Relationship between the spatial scale and biotic variability in a wetland ecotone

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Abstract

We studied potential effects of the expansion of a wetland ecotone on phytoplankton communities. The expansion of ecotone width and emergence of a mosaic of habitats are expected outcomes of a reduction of carp numbers and a consequent managed vegetation recovery. Specifically, we investigated the effects of decreasing size of open water cells on species richness, abundance and diversity. In a set of experimental enclosures of four different sizes we sampled phytoplankton weekly during 1991. The phytoplankton communities showed similar patterns of seasonal change but no clear differences in species abundance or richness that could be attributed to the system size. Notably, however, the magnitude of variation in the community structure metrics responded strongly to the enclosure size. This indicates that the importance of scale may not be fully appreciated when analyzed in the light of standard community measures. We tentatively conclude that the variation in species composition, individual responses, richness, and abundance may result in an increasing diversification of the wetland ecotone as the recovery of vegetation advances.

Introduction

An ecotone is a zone of transition between adjacent ecological systems such as a uniform macrophyte stand and open water (Holland, 1988). Wetland ecotones may vary from sharp and narrow to wide and diffused. In the case of a spreading vegetation front, the transition zone may take the form of an abrupt change in plant presence and density or may extend over a wider area with gradual and heterogeneous decrease in macrophyte densities. In the latter case, the ecotone appears as a mixed zone of vegetation and open water patches. Characteristics of such patches and their role in wetland function are unknown (Holland *et al.,* 1990). Cootes Paradise, a coastal wetland of Lake Ontario, presents an opportunity for postulating and testing hypotheses addressing the properties of ecotone internal patches. We will articulate a specific hypothesis later on.

In Cootes Paradise, both emergent and submergent macrophyte vegetation is currently at its lowest compared to the past patterns (Painter *et al.,* 1989). Several factors are implicated in the demise of macrophytes, and they appear to interact. Carp reproduction and feeding, wind driven sediment resuspension resulting in low light penetration, long-term water level fluctuations, and excessive algal densities were postulated. Fish role in the demise of the wetland **is** of particular interest because of its complexity and amenability to remedial manipulation. Carp has a direct or
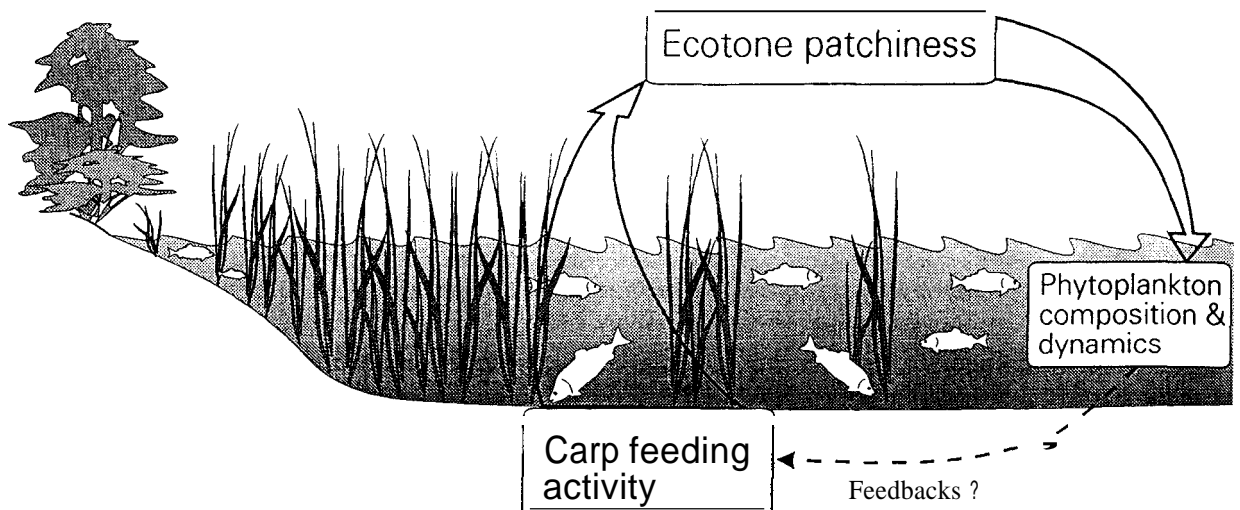
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Fig. 1. Major links between carp. *Cyprinus carpio*, emergent vegetation, habitat heterogeneity, and other components of the wetland ecosystem. Carp is a 'keystone' species

indirect impact on macrophyte development and spread, amount of suspended sediments, light availability, nutrient dynamics, benthos composition and abundance. Many of these factors influence algal ecology (Fig. 1). A restoration plan under development aims at the reduction of carp densities and activities. Preliminary experiments indicate that the reduction of carp density will allow plant recovery (unpublished). Based on the past states of Cootes Paradise documented by aerial photographs, we expect to observe the following trends in the wetland characteristics to be associated with the carp control (Fig. 2): (a) a reduction in open water areas, (b) increase in plant, fish and wildlife diversity, (c) improvement in water clarity, (d) increase in the amount of 'edge' habitats and (e) a decline in the size of remaining open water patches or cells.

The last two expected trends represent changes in spatial scale and patterns and can be addressed experimentally. Furthermore, biological trends associated with these changes can be predicted and tested within the framework of hierarchy theory (cf. Allen & Hoekstra, 1992). Specifically, this theory predicts that population and community parameters should be more variable at smaller spatial scales (Kolasa & Waltho, **1994).**

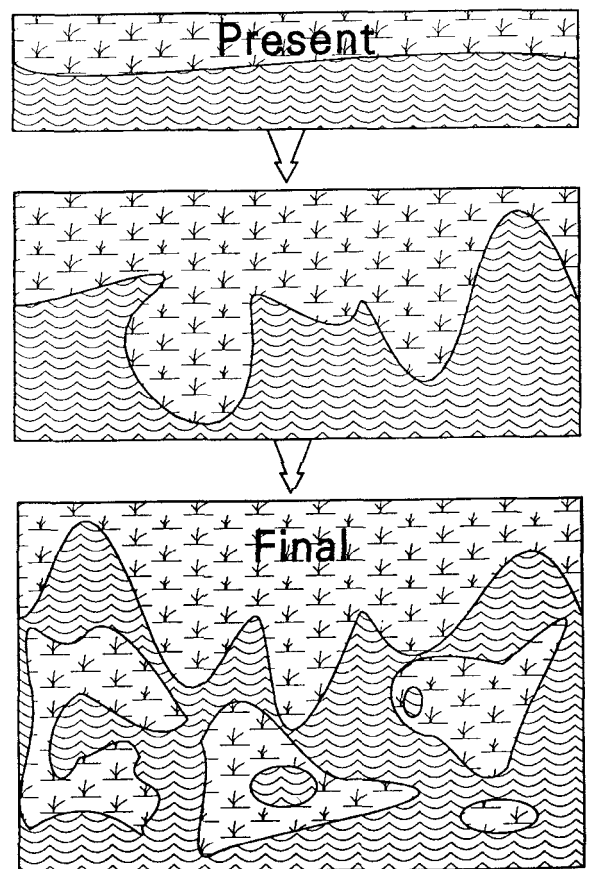The goal of the study was to test this prediction and provide a quantitative evaluation of the vari-

Fig. 2. Schematic expected trends in wetland development based on the past known conditions in Cootes Paradise.

ability of selected community parameters. Our approach to achieve this goal was experimental.

Study site and methods

Emergent macrophytes persist in the shallowest littoral zone only. They consist primarily of cattails (*Typha angustifolia*) and occasional patches of manna grass (*Glyceria aquatica*), and bur reed (*Sparganium sp.*). Submersed plants are absent throughout most of the season but may appear in small numbers towards the end of summer.

We established a total of 12 enclosures of four different sizes (three replicates of each $1 m^2$, $4 m^2$, $9 m^2$, $16 m^2$) and 3 control plots at a site near the western end of Cootes Paradise Fig. 3), about 15 m away from the nearest emergent vegetation. The enclosures were constructed of plastic foil reinforced externally by chicken wire. The placement of enclosures and controls was randomized on a grid of 5 m by 5 m squares, in four rows
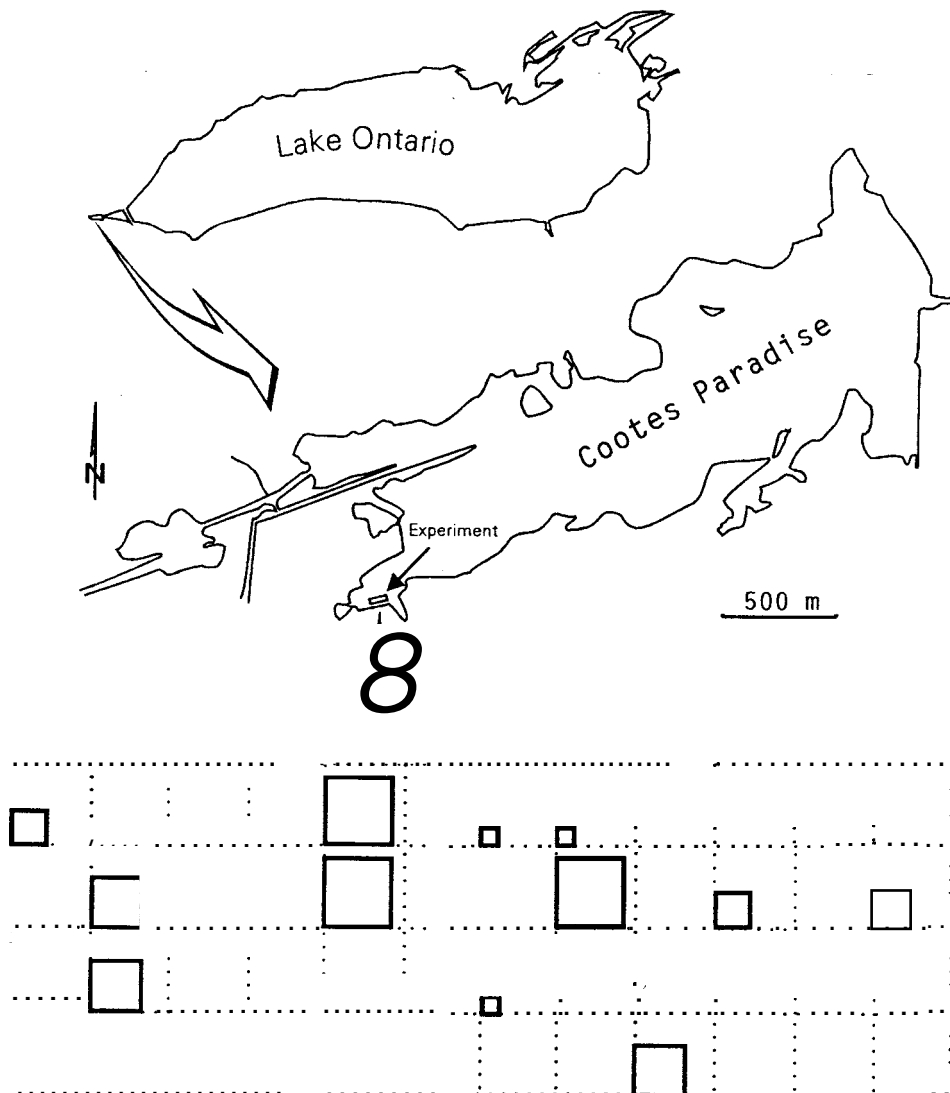

Fig. 3. Geographical location and placement of treatment enclosures in the field. Bold squares represent plastic enclosures of different sizes. Other enclosures and controls (not shown) were randomly spread in the remaining cells of the grid.

parallel to the shore (Fig. *3*). We measured basic physical parameters within the enclosures and in controls. Light conditions were assessed using a Secchi disk. Oxygen and pH were measured using portable meters.

Sampling commenced June 21, 1991 and ended August 15, 1991. One sample was taken from each enclosure and control site, at a sampling frequency of every third day. Samples were taken at approximately the same time each day, 10:00 am ± 1 hour.

A sampling device was applied to ensure that the composite sample contained plankton from the whole water column. The device consisted of a 1 l NALGENE® bottle fitted between 2 square plates of plexiglass, with a hole drilled in the top plate to accommodate the neck of the bottle. The plates were maintained in position by the use of four metal posts screwed tightly to each corner. The apparatus was weighted by a brick wedged between the plexiglass at the bottom of the bottle and another piece placed below it. The entire apparatus was attached to a rope and lowered and lifted twice before the 1 l bottle was filled. A portion of the integrated sample was then transferred to a labelled 25 ml glass scintillation vial. After the fifteen scintillation vials were filled with their respective samples, they were taken to the lab and preserved with 0.2 ml of LUGOL's iodine within an hour of finishing sampling. Samples were counted using a ZEISS inverted microscope at magnification of 40 x with phase contrast. Ten random viewing fields in which all algae were identified and counted were chosen along a straight (transect) line. Organisms were identified using a variety of sources (Findlay & Kling, 1979; Prescott, 1970; Skuja, 1964; Skuja, 1956; Taft & Taft, 1971; U.S. Federal Water Pollution Control Administration, 1966).

Results

The enclosures showed almost no consistent differences among **sizes** and did not differ from controls except for the water transparency. The water transparency was higher in the enclosures (15 cm

on average) than in controls (6 cm on average; ANOVA, $p < 0.0000$). The variability of oxygen, pH, light, and temperature showed no significant differences among treatments and controls (one way ANOVA). We have not conducted post-hoc analyses with contrasts that might reveal less prominent patterns. We have found forty-eight algal taxa to occur at least on one occasion in either treatments or controls. These taxa responded in a variety of ways which we briefly characterize below. The most important aspects of this response include (1) the number of taxa involved in community changes and (2) the magnitude of variability. We concentrate on these two results because of their significance for the interpretation of the test outlined earlier.

Species abundance and richness increased steadily within the enclosures over the season and were correlated (adjusted $r^2 = 0.641$). By contrast,
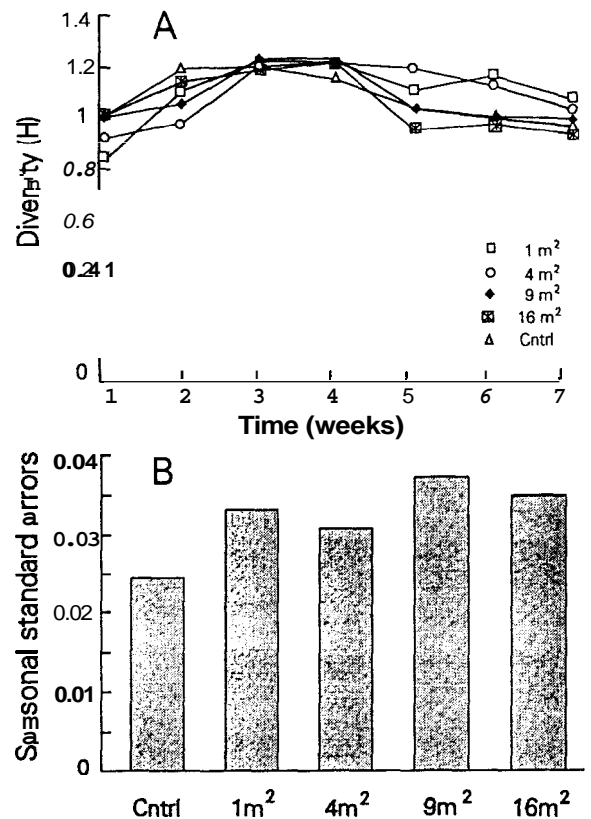

Fig. *4*. Richness (A) and abundance (B) of algae in the experimental enclosures and control areas during the summer of 1991.
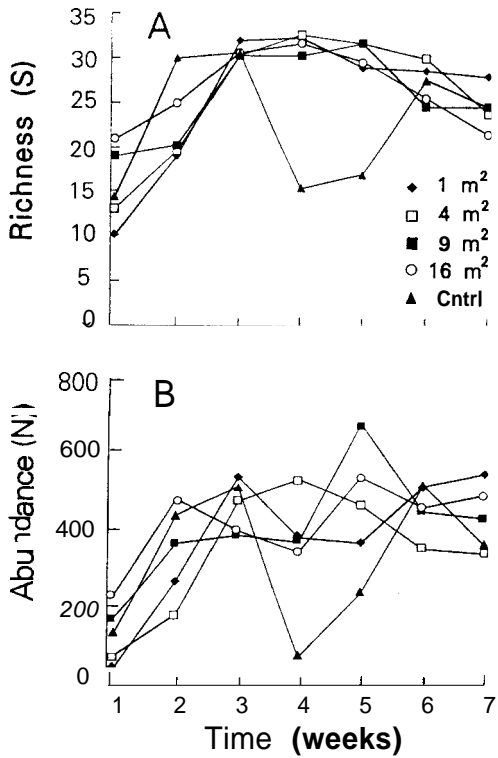
Fig. 5. Diversity means **(A)** and seasonal variation (B) in enclosures of various sizes and in control areas.

species richness and abundance outside the enclosures showed much greater variation over the season (Fig. 4A, **B**). The community structure was evaluated by the Shannon-Weaver index of diversity. This index summarizes the pattern of abundance distribution across species. Diversity showed some seasonal variation (Fig. **5A**) but, once again, we failed to find significant differences between the controls and treatments (Fig. 5B). In the next step, we examined the variation at the species level. First, we found that different sets of species were responsible for seasonal variation in different enclosures. Second, and more importantly, we found that more species contributed significantly to that variation in small enclosures than in large enclosures. We observed a striking difference between the number of species responsible for temporal density variation in large enclosures (11 and 14 species for 9 m^2 and 16 m^2 enclosures, respectively) and controls (22 species). Furthermore, as many as 32 species showed significant temporal variation in all enclosures taken together than in the control system outside. The question emerges then as to
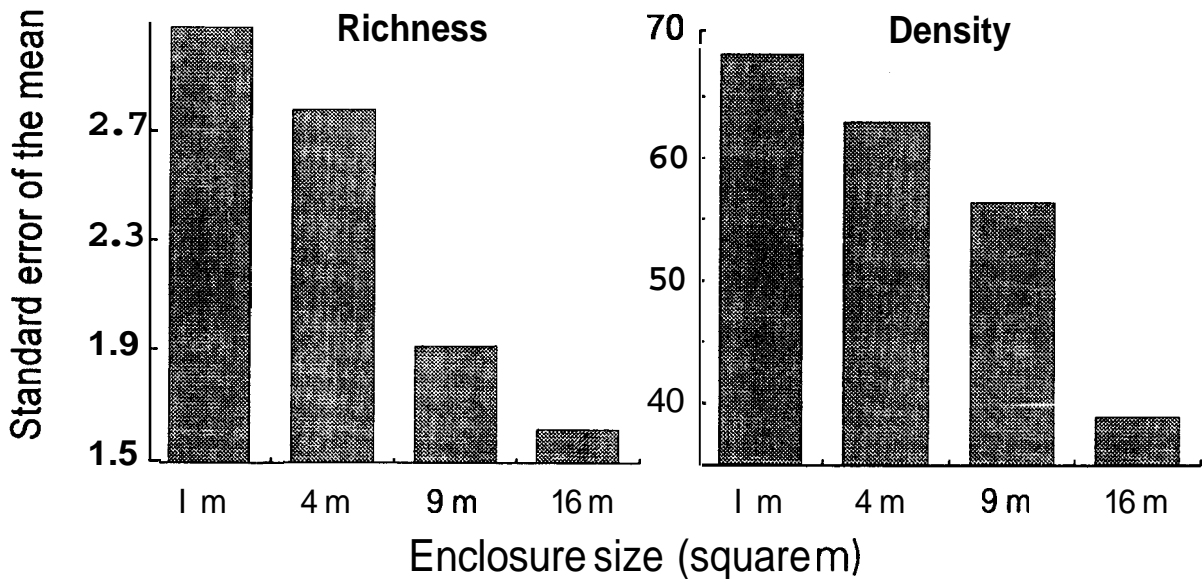

Fig. 6. Variability of algal richness and abundance (density) represented as seasonal standard errors in enclosures of various sizes. Variability in the **control** areas was substantially greater. Trends are statistically significant (see text).

the nature of this variability. An ANOVA showed that the species richness, abundance, and diversity responded in a highly variable manner but that 'differences among the means were not significant. In order to assess what was the nature of this variability, we compared standard errors of the seasonal means for both the abundance and richness of algal taxa (Fig. 6). We found that there was a clear declining trend with the increasing enclosure size (Regression fitted to standard errors, $r^2 = 0.9177$, $p < 0.042$).

Discussion and conclusions

The quality of our results might have been influenced by the taxonomic level of identification even though a generic name identifies a single species in most cases. Generally, a taxonomic detail might be expected to strengthen some of our quantitative analyses without, however, having a major impact on the conclusions (e.g. Rahel, 1990). Other sources of error potentially include changes in periphyton to phytoplankton ratios associated with the decline in the amount of enclosure material available for attached algae in larger enclosures relative to smaller ones. We have no data that would allow to explain a major decline in abundance and richness in control areas observed in the middle of the summer (Fig. 4). One possible cause of the difference between controls and treatments is wind driven water movement from other portions of the marsh. Such incoming water would not affect the community structure within the enclosures.

We are not aware of other studies varying the size of enclosures in wetlands. Various scales of variation in aquatic systems were however investigated using other organisms or measures. For example, Carpenter & Kitchell (1987) used model simulations and found that the variance of primary production and its covariance with other dynamic variables are a function of temporal sampling scales. Their observations agree with our conclusion that scale affects variability but differ in the specific pattern observed and the type of scale investigated. Specifically, Carpenter &

Kitchell(1987) found that coefficients of variation stabilized at a certain level when temporal scales larger than 7 days were treated as samples. We found variation in species abundance and richness to be less at larger spatial scales.

While this study aims at identification of the patterns of variability in the phytoplanktonic community structure, we feel obliged to provide some plausible hypotheses to address the more puzzling results. The general pattern of smaller variation in larger enclosures could be tentatively explained by cancelling effects of patch heterogeneity on the population dynamics of individual species. This idea has been first proposed by Hutchinson (1961) and further resumed by Hebert & Crease (1980) with respect to zooplankton. Such a heterogeneity would presumably increase in larger enclosures and thus could be responsible for the reduction of variation in those enclosures. The observed larger variation in controls as opposed to treatments could be explained by wind driven water movements in the marsh. Such movements are likely to bring about different communities of algae from various parts of the marsh that is known to be limnologically diverse (Painter *et al.,* 1989). Given the isolation of aquatic communities in the enclosures, water movements could not result in species substitutions directly. The difference between the number of significantly variable species in enclosures taken jointly and the control areas is of considerable interest because it indicates the importance of microhabitat isolation for the generation and maintenance of diversity. While the variation in small isolated microhabitats may threaten the persistence of some species, the interplay between the diversity of those microhabitats these habitats offer and the differential species responses to individual microhabitats appears to provide an overall enhancement of ecosystem diversity at the phytoplankton level.

In conclusion we may identify the following processes and trends:

1. Variation of phytoplankton communities declines with an increase in the spatial scale the community exists at. This variation is ex-

pressed at various levels of ecological resolution. It was observed in agglomerative parameters such as species richness or total abundance and at the compositional level.

2. Microhabitat isolation and fragmentation, as exemplified by the collection of enclosures, appears to increase overall diversity of ecological components and behaviors. This genera! observation is illustrated by the increasing number of species in small enclosures that show significant variation through time.

3. Diversity remains constant suggesting that the phytoplanktonic communities quickly compensated for major abundance changes at the species level.

All the above trends are likely to intensify with the increasing width and complexity of the ecotone postulated by the restoration plan (Fig. 2). A comparison of patterns exhibited by zooplankton and benthos with those of phytoplankton is likely to shed more light on the generality of the observations made here and on the possible interactions among all those ecotone components.

Acknowledgement

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