Nutrient release from moose bioturbation in aquatic ecosystems

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(ABSTRACT)

While the ecological importance of bioturbation is well recognized and the prevalence of aquatic foraging by terrestrial ungulates is increasingly appreciated, research linking how terrestrial ungulates function as disturbance mechanisms via bioturbation in freshwater systems is lacking. The purpose of this study was to quantify potential nutrient pulses released from benthic sediments into the water column when moose *Alces alces* feed on aquatic plants. We also determined if we could experimentally mimic the benthic disturbance and the expected nutrient pulse created when moose feed aquatically. When moose foraged aquatically, significant releases of both total and dissolved phosphorus (P) and nitrogen (N) resulted in the waters that were disturbed in foraging areas compared to adjacent undisturbed waters. Nutrient concentrations for total P and N ranged from 42.5× and 2.7× greater in disturbed than undisturbed, respectively. Dissolved P and N were 26.8× and 1.5× greater, respectively, in disturbed versus undisturbed waters. Our experimental mimic created increases of total and dissolved P and N that were equivalent to pulses created by moose. This indicates that it is possible to experimentally test by proxy the potential impact of moose bioturbation on other ecosystem processes. This study is the first quantification of moose foraging as a consumer mechanism that influences the release of limiting nutrients in aquatic systems, thereby emphasizing the potential cascading importance for nutrient uptake and productivity of plants and microbes.

KEYWORDS: *Alces alces*; disturbance; ecosystem engineer; herbivory; littoral zone; macrophyte; nitrogen; phosphorus; resource pulse; environmental heterogeneity.

INTRODUCTION

Disturbances and consumer fluxes play an important role in shaping ecological systems. Understanding the mechanisms and consequences of disturbance and consumer fluxes in ecosystems is a fundamental focus in ecology (Walker 2012, Pickett and White 2013, Sinclair et al. 2015, Allen and Wesner 2016). Disturbances and consumer effects are important causes of spatial heterogeneity across multiple scales, shaping mosaics of functional ecosystem attributes, community dynamics, biodiversity, and dynamic feedbacks (Turner 2010, Turner and Gardner 2015). Biotic disturbances are mechanisms that create heterogeneity, especially those linked to consumer effects on ecosystems processes (Leroux and Loreau 2010, Schmitz et al. 2010). Such effects have received much recent research attention because of the reciprocal relationship between an individual organism's ability to both create and respond to spatial heterogeneity (Wisdom et al. 2006, Reichmann and Seabloom 2002, Gabet et al. 2003). Consumers respond to patterns of patchiness and through multiple feedback pathways can amplify or reduce spatial heterogeneity in ecosystem processes (McIntyre et al. 2008, Allen and Wesner 2016). For example, top predators such as wolves (*Canis lupus*) can strongly modulate prey carcass distribution in time and space (Bump et al. 2009a, Wilmers and Getz 2004), which influences the distribution of biogeochemical hotspots at carcass sites (Bump et al. 2009c) and the subsequent response of herbivores and scavengers. Such feedbacks that affect environmental heterogeneity are important because shifting heterogeneity is theoretically (Franklin 2005) and increasingly empirically (Pickett et al. 1997) linked to the maintenance of biodiversity.

Bioturbation is a consumer and disturbance mechanism creating feedbacks. In the broad sense, bioturbation is the biological reworking of soils and sediments (Darwin 1881, Thayer 1979, Levinton 1995, Meysman et al. 2006, Wilkinson et al. 2009, Kristensen et al. 2011). As such, bioturbation has significant effects on sediment texture, water and solute transport, and dispersal of solid particles, thereby coupling aboveground-belowground and benthic-water column interactions. 'Bioturbators' have been categorized as ecosystem engineers, as their disturbance effects can produce strong, lasting, and disproportionally large impacts on ecosystems (Moore et al. 2006). Small invertebrates are the most abundant and ubiquitous bioturbators globally (Bottinelli et al. 2015). However, some large vertebrates also create significant bioturbation effects. For example, in terrestrial systems digging mammals such as moles, gophers, and prairie dogs significantly disturb soils by creating subterranean burrow systems, thereby affecting hydrology and nutrient cycling (see e.g., Davidson et al. 2012). In marine systems, grey whales and walruses plough trenches and create conspicuous pits in the surfaces of benthic sediments. In

seagrass meadows dugongs and stingrays create similar disturbances when feeding, resulting in multiple ecosystem effects (reviewed in Meysman et al. 2006). Freshwater systems have comparatively fewer conspicuous vertebrate bioturbators, with the exception of some fish species (Vanni 2002, Vanni et al. 2002, Moore et al. 2006, Janetski et al. 2009). Fewer still are mammals that are biotubators in freshwater systems, such as North American beaver (*Castor Canadensis*; Hood and Larson 2015) and hippopotamus (*Hippopotamus amphibius*; McCarthy et al. 1998, Deocampo 2002, Moore 2006, Mosepele et al. 2009, Subalusky et al. 2015). Additionally, while the cross-ecosystem impact of cervid herbivory on aquatic macrophytes is recently recognized (Ceacero et al. 2014, Takafumi et al. 2015, Bakker et al. 2016), cervid bioturbation effects on aquatic nutrient cycling is under examined.

Here we report on the previously unquantified role of moose (*Alces alces*) as an important bioturbator in aquatic ecosystems. Large herbivores such as moose are generally recognized as significant sources of physical (i.e., trampling, wallows, tree toppling) and biogeochemical (i.e., dung, urine, carcasses) disturbance in terrestrial ecosystems (Hobbs 1996, Moore 2006, Wisdom et al. 2006), affecting plant community composition, nutrient cycling, and patch use among herbivores. Moose are also recognized as important aquatic-terrestrial interface specialists and resource vectors (Ballinger and Lake 2006, Doughty et al. 2015, Bakker et al. 2016), foraging on aquatic macrophytes and transporting significant amounts of aquatic-derived nitrogen (N) to terrestrial systems (Bump et al. 2009b). However, the effect of bioturbation of lake sediments by moose while foraging for aquatic plants is unknown. Moose foraging in aquatic systems likely suspends nutrient-rich sediment and interstitial waters, where concentrations of productivity limiting elements are orders of magnitude greater than in overlying water (Levine and Schindler 1992; Søndergaard et al. 1992, 2003). Even though the evolution of the muzzle anatomy in moose has been suggested as a morphological adaptation for underwater feeding (e.g., moose are able to seal their nostrils underwater; Clifford and Lawrence 2004), their functional role as disturbance agents in aquatic ecosystems is unexamined. A better understanding of the role of moose in aquatic ecosystems and development of experimental approaches for exploring their role is warranted (Bakker et al. 2016).

We focus on quantifying nutrient release because key elements [e.g., phosphorus (P) and nitrogen (N)] are generally limiting to primary production in boreal freshwater systems (Elser et al. 2007; Bergström 2010). Even low frequency, short duration pulsed episodes of increased resource availability affect community dynamics and ecosystem processes (Nowlin et al. 2008, Yang et al. 2010, Marcarelli et al. 2011, Greenville et al. 2014). Resource pulse events affect consumers at various levels, including individual level behavioral and life history traits, population level numerical responses, and community

level indirect effects (Holt 2008, Yang et al. 2008, 2010). Even when resource pulses are low in frequency and short in duration, consumers employ opportunistic strategies to capitalize on ephemeral resource increases (Yang et al 2010) and short-term responses to recurrent pulses can alter community structure by affecting coexistence dynamics and transitions between alternative states (Holt 2008). Opportunistic response strategies can reduce average resource availability over larger spatial scales (e.g., Yang et al 2010, Greenville et al. 2014). Such strategies allow consumers to tolerate prolonged inter pulse periods of decreased resource availability (Takimoto et al. 2009), which is especially important in resource limited systems such as the north-temperate lakes in this study. We expect then that moose bioturbation releases nutrient pulses at ecologically significant quantities.

In this study we quantified possible pulses of total and dissolved nutrients released into the water column when moose forage on aquatic plants. We also experimentally tested our ability to in-situ create an analogous mimic of moose-derived nutrient pulses. The ability to experimentally mimic moose aquatic disturbances is important because 1) sampling water after mimicked disturbances is logistically more feasible than sampling after opportunistic observations of moose foraging in aquatic habitats and 2) experimental approaches are likely to increase mechanistic understanding and inference (Ford and Goheen 2015). The effective mimicking of moose aquatic disturbances would support experimental research on how moose bioturbation affects aquatic systems. Such experiments are necessary to advance our understanding of feedbacks between animal populations and ecosystem processes across ecological interfaces (Polis et al. 2004). For example, if moose bioturbation creates significant nutrient pulses in freshwater systems, internal nutrient availability could hypothetically increase, producing positive effects on biotic uptake and microbial productivity. Testing such hypotheses is appreciably more feasible if we are able to experimentally mimic moose bioturbation in aquatic ecosystems (e.g., Valentine et al. 1994, Usio and Townsend 2004).

MATERIALS AND METHODS

Study system and experimental design – We conducted field observations and collected water samples in aquatic ecosystems within Isle Royale National Park, an archipelago of islands in northwestern Lake Superior, USA (48°N, 89°W). The largest island, Isle Royale (~530 km^2), is approximately 72 km long and 14 km wide, 24 km from the nearest mainland shoreline, and is surrounded by numerous small islands. Isle Royale exhibits a distinctive topography of fingered peninsulas, indented bays, and a series of parallel ridge-and-valley landforms along a northeast-southwest alignment (Huber 1975). Drainage is

poorly developed due to these topographic features. As a consequence Isle Royale exhibits numerous

inland, lacustrine water bodies. Lakes and ponds ($n = 84 \geq 1$ ha) cover ~36 km^2 of the island's surface;

palustrine emergent wetlands cover another 8 km^2 (Tischler 2004). Plant communities reflect Isle

Royale's geographic position between boreal and the northern hardwoods regions (Hansen et al. 1973),

with forest mosaics of evergreen, mixed-evergreen and deciduous trees of two major associations: sugar

maple-yellow birch and birch-balsam fir-white spruce (Hansen et al. 1973). Moose density over the past

five decades ranged from ~1-5 moose per km^2 at the landscape level and is currently increasing (Peterson

et al. 2014).

Within this system moose consume aquatic macrophytes extensively between May and

September. Average daytime aquatic foraging bouts per individual are ~40 minutes and multiple bouts

have been observed in a day (Belovsky and Jordan 1978). The mean aquatic-derived proportion of the

diet during this time period is 14-37% (95% CI 9 - 54%) based on isotopic diet analysis (Tischler 2004,

Bump et al. 2009b). During aquatic foraging bouts, plant consumption and feeding movements create

notable disturbances that entrain and distribute presumably nutrient-rich benthic sediments and interstitial

water vertically and horizontally (Figure 1). Adult moose may submerge completely during aquatic

foraging (Supplementary materials Video1) and create disturbances that spread over an extended area

(e.g., >100 m^2). Field observations of benthic sediment clinging to moose hide indicate that moose can

penetrate the benthos to a depth of $\geq$ 1 meter, depending on bottom firmness.

We used a paired design in sampling and analysis to test for nutrient pulses in lake water caused

by moose foraging and to test our ability to experimentally mimic aquatic disturbances events created by

moose. The moose treatment was contingent upon opportunistic sightings and accessibility, hence

sampling occurred in the zone where moose were foraging and in adjacent, upwind zones of the same

depth and bottom firmness that were beyond the area of foraging activity, hereafter "disturbed" and

"undisturbed" respectively (Figure 1). Water sampling and analyses included two water conditions

(disturbed and undisturbed), two disturbance sources (moose and investigator mimic), and an

undetermined number of replicates (i.e., n) for each treatment. The number of replicates was contingent

upon opportunistic sightings and accessibility of moose foraging in aquatic environments. Sites of moose

disturbance and mimic treatment occurred in the same lakes as moose sites. Both filtered and unfiltered

water samples were collected to partition dissolved fractions of nutrients from particulate-derived

fractions.

Field sampling - Aquatic feeding bouts average 43 min on Isle Royale and occur on an average on 108

days seasonally (Belovsky and Jordan 1978). In spring (May-June) of 2010 and 2011 moose were

opportunistically observed foraging in littoral zones of three inland lakes that were comparatively small

(Daisy Farm Trail, 0.01 km^2), medium (Ojibway, 0.15 km^2), and large (Feldtmann, 1.86 km^2). Lakes

spanned both the east and west ends of Isle Royale. Littoral zone benthic sediments in foraging areas

were of similar firmness and exhibited a mix of silt and sand. Once moose ceased foraging (moose were

observed foraging for at least 10 minutes for all sampling) and exited the water, samples of lake water

were collected ~0.25m below the water surface in paired disturbed and undisturbed waters (Figure 1).

Distance between undisturbed water samples and the edge of the disturbed water sample area was at least

4 m. Subsequently, when moose were not present in the water, experimental attempts were made to

mimic the moose disturbance and bioturbation effect by wading, walking, and stomping in littoral zone

areas that were adjacent to, but not overlapping with, previous foraging sites (hereafter 'mimic').

Disturbance mimicking lasted 10 minutes, occurred in waters from ~0.75-1.25 m deep, and was done by

the same, single investigator each time. The duration of disturbance mimicking was based on the

observation that surface waters often appear clouded with sediments within ≤ 2 min of aquatic foraging

by moose even though foraging bouts typically last longer. Paired water samples were collected from

mimic disturbed and undisturbed areas respectively. To examine pulses of dissolved nutrients in the same

lakes, in 2011 and 2012 duplicate water samples for each treatment, i.e., moose or mimic, were collected

and filtered through a syringe filter (0.2 µm nylon membrane, Acrodisc®). Material that could pass a

0.2 µm filter was considered dissolved and more readily available for biotic uptake.

Observations of adult moose foraging during May and June 2010 and 2011 led to a total of 15

paired samples of disturbed versus undisturbed treatment for total nutrient analysis, which were

associated with 13 paired mimic samples of disturbed versus undisturbed. All samples from moose

foraging occurred from different individuals based on observations of distinct body characteristics (e.g.

hair pattern, antler development). The mimic sample size was less than the moose sample size because on

two occasions, comparable areas for the experimental mimic were unavailable due to extensive moose

disturbance (e.g., foraging lasted >1hr in one instance) and significantly different littoral zone

characteristics (e.g., abrupt depth increases and bottom firmness).

Laboratory and data analyses – In 2010, water samples were acidified with sulfuric acid in the field and

stored in opaque, high-density polyethylene containers. Samples were refrigerated and subsequently

analyzed within three weeks for total phosphorus (TP) and total nitrogen (TN) at the University of

Michigan's Biological Station using a Seal Analytical AA3 segmented flow analyzer. The chemistry

followed the Standard Methods procedures (REF methods manual, 20th edition): TP was digested using acidified persulfate (SM 4500-P(B.5)) followed by method SM 4500-P(F) then quantified using the ascorbic acid method (Ameel et al. 1993).   TN was digested using basic persulfate followed by quantification using cadmium reduction SM 4500-NO$_3$(F). TP detection limit was 2.5 µg L^{-1} with a precision of +/- 12%; TN detection limit was 44 µg L^{-1} a precision of +/- 18%. In 2011, samples were not acidified, but received the same storage and analysis within two weeks.   Filtered water sample values indicate total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) availability.

Total and dissolved nutrient data were analyzed using nonparametric paired analysis (Wilcoxon signed rank tests) to test the expectation of no difference in total and total dissolved P or N between disturbed and undisturbed samples, separated by moose and mimic treatments (JMP Pro 10 SAS Institute); a non-parametric test was used so as to not assume the data belong to a particular distribution. The paired design accounts for across site differences among lakes, times, years in which moose were opportunistically observed foraging (Zar 2010). In sum, each paired set of samples were collected and analyzed in the same way. Estimates of effect size (difference between disturbed and undisturbed lake surface water samples) were compared to test the expectation that the effect of moose disturbance could be accurately mimicked experimentally by human disturbance as described above.

RESULTS

Our analysis indicates that moose cause significant ($n = 15$ F = 8.3, $p < 0.0001$) increases in both total P concentrations (mean increase = 621 µg/L) and total N concentrations (mean increase = 885 µg/L) in the waters that are disturbed in foraging areas approximately 5 minutes after foraging (Figure 2); total P and N measured in waters disturbed by moose were 42.5× and 2.7× greater than undisturbed, respectively. Similarly, moose foraging resulted in significant ($n = 15$, F = 4.1, $p \leq 0.008$) increases of both dissolved P concentrations (mean increase = 335 µg/L) and N concentrations (mean increase = 179 µg/L) relative to undisturbed waters; concentrations of dissolved P and N were 26.8× and 1.5× greater, respectively (Figure 2). The increase in nutrient concentrations for both total and dissolved nutrients created by moose disturbance was not significantly different for P nor N from the effect size created by attempts to mimic moose bioturbation ($n = 13$, p-values between 0.45 – 0.75; Figure 3). The experimental mimic increased total P and N 45.6× and 2.1× greater than undisturbed, respectively, and dissolved P and N 35.2× and 1.7× greater than undisturbed, respectively. Based on qualitative observations, disturbance was readily visible in water for at least three hours following moose foraging.

DISCUSSION

Moose bioturbation during aquatic foraging resulted in increased concentrations (total and dissolved) of P and N in the water column in the north-temperate/boreal lakes we sampled. These moose-released nutrients are then available to primary producers (Wetzel 1992, Christiansen et al. 2016), providing an ecologically significant resource pulse for pelagic food webs. Similarly, benthic, aquatic bioturbators (such as macroinvertebrates and bivalves) can have rapid effects on nutrient cycling by facilitating nutrient transport across the sediment-water interface and enhancing nutrient availability to pelagic organisms (Anschutz et al. 2012, Blankson and Klerks 2016, Remaili et al. 2016). While the significant influence that aquatic consumers have on internal P and N cycling has been recognized (reviewed by Vanni 2002, Vanni et al. 2013, Capps et al. 2015, Hölker et al. 2015), such analyses have not included moose. Moose and other large herbivores may not be as numerous as smaller consumers but larger organisms are expected to have larger per capita impacts as bioturbators (Moore 2006, Bakker et al. 2016).

The net effect of moose biotubation on water nutrient concentrations depends on a combinations of variables, e.g. moose population density, total days spent feeding on aquatic plants, length of foraging bouts, area disturbed, and littoral zone area. Based on the mean total P and N released in a single foraging bout (Figure 2), conservative estimates of the mean days spent foraging on aquatic plants (108; Belovsky and Jordan 1978), a single aquatic foraging bout per day, and a minimal volume of water disturbed per feeding bout based on field observations (25 m^3), a single moose could resuspend 1.68 kg of P and 2.39 kg N per year. These estimates assume that the increased total P and N concentrations (Figure 2) result from a single release and not a continued resuspension during a foraging bout, which is likely conservative because moose are moving and disturbing the benthos frequently when feeding aquatically. Additionally, moose often feed on aquatic plants more than once per day; for example, at least 6 moose were observed feeding in the same lake during our study.

To put moose-released nutrients into context, the annual surface N deposition for our study lakes is estimated to be approximately 2 kg (Daisy Farm Trail), 25 kg (Ojibway), and 311 kg (Feldtmann). This range reflects differences in lake area, not variable atmospheric deposition rates. In small, relatively pristine lakes with low landscape inputs of nutrients such as those on Isle Royale , atmospheric deposition has been estimated at 50 – 90% of N inputs to the system (Likens 1985, Stottlemyer et al. 1998, Winter and Likens 2009). Therefore, for a small lake such as Daisy Farm Trail, a single foraging moose would nearly double the rate of N input to the system. Estimating the effects of moose on lake P budgets is less clear; for example, estimates of atmospheric deposition of P are variable, from less than 5% to 100%

(Schindler et al. 1976, Whalen and Cornwell 1985, Winter and Likens 2009). However, the importance of internal P resuspension in lake P budgets is clear (Søndergaard et al. 1992). For example, Chaffin and Kane (2010) suggested that sediment bioturbation by burrowing mayfly (*Hexagenia spp.*) in the western basin of Lake Erie was capable of releasing 1.40 mg/m^2 P per day, (504 mg/m^2 P per year) leading to a significant source of phosphorus loading. Our estimates suggest that one moose could add 168 mg/m^2 P per year to lake systems (e.g., Daisy Farm Trail), an amount that would likely influence nutrient limited primary producers. Understanding the net effect of aquatic nutrient releases by moose also requires more intensive analyses of time-series samples and detailed partitioning of chemical composition because both total and dissolved fractions of P and N likely contain components that vary in their availability. In general the dissolved fractions of P and N are considered more biologically available, but there is variation in the ability of microbes to directly uptake and utilize different inorganic and organic forms (Cotner and Wetzel 1992, Berman and Chava 1999), as well as the potential to access particulate-bound nutrients via extracellular enzyme activity (eg. alkaline phosphatases; Jansson et al. 1988). However, even our conservative, estimates of the effects of moose bioturbation on nutrient release suggest that moose foraging can have lake-level ecological consequences, especially for nutrient poor systems.

Pulses of dissolved P and N (Figure 2) at levels similar to those measured in this study are typically available for immediate uptake by primary producers, both algal and macrophyte species (Wetzel 1992, Christiansen et al. 2016). For example, common bladderwort (*Utricularia vulgaris*), a carnivorous aquatic macrophyte which grows in Isle Royale lakes, can reduce its investment in carnivory as more nutrients become available in the water column (Kibriya and Jones 2007), which can lead to significant increases in the populations of certain prey species, including insect larvae (Gordeev and Sibataev 1995, Harms 2002). Reductions in *U. vulgaris* carnivory occurred at water nutrient levels lower than the moose mediated release levels observed in our study. Furthermore, there are numerous studies suggesting that addition or enhanced recycling of nutrients in small, nutrient limited lake systems have transmitted effects up the food web (reviewed in Vanni et al. 2002, Meunier et al. 2016) suggesting the nutrient releases we recorded can indirectly affect community and nutrient dynamics.

Our understanding of how large herbivores influence nutrient cycling is largely dominated by a terrestrial understanding (Danell et al. 2006, but see Bakker et al. 2016). The net effect of moose foraging and excretion in forests is largely considered to decelerate (*sensu* Ritchie et al. 1998, Singer and Schoenecker 2003) N cycling as these animals selectively avoid less palatable forage that is more recalcitrant to microbial decomposition (Pastor et al. 1988, Christenson et al. 2014). The potential for ungulates to influence terrestrial P mineralization appears less than that found for N (e.g., Frank 2008,

Abbas et al. 2012). In contrast to the functional role of moose in terrestrial systems, this study indicates that aquatic herbivory by moose potentially accelerates the internal cycling and increases the availability of limiting nutrients in lakes. This role is important as the geographic range occupied by moose is extensive (e.g., ~28% of North America north of Mexico; Larsen 1980), circumpolar, characterized by a wide spectrum of freshwater ecosystems, and across these aquatic systems, both P and N are generally limiting nutrients (Elser et al. 2007).

To address the importance of moose or other ungulate bioturbation by directly studying ungulates is ideal, but can be a significant challenge to researchers. Our mimic results indicate that experimental disturbance can likely serve as a valid surrogate for moose bioturbation effects on water column dynamics to complement direct observations. These results suggest then that it is possible to begin to test the potential impact of a proxy of moose bioturbation on other ecosystem processes, such as structuring littoral zone habitat, modifying sediment mixing and oxygenation, and influencing turbidity and light penetration (Bakker et al. 2016). When impacts of moose bioturbation on such processes are experimentally estimated, we can more readily scale bioturbation effects to the lake and landscape level, identify explanatory mechanisms, and make stronger inferences (Ford and Goheen 2015). Further testing is needed to reveal whether or not an investigator mimic can successfully be used to examine benthic dynamics, e.g. mixing depth or surface area disturbance. Appreciation for ungulate effects on aquatic macrophyte communities has recently expanded (Ceacero et al. 2014, Takafumi et al. 2015, Moss 2015, Bakker et al. 2016) and similar testing of experimental mimics is recommended in other systems.

The extent to which bioturbation by moose affect other ecosystem conditions, components, and processes in addition to nutrient pulses is unexplored (Bergman and Bump 2015). For example, bioturbation has the potential to alter contaminant (e.g., mercury) transport across the sediment-water column interface and to terrestrial systems (e.g., Bergman and Bump 2014), which can affect the metal bioavailability, bioaccumulation and toxicity to organisms (Anschutz 2012, Blankson and Klerks 2016, Remalli et al. 2016). While we focused on limiting nutrients in north-temperate freshwaters, observations of bioturbation by moose indicate that sediment mixing, oxygen, and turbidity are potentially affected as well (Figure 1). Bioturbation in lake ecosystems generally causes a significant increase in oxygen at the sediment-water interface (Mermillod-Blondin and Rosenberg 2006, Mermillod-Blondin 2011). The mere movement of large mammals in water can significantly increase subsurface dissolved oxygen levels, preventing anoxia in waters with extreme nutrient loading (Gereta and Wolanski 1998, Wolanksi and Gereta 1999, Deocampo 2002). Such oxygen addition may affect P storage and the cycling of nutrients sensitive to redox state. Water clarity affects primary production of both macrophtyes and algal species

(Middleboe and Markager 1997, Karlsson et al. 2009), which in turn are important to primary (e.g., zooplankton) and secondary (e.g., fish) consumers. Hence future studies on this topic should include not only a broader analysis of the direct effects of moose bioturbation, but an examination of cascading, indirect effects as well.

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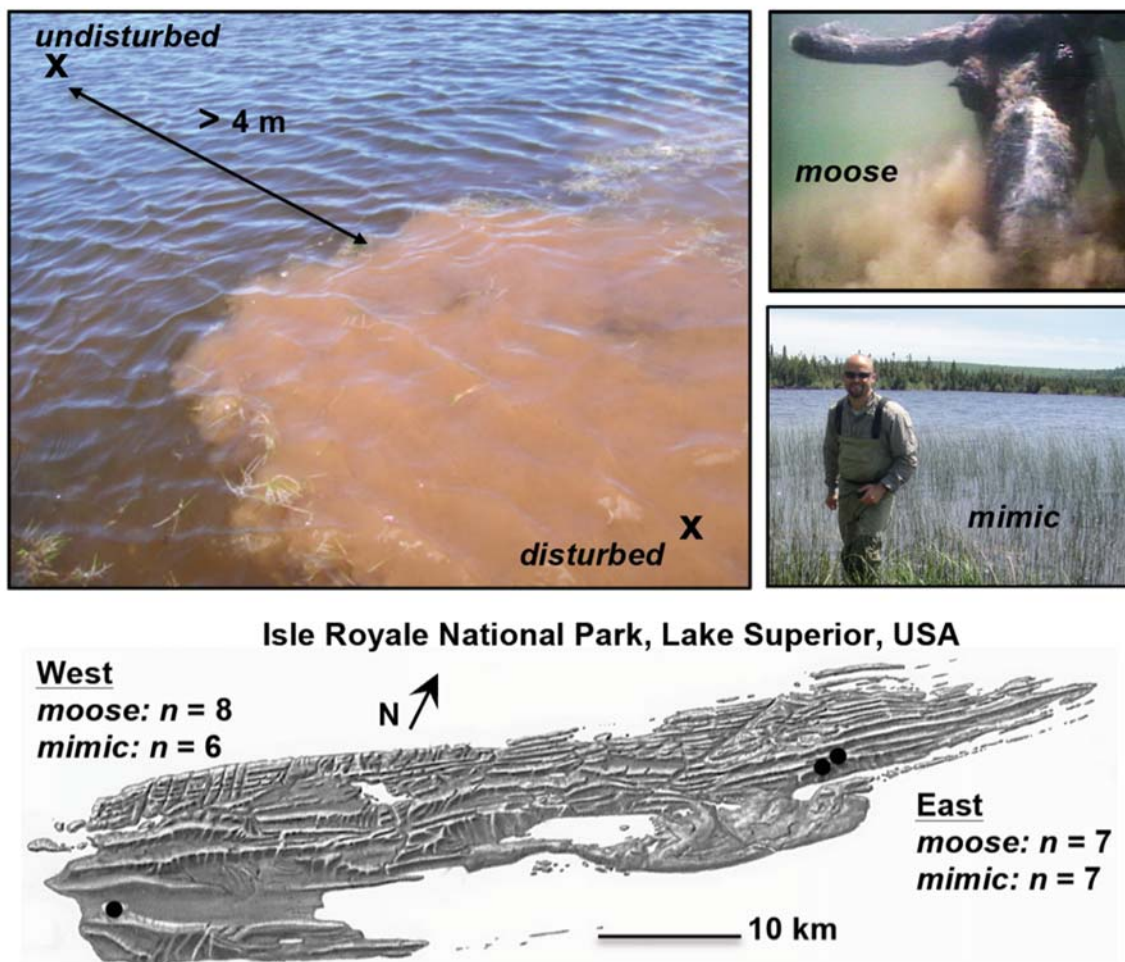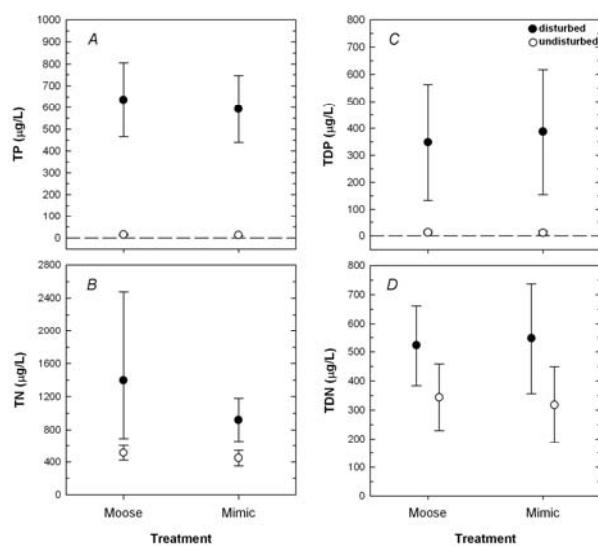
Fig. 2

FIG. 3