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Expanding American Lotus and Dissolved Oxygen Concentrations of a Shallow Lake

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ABSTRACT.—Lakes and reservoirs often experience sudden increases in macrophyte biomass. These changes have the potential to alter the abiotic environment in ways that affect other species. The American lotus (*Nelumbo lutea*) is expanding its distribution across portions of North America. *N. lutea* forms a dense canopy over the shallow margins of lakes and may influence the abiotic properties of the littoral zone, but this hypothesis has not been tested. Here we investigate the effects of a growing bed of *N. lutea* on water quality in Pymatuning Reservoir. In summer 2007 we deployed remote logging sensors to measure dissolved oxygen and temperature inside of a *N. lutea* bed and in adjacent open water. Dissolved oxygen concentrations were consistently lower in the lotus bed than in open water and oxygen concentrations within the *N. lutea* bed declined over the course of the summer. In Jul. and Aug. the *N. lutea* beds experienced hypoxia while oxygen concentrations remained high in open water. Low dissolved oxygen levels in *N. lutea* beds may affect the distribution of fish and invertebrates and alter biochemical processes in the epibenthos.

INTRODUCTION

Lakes often experience sudden increases in macrophyte biomass due to colonization or rapid expansion of an invasive species (Jeppesen *et al.*, 1997; Scheffer, 1998; Unmuth *et al.*, 2000). Most studies of aquatic invasive macrophytes focus on how environmental conditions facilitate invasion, but relatively few studies examine how changes in macrophyte abundance affect the abiotic environment (Rai and Munshi, 1979; Carpenter and Lodge, 1986; Caraco and Cole, 2002; Veitch *et al.*, 2007). Increased macrophyte biomass can dramatically influence aquatic ecosystem function because macrophytes fix carbon, attenuate light, produce oxygen, restrict water movements, cycle nutrients and stabilize sediments (Wetzel, 2001). Especially important are the potential effects of macrophytes on dissolved oxygen concentrations. A few studies suggest that dense beds of submerged macrophytes can cause localized oxygen depletion in lakes and reservoirs by reducing turbulent mixing, blocking light penetration

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and contributing to ecosystem respiration (Unmuth *et al.*, 2000; Mohseni *et al.*, 2001; Colon-Gaud *et al.*, 2004). Warm-water fish and invertebrates begin to experience acute physiological stress when dissolved oxygen falls below 2.5 mg/l (*e.g.*, Moss and Scott, 1961; Smale and Rabeni, 1995; Killgore and Hoover, 2001; Landman *et al.*, 2005), so hypoxia associated with high macrophyte density will likely lead to depauperate fish and macroinvertebrate assemblages (Saint-Paul and Soares, 1987; Cardinale *et al.*, 1997; Miranda and Hodges, 2000; Burlakova and Karatayev, 2007). Oxygen deficits may also alter the nature of biogeochemical reactions and sediment oxidation-reduction potentials (Wetzel, 2001).

Studies of macrophytes and dissolved oxygen depletion have focused on submerged macrophytes, but we expect that floating and emergent macrophytes will have the strongest tendency to reduce dissolved oxygen concentrations (Rose and Crumpton, 1996; Caraco and Cole, 2002). Floating and emergent foliage contribute little oxygen to the water during photosynthesis but dense growths can block light, thereby limiting in-water photosynthesis by submerged macrophytes, periphyton and phytoplankton (Cataneo *et al.*, 1998; Frodge *et al.*, 1990; Caraco and Cole, 2002). A number of highly invasive aquatic plant species are characterized by floating or emergent leaves (*e.g.*, water chestnut *Trapa natans*, water hyacinth *Eichornia crassipes*, floating fern *Salvinia molesta*, water lettuce *Pistia stratiotes*, narrow leaf cattail *Typha angustifolia*), but there are relatively few studies of how these species affect oxygen concentrations in shallow lakes and wetlands (but *see* Frodge *et al.*, 1990; Caraco and Cole, 2002).

Here we evaluate the effect of *Nelumbo lutea*, the American lotus, on oxygen concentrations in a shallow reservoir. *Nelumbo lutea*, a perennial, is native to eastern and central North America and locally abundant. In some localities, *N. lutea* is rapidly expanding its local distribution (*e.g.*, Whyte *et al.*, 1997; Burlakova and Karatayev, 2007). Colonies of *N. lutea* expand by growth of large rhizomes. Colony expansion can exceed 15 m per year (Hall and Penfound, 1944; Rogers, 1981). The plants produce a very dense growth of large floating and emergent leaves. The dense growth habit of *N. lutea* potentially restricts water movement and the layers of floating and emergent leaves block most light from entering the water column, shading submerged vegetation. Floating and emergent leaves add little oxygen to the water column during photosynthesis (Pokorný and Rejmanková, 1984), and the floating leaves likely inhibit gas exchange between water and the atmosphere. This growth architecture leads us to predict that oxygen concentrations will be lower within *N. lutea* beds than in uninvaded open water locations.

METHODS

We assessed oxygen concentrations in the *Nelumbo lutea* beds of Pymatuning Reservoir, Pennsylvania's largest inland lake (surface area = 6645 ha). The lake is shallow, turbid and very eutrophic (*see* Turner and Ruhl, 2007 for a more complete limnological description). *Nelumbo lutea* populations have been present in the lake for decades but were restricted to a few small and stable populations. In 1998 *N. lutea* simultaneously colonized several disjunct areas in the northern portion of the reservoir, presumably via seed dispersal and germination, and began rapid expansion via clonal growth. By 2007 *N. lutea* dominated more than half of the shoreline in the northern portion of the reservoir. *Nelumbo lutea* forms an approximately 80-m wide belt of vegetation in shallow water along the shoreline and extending to the 1-m depth contour.

This is a comparative study of oxygen concentrations in the littoral zone and open water in one portion of the reservoir. We used two YSI-7960 data logging sondes (Yellow Springs Instrument, Yellow Springs, Ohio, USA), equipped with Clark style polarographic oxygen

TABLE 1.—Dissolved oxygen concentrations and temperature within a bed of *Nelumbo lutea* and an adjacent open water location in Pymatuning Reservoir. All oxygen concentrations are mg/l. Hypoxia is defined as dissolved oxygen concentrations less than 2.5 mg/l

	Jun.		Jul.		Aug.	
	Lotus	Open water	Lotus	Open water	Lotus	Open water
Daily mean concentration	5.9	5.9	4.3	9.7	1.6	7.5
Minimum concentration	3.02	4.50	1.74	7.81	0.81	4.84
Frequency of hypoxia (%)	0	0	10.6	0	100	0
Temperature (C)	25.1	25.0	25.1	25.5	27.1	27.0

electrodes, on 28–29 Jun., 8–9 Jul. and 2–3 Aug., 2007 to collect oxygen and temperature data at 10 min intervals over 24 h. On each date we deployed one sonde 10 m inside the outer edge of the *Nelumbo lutea* bed and another sonde was deployed adjacent to the first but 10 m beyond the outer edge of the *N. lutea* bed. Thus, the two sondes were in water of similar depth (<20 cm difference) and were located just 20 m apart. Sondes were anchored to a floating buoy and deployed in water between 80 and 120 cm in depth. In Jun. and Jul. the oxygen probes were positioned 30–40 cm above the lake bottom. In Aug. the sonde-to-buoy attachment was modified so that the probes were 30 cm from the water's surface, which placed the probes 60–80 cm above the bottom of the lake. Oxygen sensors were calibrated to atmospheric saturation prior to deployment. After retrieval, we recalibrated each sonde and noted instrument drift. Oxygen readings after retrieval were always within 0.2 mg/l of the calibration value.

RESULTS

In Jun., time averaged oxygen concentrations were the same in *Nelumbo lutea* beds and in open water, but minimum dissolved oxygen concentrations were slightly lower within *N. lutea* beds (difference = 1.48 mg/l, Table 1). Neither location experienced hypoxia (defined as dissolved oxygen concentrations lower than 2.5 mg/l) during the 24 h study period. Oxygen concentration in open water showed the diel pattern of variation typical of lakes, peaking in midafternoon, but oxygen concentration in *N. lutea* beds followed an anomalous diel pattern as it peaked near midnight and reached its minimum at midday (Fig. 1). This pattern is likely due to bulk transport of oxygenated water from outside the beds driven into lotus beds by wind or internal waves. Water temperature, averaged across the day, differed between the two sites by just 0.1 C.

As the summer progressed, dissolved oxygen concentrations within *Nelumbo lutea* beds fell steadily while oxygen remained high in open water, so differences in oxygen concentrations between *N. lutea* beds and open water became more pronounced (Fig. 1). In Jul., minimum oxygen concentrations were 6.07 mg/l lower in *N. lutea* beds than in open water, and time-averaged oxygen concentration were 5.4 mg/l lower in *N. lutea* than in open water (Table 1). The *N. lutea* bed experienced hypoxia at a frequency of 10.6%, but oxygen concentrations in open water remained above 2.5 mg/l throughout the diel cycle. Oxygen concentration at both sites followed typical diel patterns, peaking in late afternoon. Peak diel oxygen concentration in the *N. lutea* occurred 1 h later than in the open water. The temperature difference between open water and *N. lutea* beds was 0.4 C.

By early Aug. hypoxia was persistent in the *Nelumbo lutea* beds, even though dissolved oxygen concentrations in open water were near saturation (Fig. 1). The mean dissolved oxygen concentrations within *N. lutea* beds were lower than in Jun. or Jul., but mean oxygen

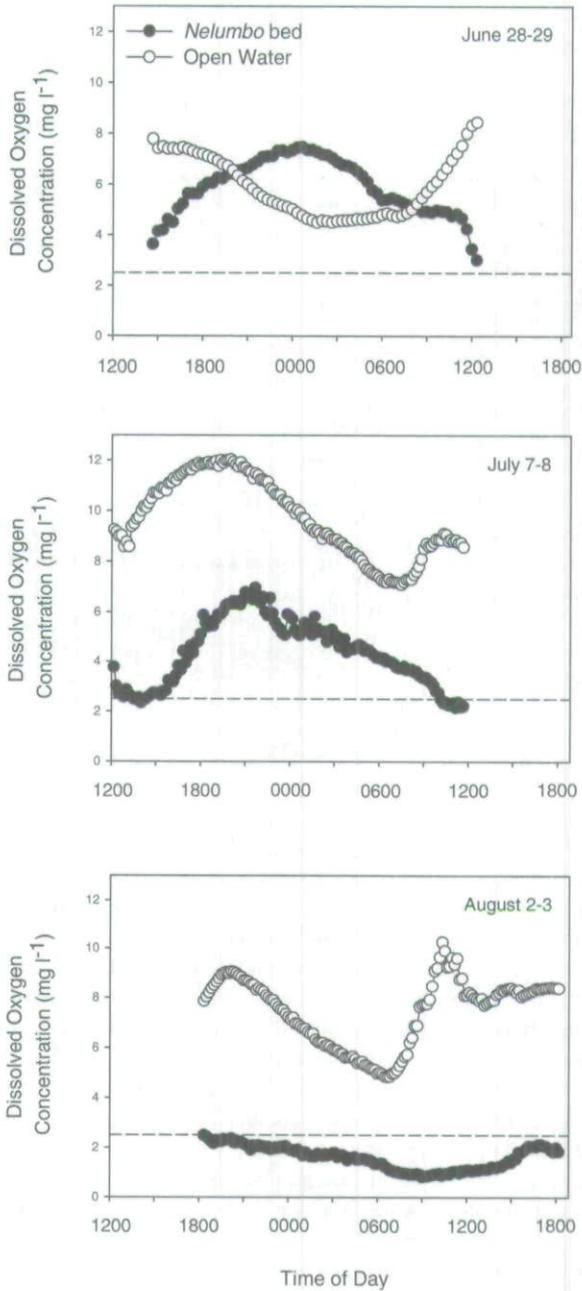


FIG. 1.—Diel variation in dissolved oxygen concentrations in a bed of *Nelumbo lutea* and an adjacent open water location in Pymatuning Reservoir. Dashed line denotes 2.5 mg/l

concentrations in open water were similar to that in earlier months, so differences in mean oxygen concentrations in open water and *N. lutea* beds were most pronounced in Aug. (difference in means = 5.9 mg/l; Table 1). Minimum oxygen concentrations were 4.03 mg/l lower in the *N. lutea* beds than in open water (Table 1). As in previous months, temperature differences between sites were small, averaging just 0.1 C.

DISCUSSION

Hypoxia plays a central role in organizing aquatic communities and is a primary water quality concern. The effects of increased loadings of organic material or nutrients on hypoxia are well established. Less studied is how introduced or invasive (e.g., rapidly expanding native or introduced) species may affect oxygen concentrations (but see Rai and Munshi, 1979; Carpenter and Lodge, 1986; Caraco and Cole, 2002; Veitch *et al.*, 2007). *Nelumbo lutea* is a rapidly expanding species and is of concern in many areas, but we are not aware of any other studies of how the widespread expansion of *N. lutea* may affect oxygen concentration in littoral areas of lakes. Our data show that oxygen concentrations were lower in the *N. lutea* bed than in open water, and that these differences became more pronounced as the summer progressed.

Environmental alteration by *Nelumbo lutea* likely caused lower oxygen concentrations in the *N. lutea* beds. Ongoing investigations show that the biomass of submerged macrophytes and phytoplankton abundance are lower in the *N. lutea* beds than in the open water (Turner *et al.*, pers. obs.). Submersed macrophytes and phytoplankton are likely limited because of shading by *Nelumbo*, and there is evidence that *Nelumbo* may produce allelopathic agents that reduce the growth of submersed macrophytes (Vance and Francko, 1997; Whyte and Francko, 2001). Reductions in primary production in the water column as a result of shading or allelopathy would decrease oxygen added to the water through photosynthesis.

The negative effects of *Nelumbo lutea* on dissolved oxygen concentrations may be exacerbated by its architecture and formation of large stands through rhizome expansion. Water circulation is likely reduced by the structural complexity of *N. lutea* beds. This effect has been found with other invasive macrophytes; Caraco and Cole (2002) found that dissolved oxygen concentrations in *Trapa* beds were higher in smaller, less dense stands than larger, denser stands. Dissolved oxygen concentrations in *N. lutea* beds may be further reduced because leaves on the water surface reduce gas exchange with the atmosphere. Water temperature of the lotus bed was similar to temperature in the open water, so differences in storage capacity do not explain the observed differences in the oxygen concentration.

Our study only ran through early Aug., but we expect that oxygen deficits would be even more prevalent in late summer as *Nelumbo lutea* begin to senesce and provide high quality substrate for microbial decomposition. Late summer oxygen depletion caused by intense decomposition of macrophyte tissue is a common occurrence in shallow, eutrophic lakes (Wetzel, 2001) and studies show that *N. lutea* leaves are rapidly reduced to fine particulate organic matter by microbial and physical breakdown after the peak growing period (Lubinski and Sparks, 1986).

Dissolved oxygen concentrations of less than 5 mg/l will be stressful to sensitive fish species, and concentrations less than 2.5 mg/l are stressful to most fish as well as some amphibian and invertebrate species (Cardinale *et al.*, 1997; Killgore and Hoover, 2001; Miranda and Hodges, 2000; Toft *et al.*, 2003; Colon-Gaud *et al.*, 2004; Burlakova and Karatayev, 2007). The littoral zone of lakes typically functions as a refuge from predation for juvenile fish (Werner and Hall, 1977; Werner *et al.*, 1983; Lehtiniemi, 2005). Hypoxia in the

littoral zone potentially has large effects on fish populations by making juveniles vulnerable to predators (Saint-Paul and Soares, 1987). For example, Toft *et al.* (2003) found that invertebrate assemblages in water hyacinth (*Eichhornia crassipes*) beds had low species richness during hypoxic episodes and that invertebrates found in hyacinth beds were less likely to be consumed by fish than those found in native floating aquatic vegetation. Further investigation should assess the effects of *Nelumbo lutea* on fish and invertebrate assemblages and the repercussions of these effects on higher trophic levels.

Increases in the severity and extent of hypoxia could result in altered biogeochemical processes in the hypolimnion and in the epibenthos. Increased use of available electron donors could lead to a reduced redox potential earlier in the summer. For ponds and rivers with abundant beds of *Nelumbo lutea*, low redox potential may increase rates of denitrification and methanogenesis and constitute a significant proportion of permanent gaseous loss of N₂ from the system (Knowles, 1982; Wetzel, 2001; Caraco and Cole, 2002). *Nelumbo lutea* may also prevent uptake of biologically available nitrogen by limiting primary productivity in the water column.

A review of the literature shows that natural resource managers have a Jekyll and Hyde relationship with the American lotus. The species' native range encompasses the eastern and central portions of the United States from Maine to Wisconsin and southward from Florida to Texas (USDA, 2009). The species is currently listed as an endangered species in New Jersey and Pennsylvania and as threatened in Michigan, where it was named the official state symbol for clean water quality (Michigan Senate Bill 106, 2004). Yet, it is listed as "a noxious and invasive weed" in Connecticut and intentional plantings are banned (Connecticut Invasive Plants Council 2004). The species has traits associated with invasive species (*sensu* Colautti and MacIsaac, 2004), as it is capable of rapid expansion (*e.g.*, Whyte *et al.*, 1997), particularly in human-altered habitats, and it likely displaces other species. We have shown here that its expansion has ecosystem level consequences. Such situations in which a native species responds to disturbance with aggressive expansion and displacement of other species raises difficult questions with regard to appropriate management strategies. Other examples of such situations include the double crested cormorant, the giant Canada goose, and the narrowleaf cattail *Typha angustifolia*. Resolving such questions ultimately requires an examination of societal values and an evaluation of competing priorities.

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