferous expansion percentage rates were characterized by the transition from the absence of rooted growth within a quadrat during one sampling period to the presence of rooted growth during the next sampling period. Mortality was characterized by the transition from rooted growth present during one sampling period to no rooted growth present within the quadrat during the next sampling period.

Population expansion rates by fragments were categorized as fragment settling, fragment persistence, establishment of fragments, and fragment mortality. Percentage of fragment settling was characterized by the transition within a quadrat from the absence of fragments in one sampling period to their presence in the next sampling period. Persistence of fragments was characterized by the presence of fragments in two consecutive sampling periods. Establishment of fragments into rooted growth was characterized by the transition from fragments present in one sampling period followed by rooted growth present in the next sampling period. Fragment mortality or resuspension was characterized by the transition from the presence of fragments within a quadrat in one sampling period to the absence of the fragment in the next sampling period.

RESULTS AND DISCUSSION

During the expansion period of November 1992 through early June 1993, 74% of the population expansion was attributable to stolons while 26% was attributable to fragments. Expansion of the colonies began when temperatures approached 10°C after a prolonged cold-water period, and declined when temperatures increased to above 25°C (Figure 2A). Furthermore, during this key expansion period, stolon production radially increased the vegetative coverage from 21.4 quadrats to 177.3 quadrats which equates to a 3.1 cm^{-1} d^{-1} average radial expansion for the 229 day interval. Combined coverage by stolons and fragments which established new plants increased from 23.5 quadrats to 269.8 quadrats during this period. Therefore, the population expanded radially at a rate of 3.9 cm^{-1} d^{-1} during the key expansion period. Expansion in pond 19 lagged slightly behind pond 18, possibly due to higher turbidity early in the experiment. Otherwise, environmental factors were similar between the two ponds.

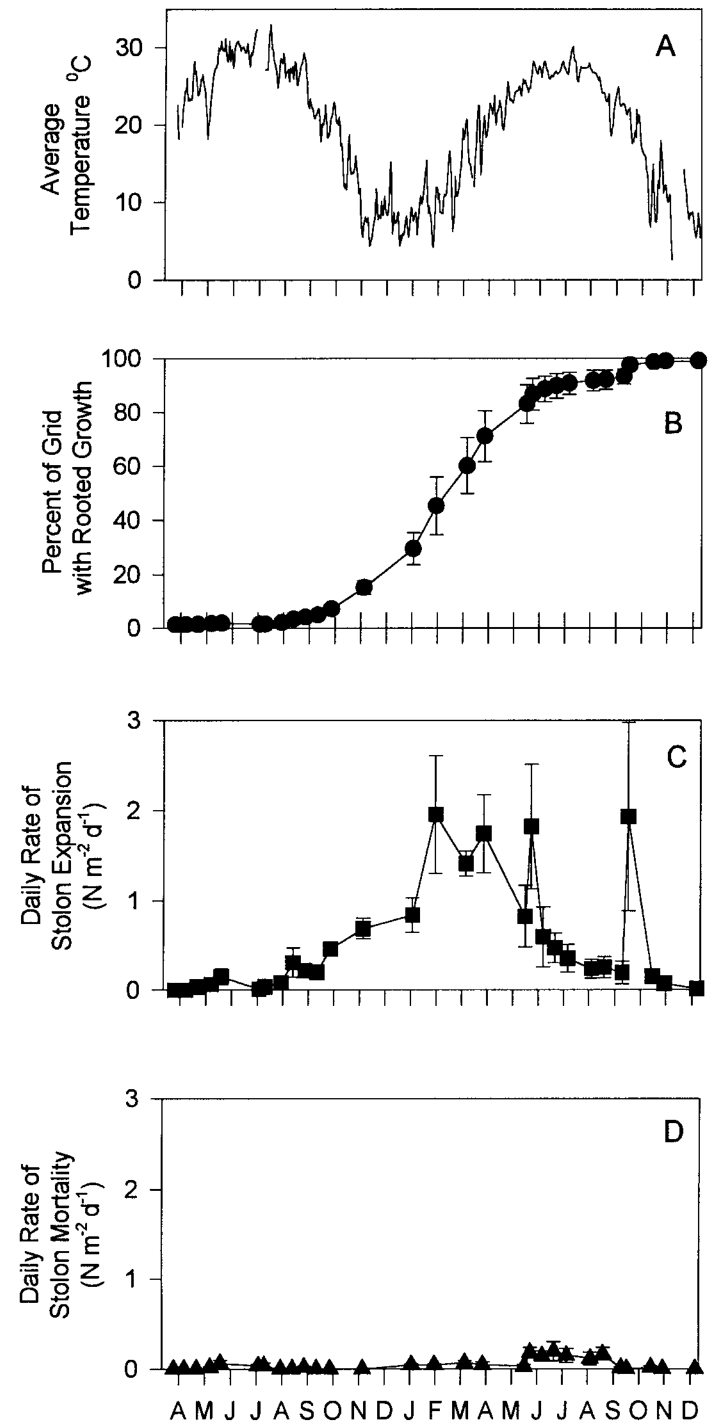

Figure 2. Stolon dynamics in experimental ponds. (A) Daily average water temperature during study period; (B) Percentage of sample areas vegetated by rooted growth; (C) Daily rate of expansion by stolons; (D) Daily rate of stolon mortality.

The interval from colonization, when the four shoot apices were planted, to dominance to dominance by Eurasian watermilfoil was April 1992 to June 1993. Between November 1992 and June 1993, the presence of rooted Eurasian watermilfoil increased from 15% to 83% of the sampling quadrats. Expansion continued at a reduced rate from late June through December 1993, resulting in 99% coverage by Eurasian watermilfoil (Figure 2B).

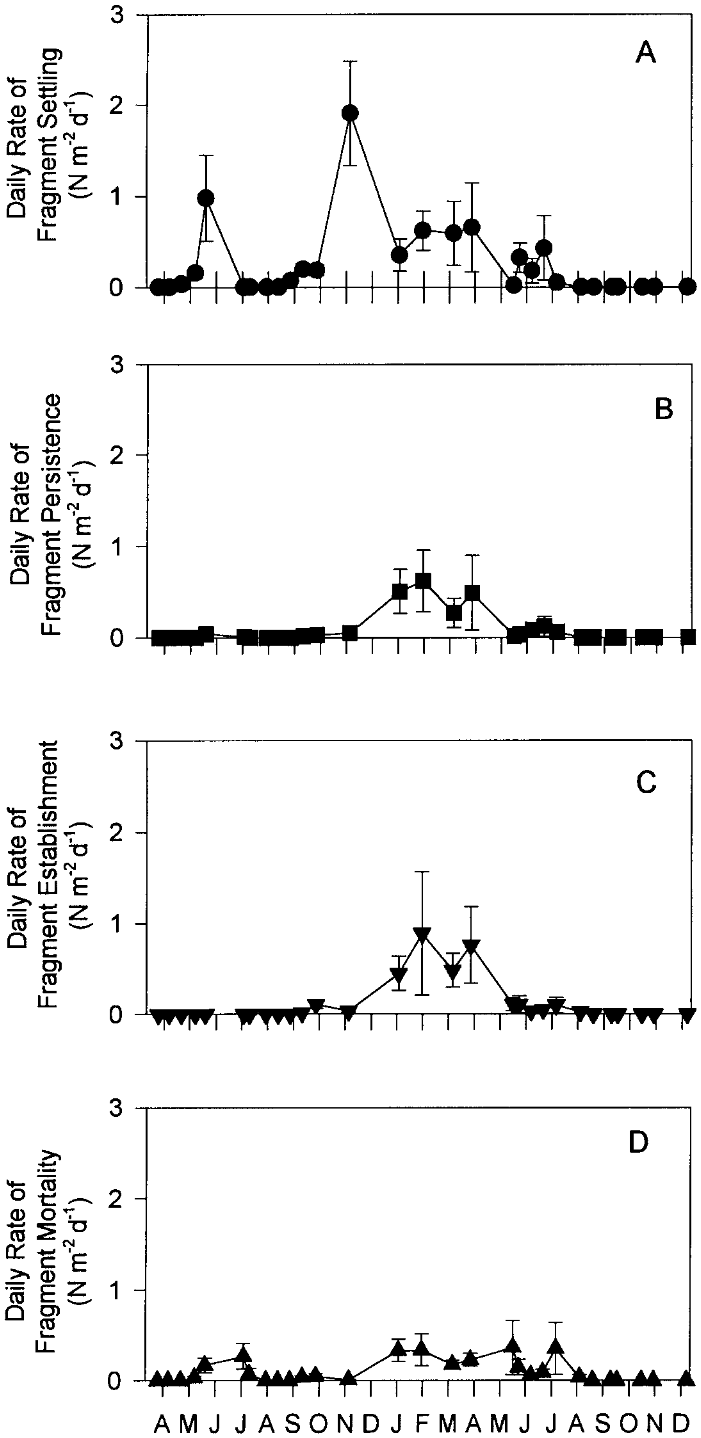

Figure 3. Fragment dynamics in experimental ponds. (A) Daily rate of fragment settling; (B) Daily rate of fragment persistence; (C) Daily rate of fragment establishment into rooted plant; (D) Daily rate of fragment mortality.

The peak expansion interval occurred between November 1992 and June 1993 when the linear rate of daily expansion between sampling periods ranged from 0.68 ± 0.12 N m^{-2} d^{-1} to 1.95 ± 0.65 N m^{-2} d^{-1} (Figure 2C). Throughout the investigation, observed stolon mortality was $\leq 0.20 \pm 0.11$ N m^{-2} d^{-1} (Figure 2D). Thus, once stolon expansion was initiated, the colony maintained a continual increase in size, since little mortality of stolons was observed.

In comparison to the northern study where rapid expansion was found in July through August (Madsen et al. 1988), the southern study found the interval of rapid expansion by stolons to be November through June. Additionally, the New York study found that mortality had a significant role in the dynamics of colony expansion, with a peak mortality rate of 10% during September. In contrast, the Texas study found mortality to be negligible.

These seemingly opposed conclusions may be due to differences in the successional state, water depth of study areas, light attenuation, photoperiod, temperatures and sediment nutrient levels. The northern study was conducted in a well developed ecosystem in which the Eurasian watermilfoil had to compete with an established native plant community. Conversely, the southern study was conducted in a recently flooded, unvegetated ecosystem. Competition from native plants was minimal; the only competing species within the study areas were two native annuals, muskgrass (*Chara vulgaris* L.) and southern naiad (*Najas guadalupensis* (Sprengel) Magnus). The northern study was conducted in 1 m to 5 m of water whereas the southern study was conducted in less than 1.5 m. Water depth and turbidity would account for differences in light attenuation. Photoperiods were also dissimilar. The northern study received more pronounced changes in photoperiod, with shorter days in fall and winter compared to summer months. The northern study experienced a greater temperature fluctuation than the more moderate temperature regime of the southern study. While the southern study had its peak expansion during the late fall and winter months, the northern study showed increased mortality as the winter approached. Additionally, the northern site was characterized by lower nutrients and alkalinity than the southern site, and this could have increased milfoil mortality in the northern study.

However, the greatest difference is change in phenology that Eurasian watermilfoil undergoes from the northern sites

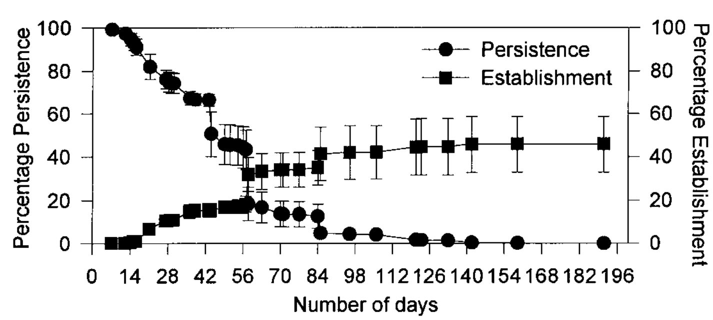

Figure 4. Number of days fragments persisted before rooting in the sediment and establishing new plants.

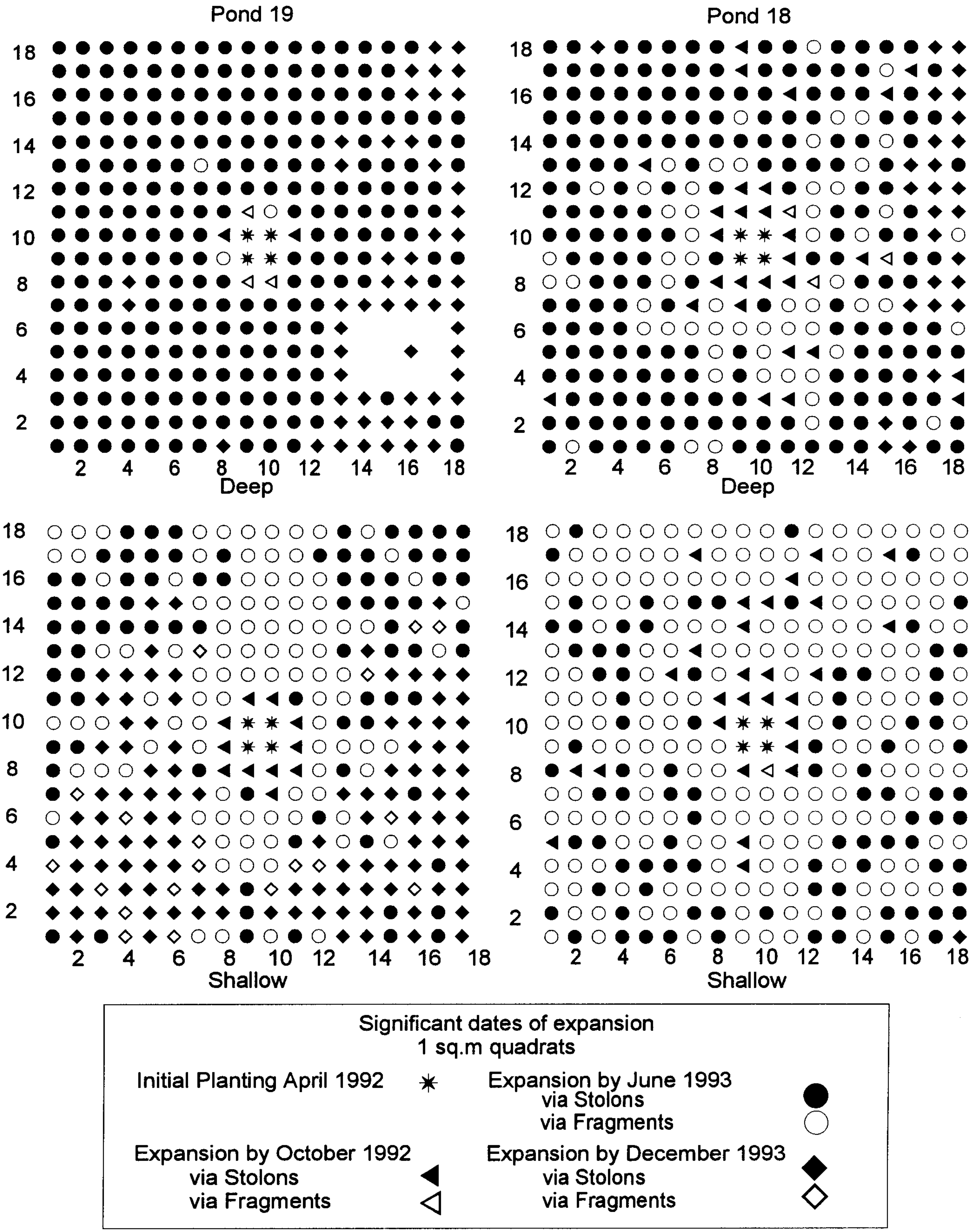

Figure 5. Significant dates of expansion per sampling area by stolons versus fragments.

to southern sites. In the northern part of its range, the phenology of Eurasian watermilfoil has active growth in the summer, with a winter senescence period. In southern regions, Eurasian watermilfoil appears to slow in growth during the summer months when water temperatures exceed 25 to 28°C, with plant growth active throughout periods with water temperatures above 10°C (Madsen 1997).

A major episode of settling occurred during November 1992. These fragments settled into new quadrats at a rate of 1.91 ± 0.58 N m^{-2} d^{-1} (Figure 3A). After the November 1992 fragment settling episode and continued settling through April, the persistence rate ranged from 0.27 ± 0.16 N m^{-2} d^{-1} to 0.62 ± 0.34 N m^{-2} d^{-1} (Figure 3B). Two months after the initial settling pulse of fragments there was a peak in fragment establishment. From January through April 1993, the rate of population expansion by fragments ranged from 0.45 ± 0.19 N m^{-2} d^{-1} to 0.89 ± 0.68 N m^{-2} d^{-1} (Figure 3C). Fragment mortality followed the initial pulse of fragmentation by two months and continued until June 1993 (Figure 3D).

During the study, there were a total of 714 incidents of fragment settling within the quadrats of the four sampling areas. Fragments persisted on average 44 days, before either establishing a new plant or dying. Within the four sampling areas, 46% of the fragments established new plants while 54% did not remain viable (Figure 4). The distance traveled by fragments ranged from 1 to 8 m, with a median distance of 5 m traveled from the original colony.

Additionally, significant difference in expansion by fragments versus stolons was observed in the shallow versus deep survey areas (Chi-square $p < 0.01$). Wind direction was predominately from the southwest to northeast and expansion by fragments appeared to increase from the leeward side toward the windward side (Figure 5).

Although conditions in this experiment may have reduced the significance of fragment propagation (low current, limited space), nonetheless it is apparent that, whereas stolon growth may be more successful than spread by fragment, it is more restricted spatially. Autofragments, while less certain of success than stolons, are a reproductive strategy that can vegetatively spread Eurasian watermilfoil large distances, with higher success rates than seed propagation or vegetative propagules of some other aquatic plant species.

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