Wetlands (2010) 30:211–219
DOI 10.1007/s13157-010-0034-x

ORIGINAL PAPER

Muskrat Abundance Responses to Water level Regulation Within Freshwater Coastal Wetlands

Jason Toner · John M. Farrell · Jerry V. Mead

Received: 3 February 2009 / Accepted: 8 October 2009 / Published online: 9 March 2010

Abstract Muskrats (*Ondatra zibethicus*) are aptly described as "ecosystem engineers" for their influences associated with herbivory, house building, and movement within freshwater wetlands. Sensitivity to flow regime alteration via hydrologic regulation, however, may limit their populations and ability to facilitate wetland diversity and heterogeneity. Muskrat house surveys in coastal wetlands in tributaries (reference wetlands) subject to regional scale water level regulation were compared to treatment sites where local scale water-control structures were installed to alter the regulation effect. Data were used to develop a two-step model to predict wetland occupancy then house density to assess effects associated with proposed water level regulation plans. Field surveys indicated low house densities for cattail-dominated reference wetlands, and nearly 85% of houses located were in treatment sites. House distribution at reference sites was limited to channel edges, whereas houses at treatment sites were found throughout the floodplain. Occupancy of wetlands by muskrats was estimated by winter water depth, and fall water depth, and winter air temperature were selected as predictors of house density. Model validation indicated complete agreement for wetland occupancy, but density tended to be underestimated. Simulations provided a tool to evaluate water management plans and indicated that muskrat populations are suppressed under the current water level regulation regime.

Keywords Drowned river mouth wetlands · Ecological modeling · Hydrologic regulation

J. Toner · J. M. Farrell (✉)
Department of Environmental and Forest Biology,
State University of New York College
of Environmental Science and Forestry,
Syracuse, NY 13210, USA
e-mail: jmfarrell@esf.edu

Present Address:
J. V. Mead
Academy of Natural Sciences,
Patrick Center for Environmental Research,
1900 Benjamin Franklin Parkway,
Philadelphia, PA 19103-1195, USA

Introduction

Muskrats (*Ondatra zibethicus* L.) are known to influence ecosystem structure and function within freshwater coastal emergent wetlands. Foraging, house construction, and transportation networks associated with muskrats promote habitat heterogeneity and may influence wetland succession processes (Lynch et al. 1947) and faunal diversity, including vertebrate and invertebrate communities (Voigts 1976; Kiviat 1978; Bishop et al. 1979; Kaminski and Prince 1981; Clark and Kroeker 1993). Muskrat disturbance positively impacts wetland vegetation composition and structure through reduction of standing crop biomass (Clark 2000), leading to increased plant species richness (Nyman et al. 1993) and biomass of less abundant plant species (Kangas 1985). Furthermore, muskrats facilitate decomposition processes by increasing litter breakdown (Davis and van der Valk 1978; De Szalay and Cassidy 2001) and altering wetland topography thereby promoting accelerated organic decomposition (Wainscott et al. 1990) and higher microbe densities (Conners et al. 2000).

Seasonal hydrologic conditions and the presence of adequate forage are known to influence population dynamics and distribution of muskrats (Aldous 1947; Danell 1978b; Bishop et al. 1979; Thurber et al. 1991). Dispersal mechanisms are related to house construction activities in fall (Errington 1939; Bellrose 1950; Danell 1978b;

Herdendorf 1987; Thurber et al. 1991), and water depth is a primary factor in site selection. Low water levels may limit forage procurement, and freeze outs may lead to house abandonment and mortality (Errington 1961; Friend et al. 1964). Coastal emergent wetlands of the Lake Ontario-St. Lawrence River (LOSLR) system of the lower Great Lakes are characterized by a dense emergent zone composed primarily of invasive *Typha* x *glauca* hybrid (Wilcox et al. 2008; Farrell et al. 2010), a highly preferred muskrat forage and house building material. Construction of the St. Lawrence Seaway in 1958, however, created a regional scale hydrologic alteration affecting Lake Ontario and the St. Lawrence River through reduced periodicity and magnitude of levels (Wilcox and Xie 2007; Farrell et al. 2010) that may have affected muskrat populations and their potential to influence coastal wetlands. The International Joint Commission (IJC) administers water level policy through the regulation plan 1958D that has been in place for over 40 years. Relationships between water level periodicity and its regulation, resulting wetland water depth conditions, and the status of muskrat populations needed to be evaluated in a modeling framework to assist in revising the regulatory process.

We sought to investigate the influence of water level regulation on muskrat populations by comparing winter house building responses in existing wetlands to those where we artificially manipulated water levels. Additionally, we used these relationships to evaluate proposed alternative water-level-regulation plans generated by the recent IJC LOSLR Water Levels Study intended to balance multiple interests of the shipping industry, hydropower, riparian shore owners, municipalities, recreational boating, and the environment. Our approach was directed toward 1) use of field estimates of muskrat house density within reference (IJC water level regulated) and treatment (independent regulation) sites to investigate relationships between muskrat house density and environmental conditions and 2) development and validation of a model designed to predict house density for use in evaluation of proposed water level regulation plans.

Methods and Materials

Study Sites

Our study was conducted in US waters of the International Section of the upper St. Lawrence River, near its confluence with Lake Ontario. Six drowned river mouth coastal wetlands located in the Thousand Islands region of the upper river were used as study sites (Fig. 1). Most drowned river mouth wetlands in this area are cattail-dominated, as were our study sites. Water levels in reference sites were regulated by IJC in accordance with plan 1958D since the St. Lawrence Seaway opening in 1959. Water levels within reference locations experience a fall drawdown, a management action to accommodate winter storage (Fig. 2). We compared reference sites to treatment sites that were managed independently via water-control structures. Water-control structures were installed and managed at road overpasses at two treatment sites (Cranberry Creek 2000–2004 and Carpenters Branch 2004–2006) to measure the response of wetlands to hydrologic modifications by providing conditions of higher water levels during winter months and provide a greater range of water-depth conditions to facilitate modeling. Water levels for treatment sites averaged 75.4 m (SD=0.20) elevation, International Great Lakes Datum (IGLD 1985) compared to 74.7 m IGLD (SD=0.23) at reference sites, a difference of 0.7 m (Fig. 2). Carpenters Branch also served as a comparison of pre-treatment (2001–2002) and post-treatment (2004–2006) conditions; 2003 was considered transitional.

Muskrat House Surveys

Active muskrat house counts were conducted in winters of 2001–2004 for model development and 2005–2006 for model validation during periods of safe ice cover and low snow depth to facilitate house visibility. Coordinates of each muskrat house were determined with Trimble GPS. Locations were plotted onto site-specific digital elevation models (DEMs) (Toner 2006) and were assigned to one of five elevation classes (1 = 74.12–74.43; 2 = 74.44–74.66; 3 = 74.67–74.81; 4 = 74.82–74.96; 5 = 74.97–75.19 m IGLD) to quantify house distribution along the wetland elevation gradient.

Descriptive comparisons of active muskrat house density were made among individual sites and elevation classes for each site and year, among years for both sites, and before and after water-control structure installation at Carpenters Branch.

Model Development

Two independent models, one to predict the probability of occupancy for a wetland and a second to predict house density, were developed using SAS (1998). For occupancy, a logistic regression with stepwise selection of 12 water level and air temperature variables (Table 1) against a muskrat house presence or absence dependant variable was performed with a significance level for entry (SLE=0.70) and stay (SLS=0.10). Environmental variables were selected to represent importance to muskrat life history including seasonal water depth, mean seasonal air temperatures, frequency of below freezing temperature, and seasonal water level variation.

Water levels from the St. Lawrence River Alexandria Bay, New York NOAA gauging station (reference sites) and

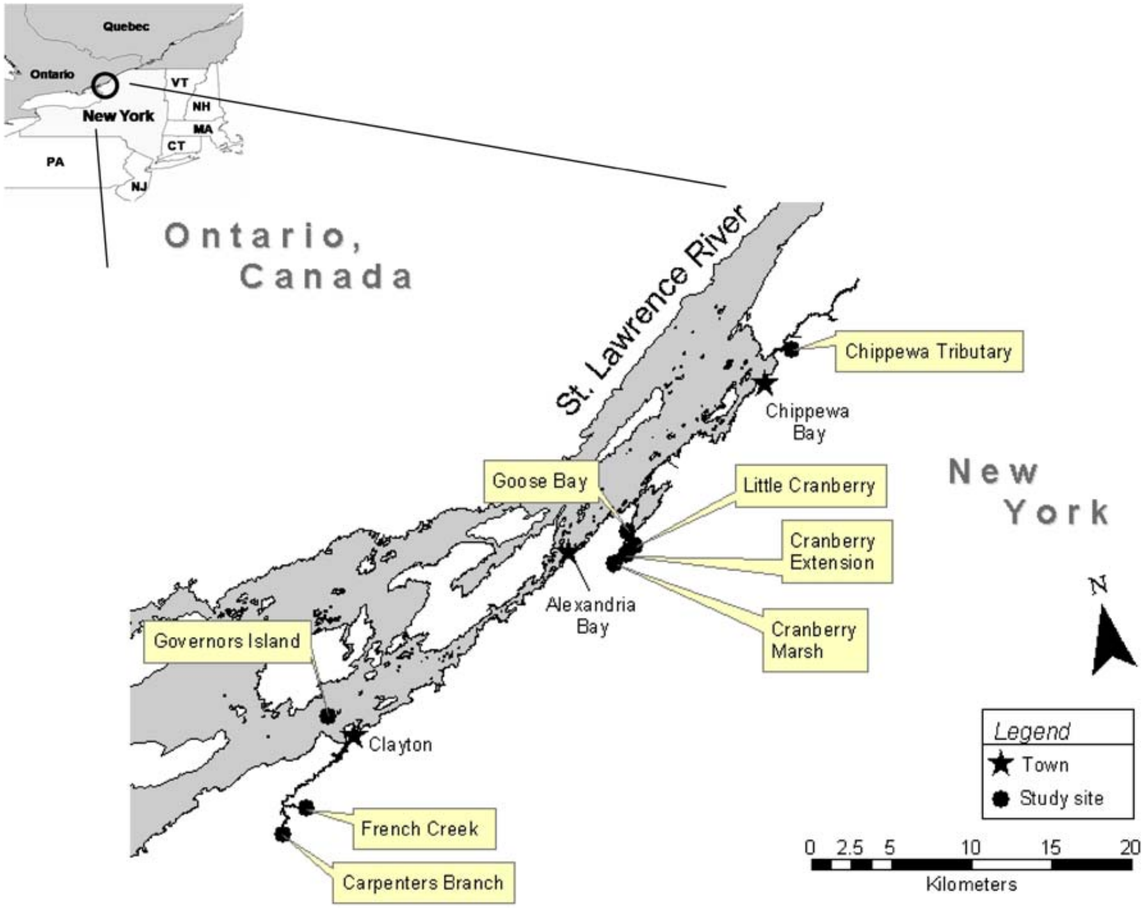

Fig. 1 Study wetlands in the Thousand Islands Region of the upper St. Lawrence River in Clayton and Alexandria Bay, New York, including French Creek and Carpenters Branch, Little Cranberry Creek, Cranberry Extension, Cranberry Creek, and Chippewa Tributary. The Thousand Islands Biological Station is located on Governors Island, Clayton, New York

staff gauge reading (2001–2002) and Solinst™ water level loggers (2002–2005) (treatment sites) were used with DEMs to determine water depths for specific elevations. Wetland water depth was estimated for each tributary by applying a water level to each grid cell of site-specific digital elevation models (DEM) developed using IDRISI™ (Toner 2006). The mean monthly water depth output (m) represented a mean of all 1 m^2 cells within the specified elevation ranges and was converted to seasonal averages for model input. Mean daily air temperature for December through February was used as an indicator of winter severity. Air temperatures (°C) were obtained from the NOAA station at the Watertown International Airport, New York.

Muskrat occupancy (presence/absence) was determined from the winter field surveys of muskrat density (2001 through 2004). Excel Solver™ was used to determine the minimum value of the sum of the squared differences between predicted and observed house density as the threshold for entry into the density model to minimize error. Multiple linear regression with stepwise variable selection (entry=0.40 and stay=0.10) was conducted with sites containing muskrat houses (n=12) and eight water level and air-temperature variables to predict active house density (Table 1). Variable sets were the same as those to predict occupancy with the exception of those used to represent water level change. Validation for the probability of wetland occupancy and the muskrat house density model was performed with independent muskrat house surveys conducted at study areas in 2005 and 2006 not used in model development and a cattail-dominated open embayment (Cobb Shoal, Alexandria Bay, NY). House density predictions were plotted with observed counts and compared to a 1:1 relationship.

Water-level-plan Evaluation

Probability of occupancy and active muskrat house density models were used to predict muskrat responses for each water level regulation plan for 101 year simulations. Simulations were performed within the Integrated Ecosystem Response Model (IERM) developed for the LOSLR

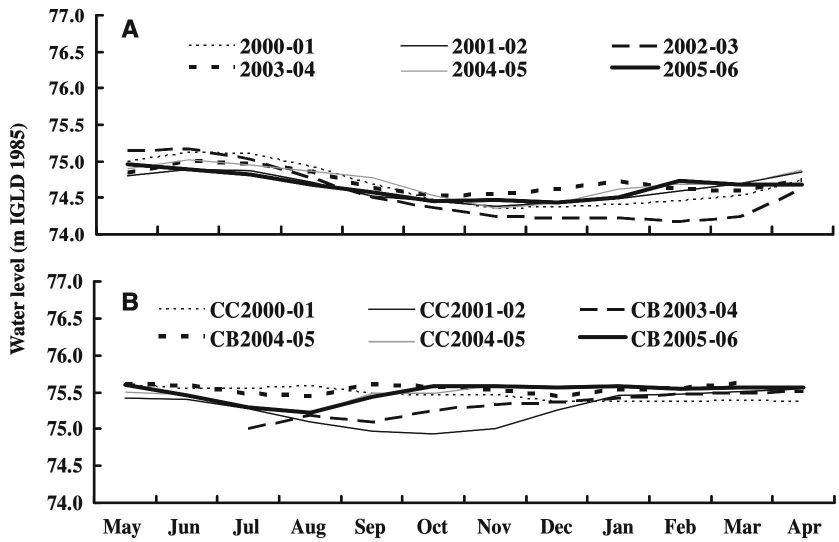

Fig. 2 Mean monthly water level (m IGLD 1985) from the Alexandria Bay NOAA gauging station, New York (A) used for tributary reference sites, and (B) water levels recorded by Solinst™ and staff gauges for treatment sites including Cranberry Creek (CC) and Carpenters Branch (CB). Data for 2005–06 were used in validation and not in model development

Water Level Study (Limno-Tech, Inc. 2005). A mean muskrat house density aggregate (using all sites and 100 years of predicted active house densities) was output from the IERM representing years 1901 to 2000. Four regulation plans were evaluated, including: (1) pre-project where levels fluctuated naturally according to water supplies and the effect of regulation was removed, (2) 1958D with deviations, the current management plan where levels are reduced to less than 74.40 m IGLD during fall and winter, (3) Plan B+ when November through February levels were maintained at 74.50 m IGLD, and (4) Plan 2007, where levels on average were lower than current regulation in fall but slightly higher during winter months (Fig. 3).

Results

Muskrat House Abundance

Winter muskrat house surveys conducted from 2001 through 2006 detected a total of 380 active houses; over 85% (n=321) were found in treatment sites (Table 2). Active houses were absent during 11 of 25 reference-site surveys. Mean overall density for reference sites was 0.71 houses/ha (SD=0.79, n=25). Overall house density for treatment sites was over four times greater than reference sites at 3.01 houses/ha (SD=1.16, n=6). Reference-site house density in 2005 (mean=1.98, SD=1.47, n=6) was consistently greater than previous years (mean=0.44, SD= 0.77, n=25). Water level treatment (2004–2006) at Carpenters Branch resulted in an overall muskrat house density nearly three times greater (3.46 houses/ha) relative to pre-treatment (2001–2002) at 1.26 houses/ha (Table 2). Immediately following first flooding (fall 2002), the 2003 house density was 0.63 houses/ha and was excluded from the comparison.

Most muskrat houses (83%) within reference sites were located between low elevations, 74.14 and 74.67 m IGLD, along the channel edge. At treatment sites, houses were more widely distributed along the wetland elevation gradient; only 15% of houses were located within near channel elevations (74.14 and 74.67 m IGLD), and 80% were distributed higher in the floodplain (74.67 to 74.81 m IGLD). Following water-control structure installation at the Carpenters Branch treatment site, muskrat houses in 2004 were widely distributed. House densities within higher elevation classes (between 74.96 and 75.19 m IGLD) increased considerably from pre-treatment (0 houses/ha) to post-treatment (2.7 houses/ha). House density also increased for the high 74.81 and 74.96 m IGLD elevations from 0.13 houses/ha to 2.2 houses/ha post-treatment.

Predicting Active House Density

Winter water depth was selected as the determinant of muskrat presence/absence within a wetland (χ^2=3.1, df=21, p= 0.0774) with an intercept coefficient of −1.6692 (χ^2=4. 8, df=21, p=0.0292). For each site, probability of occupancy (PROB) for each wetland was computed as

$$\mathrm{PROB} = 1 \div \left[1 + \mathrm{e}^{(1.6692-(11.9129\times \mathrm{WINTERWD}))}\right]$$

where WINTERWD was the mean water depth (m) during winter months (December, January, February). A change in WINTERWD of 6 cm results in a ~10% change in probably

Table 1 Habitat variables used in a logistic model that predicts the probability of muskrat occupancy (variables 1–12) followed by house density (variables 1–8) for upper St. Lawrence River tributary wetlands. Water depth variables were extracted from digital elevation maps (one meter resolution) for each site during each year (2000–2004) for elevations ranging from 74.3 to 75.13 m IGLD 1985. Water levels were obtained from Alexandria Bay, NY (NOAA) gauging station (reference sites) or independent readings (treatment sites). Air temperatures were from the Watertown, NY Airport (NOAA) and were in °F in their original form that was used in model development

Variable	Description
1-Fall water depth	Mean water depth (m) during (September, October, November)
2-Winter water depth	Mean water depth (m) (December, January, February)
3-Summer water depth	Mean water depth (m) (June, July, August)
4-Fall air temperature	Mean air temperature (°C) (November and December)
5-Winter air temperature	Mean air temperature (°C) (January and February)
6-Cumulative below freezing temperature	Cumulative below freezing air temperature (°F) (December, January, February)
7-Below freezing mean air temperature	The number of quarter monthly periods from October to March with mean air temperature (°F) <32°F
8-Zero water depth	Number of months (May to April) with mean water depth (m) of zero
9-Water level change	The difference between July and August mean monthly water levels (m IGLD)
10-Water level change	The difference between August and September mean monthly water levels (m IGLD)
11-Water level change	The difference between September and October mean monthly water levels (m IGLD)
12-Water level change	The difference between the July and October mean monthly water levels (m IGLD)

of muskrat occupancy on average for values between 0.5 m and zero water depth.

Stepwise linear regression selected two habitat variables, fall water depth (t=4.0, df=34, p=0.0032) and winter temperature (t=4.3; df=34, p=0.0021), as variables for prediction of house density as

$$\mathrm{HD} = 2.05276 + (2.7395 \times \mathrm{FALLWD}) + (0.00910 \times \mathrm{WINTERTEMP})$$

where for each wetland, HD was house density/ha, FALLWD was the mean water depth within the specified elevation range for fall months (September, October, November), and WINTERTEMP was the cumulative air temperature difference from freezing (0°C; note that temperature must be converted to °F for use in model) for quarter monthly average temperatures during winter months (December, January, February). At a constant WINTERTEMP, a change in FALLWD of 3.6 cm resulted in a 0.1 change in muskrat house density for depths between 0.5 and 0 m. A 10 unit change in WINTERTEMP resulted in a 0.09 unit change in muskrat house density.

Model Validation

Observed muskrat occupancy was correctly predicted by the model in all cases. However, the density model

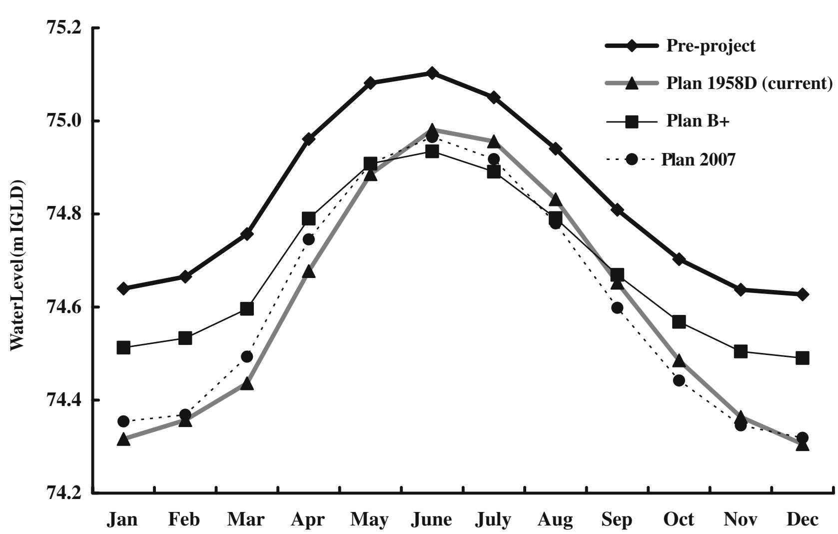

Fig. 3 Water-level-regulation plan scenarios including pre-project (unregulated), the current plan 1958D (in operation since ~1960), plan B+ (developed as part of the LOSLR Water Levels Study), and the IJC proposed plan 2007. All plans were generated over a 101 year period (1900–2000) based on the observed historical water supply

Table 2 Wetland surface area (ha) and active muskrat house density (N/ha) from winter house surveys conducted at upper St. Lawrence River wetlands from 2001 through 2006. Carpenters Branch became a treatment site in 2004 when a water-control structure was added to manage local levels; data from 2003 were transitional and not used in analyses. NA denotes data not available due to unsafe ice conditions for sampling or failure of the control structure to manage levels at Cranberry Creek following the 2004–2005 seasons

Site	Area (ha)	House Density (N/ha)					
		2001	2002	2003	2004	2005	2006
Treatment							
Cranberry Creek	35.55	2.67	2.00	NA	NA	2.03	NA
Carpenters Branch	8.00	0.63	1.88	0.63	2.50	5.00	2.88
Reference							
Cranberry Extension	1.96	0	1.02	0	0	2.04	1.02
Chippewa Tributary	3.38	0	0	0	0	0.30	0.89
French Creek	2.23	NA	2.70	0.45	0.90	2.24	0
Little Cranberry	1.69	0	0	0	1.18	2.37	1.18

underestimated individual active house densities compared to observed densities (Fig. 4). An area-weighted aggregation, used in water level regulation plan comparisons balanced variability in site-specific validation estimates and resulted in a close prediction between observed (1.78/ha) and predicted house density (1.81/ha). This is likely because of a low average residual difference in house density for observed and predicted survey outcomes (−0.03 houses/ha; $n=11$). At Cobb Shoal, an open embayment, the model also predicted an underestimate of house density at 1.1 compared to 1.6 houses/ha observed in 2005.

Water Level Regulation Plan Evaluation

Muskrat house density simulations for the pre-project plan produced greater active muskrat house density relative to the current plan 1958D (ratio=35:1) and all other plans simulated (Fig. 5). Pre-project water levels consistently produced muskrat densities > 1.0 house ha, while regulation plans rarely produced densities above zero. Simulations with plan 1958D resulted in only two predicted active house densities (0.3/ha for simulation year 73 and 0.9/ha in year 87) greater than zero, while 35 predicted densities ranging from <0.1 for year 43 to 2.8 for year 87 were observed for the pre-project plan. The house density aggregate ($n=100$ simulations) for the pre-project plan was 0.4 houses/ha (SD=0.6).

The two remaining water level regulation plans considered (B+ and 2007) resulted in highest muskrat house density ratios for Plan B+. Plan 2007 proposed by the IJC for implementation produced little change over the current plan 1958D with 5 of 100 years with muskrat house density of 0.02 house/ha (SD=0.1). Plan B+ produced house density estimates for 10 of 100 years simulated for an overall density of 0.05 house/ha (SD=0.2).

Discussion

Naturally fluctuating water levels that maintain a balance between wetland vegetation dynamics and access to suitable forage are believed to provide adequate long-term conditions for healthy muskrat populations (Hamerstrom and Blake 1939; Bellrose and Brown 1941; Allen and Hoffman 1984). Despite dominance of cattail in the upper St. Lawrence River, muskrat house density was considerably lower in reference wetlands under the influence of IJC regulation. High muskrat densities

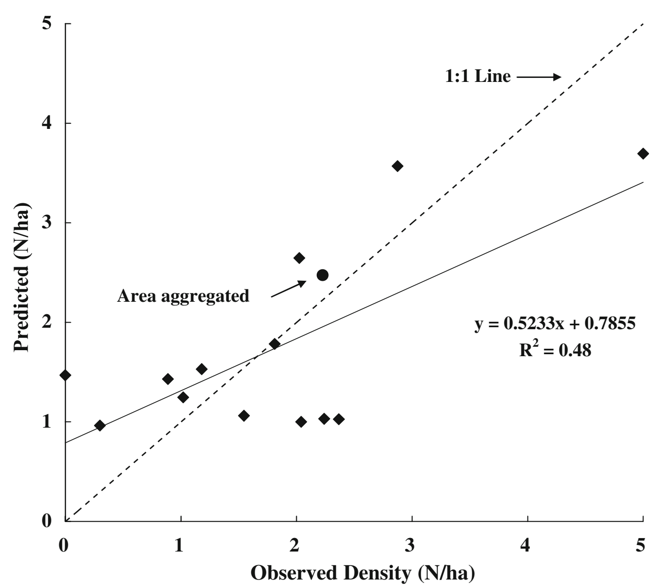

Fig. 4 Comparison of observed and predicted muskrat house density from wetland surveys 2005 and 2006. Sites included CB = Carpenters Branch; CC = Cranberry Creek; FC = French Creek; CE = Cranberry Extension; LC = Little Cranberry Creek, CH = Chippewa Tributary; COBB = Cobb Shoal Marsh. Dotted line represents a 1:1 relationship. An area-aggregate for all sites combined is shown to represent the method used for simulation outcomes

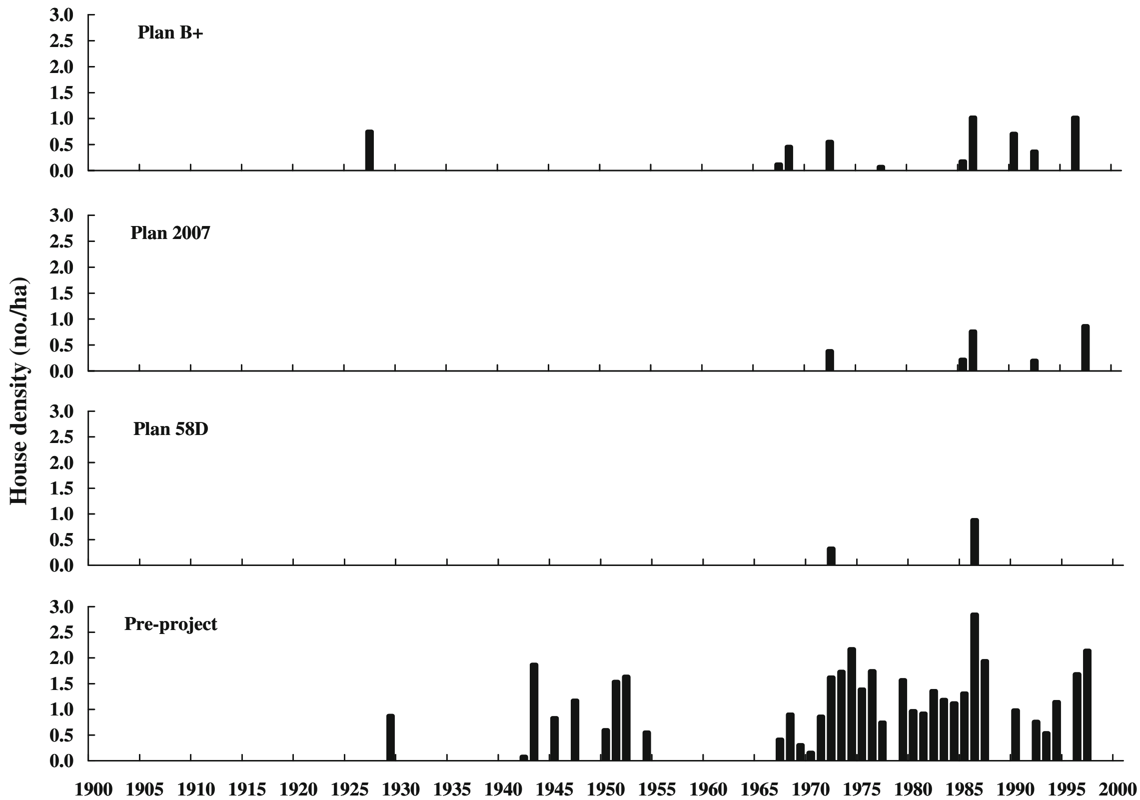

Fig. 5 Muskrat house density simulation (100 years, 1901 to 2000) in drowned river mouth geomorphic type coastal wetlands in the upper St. Lawrence River. IJC water-level-regulation plan 1958D has been in effect since 1960, pre-project represents simulated no-regulation water levels

are often reported for cattail dominated wetlands because cattails are an important food source with similar nutrient value to other vegetation types (Campbell and MacArthur 1994) and a preferred vegetation type for house building. Proulx and Gilbert (1984) estimated muskrat house density at 2.05 houses/ha in 1979 and 3.48 houses/ha in 1980 for cattail-dominated Luther Marsh, Ontario. Messier and Virgil (1992) report a maximum fall density of 3.6 houses/ha in a northern marsh (Saskatchewan).

Simulations of house density with our model indicate that water level regulation has had a negative effect on muskrats relative to an unregulated scenario. Similarly, studies conducted at Rainy and Kabetogama Lakes, Minnesota (two lakes regulated by the IJC) demonstrated that water level fluctuation negatively influenced house density (Thurber et al. 1991). Muskrat house density at Rainy Lake, at which water level fluctuated 1.0 m annually, was only 0.14 and 0.33 houses/ha in 1985 and 1986, respectively. Densities at Lake Kabetogama, with large water level fluctuations of 2.7 m annually, were 0.05 and 0.21 houses/ha during two consecutive years. Notably, these lakes lacked extensive cattail stands (Wilcox and Meeker 1991), but density estimates are comparable to those observed in our study areas.

When more adequate fall and winter levels were provided in treatment sites, muskrat house densities increased. These findings were similar to those reported for Lake Erie marshes from 1954 to 1957, where house density for dike-controlled marshes had a grand mean of 3.95 houses/ha, and uncontrolled marshes were 0.52 houses/ha (Donohoe 1966). Further, house density at Carpenters Branch increased following installation of a water-control structure and reached 5.0 houses/ha in 2005 (the highest recorded density) and remained high in 2006. The response of the muskrat population, as indicated by house density (Dozier 1948), to improved conditions at Carpenters Branch 2004 to 2006 was similar to other studies where muskrats responded within two years of flooding (Bishop et al. 1979). Population density also increased rapidly within two years in areas where muskrats were introduced (Danell 1977) and in re-flooded areas (Clark and Kroeker 1993; Clark 1994).

Winter water depth, directly influenced by water levels, was shown to be a strong predictor of presence or absence and affected the distribution of muskrat houses. Suitable winter water depth is a limiting factor cited for many muskrat populations (Bellrose and Brown 1941; Aldous 1947; Errington 1961; Clark 1994). Clark (1994) found that

>90% of muskrat houses at Delta Marsh, Manitoba were located in water depths > 10 cm, with an average depth of 38 cm. Other researchers have shown that muskrats required 15 cm of water for over-wintering in the Illinois River (Bellrose and Brown 1941) and Luther Marsh, Ontario (Proulx and Gilbert 1983). Aldous (1947) reported that all houses in the Sand Lake National Wildlife Refuge, South Dakota had frozen plunge pools by March in water depths <38 cm. Bellrose (1950) found that 70% of Illinois River Valley muskrat houses in 12 cm of water experienced freeze-out, compared to <50% at water depths of 25.4 cm.

An interaction between winter water depth, air temperature, and the active house density response was observed in the upper St. Lawrence River study sites. During years that were relatively cold with low water levels (2001 and 2003), house density was lower. Years with milder winter temperatures (2002 and 2004) produced greater house densities. Densities for 2005 were greater relative to previous years despite colder January and February temperatures. Warmer December temperatures may explain some of the observed house density response in 2005. Also in 2005, January and February water levels were higher relative to three of the four years sampled, reducing the effect of cold temperatures.

Water depths also affected the distribution of muskrat houses within the floodplain. Houses in non-treatment sites were typically located at the open water-emergent vegetation interface found along the channel edge. Earlier studies that evaluated house distribution had similar findings (Pelikan et al. 1970; Danell 1978a, Proulx and Gilbert 1983; Clark 1994). Low water depth in fall may function as a dispersal mechanism (Errington 1940; Proulx and Gilbert 1983). Upper St. Lawrence River muskrats likely select the deepest portions of marsh or may seek refuge wetlands further inland independent of the regulation effect during the fall period. During October through March, average water depths within the channel edge elevation class ranged from 0 cm in 2002–2003 to 32.2 cm in 2003–2004. Treatment sites, however, had houses widely distributed throughout the wetland. Elevation-specific house density for Cranberry Creek was greatest where water depth averaged 68 cm in 2000–2001 and 55.6 cm in 2001–2002 for October through March.

We are aware of few published accounts of the use of statistical or spatial models in understanding muskrat dynamics in relation to habitat variables. Logistic regression was used by Nadeau et al. (1995) to determine important wetland variables that help predict presence or absence of muskrat burrows along river shorelines. Brooks and Dodge (1986), in a test of a riverine burrow muskrat model, recommended that local population attributes should be combined with habitat analyses to obtain accurate quantitative estimates of muskrat abundance. Therefore, caution should be used when applying the upper St. Lawrence River muskrat house density model outside the physiographic region. Work conducted by Ouellet and Morin (2006) provides an example inverse to our results, where in a spatially explicit model of muskrat abundance house destruction via swamping was deemed an important regulatory mechanism in the lower St. Lawrence River. Therefore, different muskrat population responses to hydrologic regulation above and below the same dam were observed.

Our logistic model seems to predict muskrat occupancy of a wetland accurately, but the density model, however, tended to underestimate the number of muskrat houses. The range of environmental condition for 2005 and 2006 may have operated outside the model experience. In addition, the house density model assumed independence between consecutive estimates. Interannual dependence in observed house density estimates may have contributed to underestimates of house density in the presence of conditions favoring population growth. Despite these shortcomings results produced by the density model appear to capture the mechanisms of water level fluctuation effects on muskrat house building adequately and provided a conservative approach for estimating house abundance.

Muskrat house density, predicted from the pre-project plan (levels for November through February maintained above 74.60 m IGLD), indicated a positive response to periodic high water levels during the fall and winter months. Comparisons between alternative water level plans and plan 1958D (levels for November through February maintained below 74.40 m IGLD) reveal that regulation reduces muskrat house density relative to natural conditions. According to simulation outcomes, the influence of regulation on muskrat populations is severe, effectively dampening their cascading facilitation effects on these wetlands and their biota.

References

Aldous SE (1947) Muskrat trapping on Sand Lake National Wildlife Refuge, South Dakota. Journal of Wildlife Management 11:77–91

Allen AW, RD Hoffman (1984) Habitat suitability index models: Muskrat. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, DC, USA. FWS/OBS-82/10

Bellrose FC (1950) The relationship of muskrat populations to various marsh and aquatic plants. Journal of Wildlife Management 14:299–315

Bellrose FC, Brown LG (1941) The effect of fluctuating water levels on the muskrat population of the Illinois River Valley. Journal of Wildlife Management 5:206–212

Bishop RA, Andrews RD, Bridges RJ (1979) Marsh management and its relationship to vegetation, waterfowl, and muskrats. Proceedings of the Iowa Academy of Science 86:50–56

Brooks RP, Dodge WE (1986) Estimation of habitat quality and summer population density for muskrats on a watershed basis. Journal of Wildlife Management 50:269–273

Campbell KL, MacArthur RA (1994) Digestibility and assimilation of natural forages by muskrat. Journal of Wildlife Management 58:633–641
Clark WR (1994) Habitat selection by muskrats in experimental marshes undergoing succession. Canadian Journal of Zoology 72:675–680
Clark WR (2000) Ecology of muskrats in prairie wetlands. In: Murkin HR, van der Valk AG, Clark WR (eds) Prairie Wetland Ecology: the contribution of the Marsh Ecology Research Program. Iowa State University Press, Ames, pp 287–313
Clark WR, Kroeker DW (1993) Population dynamics of muskrats in experimental marshes at Delta, Manitoba. Canadian Journal of Zoology 71:1620–1628
Conners LM, Kiviat E, Groffman PM, Ostfeld RS (2000) Muskrat (*Ondatra zibethicus*) disturbance to vegetation and potential net nitrogen mineralization and nitrification rates in a freshwater tidal marsh. American Midland Naturalist 143:53–63
Danell K (1977) Short-term plant successions following the colonization of a northern Swedish lake by the muskrat, *Ondatra zibethica*. Journal of Applied Ecology 14:933–947
Danell K (1978a) Intra- and interannual changes in habitat selection by the muskrat. Journal of Wildlife Management 42:540–549
Danell K (1978b) Population dynamics of the muskrat in a shallow Swedish lake. Journal of Animal Ecology 47:697–709
Davis CB, van der Valk AG (1978) The decomposition of standing and fallen litter of *Typha glauca* and *Scirpus fluviatilis*. Canadian Journal of Botany 56:662–675
De Szalay FA, Cassidy W (2001) Effects of muskrat (*Ondatra zibethicus*) lodge construction on invertebrate communities in a Great Lakes coastal wetland. American Midland Naturalist 146:300–310
Donohoe RW (1966) Muskrat reproduction in areas of controlled and uncontrolled water-level units. Journal of Wildlife Management 30:320–326
Dozier HL (1948) Estimating muskrat populations by house counts. Transactions of the North American Wildlife Conference 13:372–389
Errington PL (1939) Reactions of muskrat populations to drought. Ecology 20:168–186
Errington PL (1940) Natural restocking of muskrat-vacant habitats. Journal of Wildlife Management 4:173–185
Errington PL (1961) Muskrats and marsh management. Wildlife Management Institution Publication, Wildlife Management Institute, Ames
Farrell JM, Murry BA, Leopold DJ, Halpern A, Rippke M, Godwin KS, Hafner SD (2010) Water-level regulation and coastal wetland vegetation in the upper St. Lawrence River: inferences from historical aerial imagery, seed banks, and *Typha* dynamics. Hydrobiologia. doi:10.1007/s10750-009-0035-z
Friend M, Cummings GE, Morse JS (1964) Effect of changes in winter water levels on muskrat weights and harvest at the Montezuma National Wildlife Refuge. New York Fish and Game Journal 11:125–132
Hamerstrom FN Jr, Blake J (1939) Central Wisconsin muskrat study. American Midland Naturalist 21:514–520
Herdendorf CE (1987) The ecology of coastal marshes of western Lake Erie: a community profile. U.S. Fish and Wildlife Service Biological Report 85(7.9)
Kaminski RM, Prince HH (1981) Dabbling duck and aquatic macroinvertebrate responses to manipulated wetland habitat. Journal of Wildlife Management 45:1–15
Kangas PC (1985) Vegetation on muskrat mounds in a Michigan marsh. American Midland Naturalist 13:392–396
Kiviat E (1978) Vertebrate use of muskrat lodges and burrows. Estuaries 1:196–200
Limno-Tech Inc. (2005) Development of an integrated ecological response model (IERM) for the Lake Ontario – St. Lawrence River Study. Report for the USACE-Institute for Water Resources and the International Joint Commission as a contribution to the IJC LOSL Study
Lynch JJ, O'Neil T, Lay DW (1947) Management significance of damage by geese and muskrats to Gulf Coast marshes. Journal of Wildlife Management 11:50–76
Messier F, Virgil JA (1992) Differential use of bank burrows and lodges by muskrats, *Ondatra zibethicus*, in a northern marsh environment. Canadian Journal of Zoology 70:1180–1184
Nadeau S, Decarie R, Lambert D, St-Georges M (1995) Nonlinear modeling of muskrat use of habitat. Journal of Wildlife Management 59:110–117
Nyman JA, Chabreck RH, Kinler NW (1993) Some effects of herbivory and 30 years of weir management on emergent vegetation in a brackish marsh. Wetlands 13:165–175
Ouellet V, Morin J (2006) Impact of water levels on an aquatic mammal: the muskrat. In: Talbot A (ed) Water availability issues for the St. Lawrence River: an environmental synthesis. Environment Canada, Montreal, pp 116–125
Pelikan J, Svoboda J, Kvet J (1970) On some relations between the production of *Typha latifolia* and a muskrat population. Zoologika Listy 19:303–320
Proulx G, Gilbert FF (1983) The ecology of the muskrat, *Ondatra zibethicus*, at Luther Marsh, Ontario. Canadian Field Naturalist 97:377–390
Proulx G, Gilbert FF (1984) Estimating muskrat population trends by house counts. Journal of Wildlife Management 48:917–922
SAS Institute Inc (1998) SAS/STAT User's Guide, Release 6.03 Edition. Cary, NC, USA
Thurber JM, Peterson RO, Drummer TD (1991) The effect of regulated lake levels on muskrats, *Ondatra zibethicus*, in Voyageurs National Park, Minnesota. Canadian Field-Naturalist 105:34–40
Toner JA (2006) Muskrat house abundance and cattail use in upper St. Lawrence River tributary wetlands: modeling the effects of water level regulation. MS Thesis, SUNY College of Environmental Science and Forestry, Syracuse, NY, USA
Voigts DK (1976) Aquatic invertebrate abundance in relation to changing marsh vegetation. American Midland Naturalist 95:313–322
Wainscott VJ, Bartley C, Kangas P (1990) Effect of muskrat mounds on microbial density on plant litter. American Midland Naturalist 123:399–401
Wilcox DA, Meeker JE (1991) Disturbance effects on aquatic vegetation in regulated and unregulated lakes in northern Minnesota. Canadian Journal of Botany 69:1542–1551
Wilcox DA, Xie Y (2007) Predicting wetland plant community responses to proposed water-level-regulation plans for Lake Ontario: GIS-based modeling. Journal of Great Lakes Research 33:751–773
Wilcox DA, Kowaskski KP, Hoare HL, Carlson ML, Morgan HN (2008) Cattail invasion of sedge/grass meadows in Lake Ontario: photointerpretation analysis of sixteen wetlands over five decades. Journal of Great Lakes Research 34(2):301–323