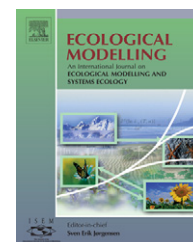


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Monitoring waterbird abundance in wetlands: The importance of controlling results for variation in water depth

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ABSTRACT

Wetland use by waterbirds is highly dependent on water depth, and depth requirements generally vary among species. Furthermore, water depth within wetlands often varies greatly over time due to unpredictable hydrological events, making comparisons of waterbird abundance among wetlands difficult as effects of habitat variables and water depth are confounded. Species-specific relationships between bird abundance and water depth necessarily are non-linear; thus, we developed a methodology to correct waterbird abundance for variation in water depth, based on the non-parametric regression of these two variables. Accordingly, we used the difference between observed and predicted abundances from non-parametric regression (analogous to parametric residuals) as an estimate of bird abundance at equivalent water depths. We scaled this difference to levels of observed and predicted abundances using the formula: $((\text{observed} - \text{predicted abundance}) / (\text{observed} + \text{predicted abundance})) \times 100$. This estimate also corresponds to the observed:predicted abundance ratio, which allows easy interpretation of results. We illustrated this methodology using two hypothetical species that differed in water depth and wetland preferences. Comparisons of wetlands, using both observed and relative corrected abundances, indicated that relative corrected abundance adequately separates the effect of water depth from the effect of wetlands.

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1. Introduction

Waterbirds comprise a large group of species including anseriformes, charadriiformes, ciconiiformes, gaviiformes, gruiformes, pelecaniiformes, podicipediformes, and procellariiformes. These species display a variety of adaptations for exploiting wetland habitats. In non-diving waterbirds, variation in morphological features, such as bill length and shape, bill lamellae distance, neck length, leg length, and body size, allow species to forage at different depths and on different foods (Baker, 1979; Pöysä, 1983; Nudds and

Bowlby, 1984; Zwarts and Wanink, 1984). Accordingly, water depth is paramount in explaining waterbird density, and determining whether or not habitat is available; waterbird diversity generally is highest at low water depth and correlated to hydrological diversity (Powell, 1987; Taft et al., 2002; Bolduc and Afton, 2004a; Kingsford et al., 2004; Robertson and Massenbauer, 2005; Holm and Clausen, 2006).

Thus, it is reasonable to assume that waterbird communities differ among areas showing different hydrological regimes at a given time. Such differences ultimately describe the confounded effects of resource availability (via water depth) and

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resource abundance, and one cannot ascertain the extent to which of the two factors affect the observed bird abundance. Indeed, several researchers have compared bird abundances among wetlands, while admitting a confounding effect of the variation in water depth on wetland comparisons, but did not include water depth in their predictive models (Hands et al., 1991; Frederick and McGehee, 1994). If water regimes are fairly predictable, as for tidal wetlands, comparing these communities can be straightforward. However, there often is a large variation in wetland hydrology among consecutive days, months or years (Mitsch and Gosselink, 1993; Bolduc and Afton, 2004b), which precludes generalizing on the short-time water depth of a given wetland, unless one examines the long-term wetland hydroperiod (defining the seasonal pattern of water levels in a given wetland type and the vegetation that developed therein). Ecological studies generally are conducted over a few consecutive years at best and use sampling techniques to optimize efforts in the field. Consequently, such studies necessarily are susceptible to unpredictable short-term events, such as sudden hydrological events in wetlands, which cause problems for census (e.g., Warnock et al., 1998). Accordingly, water depth and wetland type effects need to be controlled for and estimated separately in analyses with objectives of providing unbiased conclusions on how these habitats provide resources preferred by waterbirds.

As noted above, the general biological relationship between water depth and waterbird abundance is clear; however, its mathematical functions have not been explored thoroughly. Researchers who have examined the influence of water depth on the abundance of non-diving waterbirds generally report the average water depth used by each species (Weber and Haig, 1996; Safran et al., 1997; Isola et al., 2000) or the range of water depths used (Davis and Smith, 1998; Ntiamoa-Baidu et al., 1998). The relationships of water depth and several biotic components of wetlands previously have been analyzed in several ways. For example, variation in bird abundance and water depth sometimes are analyzed separately and their relationship discussed afterward (e.g., Connor and Gabor, 2006). Also, water depth may be transformed into categories (ranges) and the latter compared (Hoover, 2006). When possible, an experimental setup can be used with the study's subjects enclosed at specific water depths (Angeler et al., 2005). Wetlands also can be divided in cells where water depth is manipulated (Murkin et al., 2000), or water depth can be manipulated in laboratory experiments (Miller and Zedler, 2003). Often, water depth is considered as a separate environmental factor and incorporated in multivariate models to predict effects on biotic components (Bolduc and Afton, 2004a; Özsesmi et al., 2006; Vincent et al., 2006). Finally, univariate models of the effect of water depth on bird abundance have been explored using linear, exponential, quadratic and S-shaped models (Bancroft et al., 2002; Boertmann and Riget, 2006; DesGranges et al., 2006).

Some researchers have reported negative correlations between water depth and bird abundance (Epstein and Joyner, 1988; Colwell and Taft, 2000), even though the end result of this is biologically unrealistic because it implies that maximum waterbird abundance is found where water depth is zero. In general, there should be a water depth that maximizes resource exploitation, and consequently bird abundance, and a range of water depths that a species uses, which depend

on the interaction among feeding strategy, morphological features and resource abundance at various water depth. Quadratic models generally follow the above pattern, but there are no bases for a parametric function between bird abundance and water depth. Although useful to identify the cutoff point where the relationship between bird abundance and water depth changes rapidly, the S-shaped model of Boertmann and Riget (2006) is relevant to local conditions only.

In this paper, we argue that the relationship between water depth and bird abundance is non-linear in most non-diving waterbird species, with low abundance at water depth 0 (except for shorebirds), followed by an increase afterward until a maximum is reached, and then a decrease to abundance 0 when water depth is too deep for a species to forage. Moreover, the mathematical functions of such relationships are unknown, and probably vary among species. We therefore suggest that non-parametric regression be used for modeling relationships between species-specific waterbird abundance and water depth.

Developments in non-linear modeling (Cleveland et al., 1988) and its integration in statistical software facilitate examinations of the relationship between water depth and waterbird abundance. Curve-fitting techniques using non-parametric smoothing (locally weighted regression, LOESS) also can be integrated into parametric analysis using generalized additive models (Hastie and Tibshirani, 1990). Here, we use non-parametric regressions to estimate bird abundance in relation to water depth. We compute differences between observed abundances and those predicted by the non-parametric regression at recorded water depths (analogous to residuals in parametric models) for two hypothetical species. We subsequently compare four hypothetical wetlands, using both observed and corrected abundances within an analysis of variance, to illustrate differences between these two estimates. Finally, we discuss the pros and cons of our method and alternatives, and provide an Appendix A with instructions for use of our method by field biologists.

2. Methods

2.1. Modeling abundance of hypothetical species

To illustrate our methodology, we created hypothetical survey data for two waterbird species that differed in their water depth and wetland selection. Species G (i.e., a generalist species) uses a large range of water depths and its abundance is maximized at a water depth of 15 cm. Species S (i.e., a specialist species) uses a narrow range of water depths and its abundance is maximized at a water depth of 5 cm. We built a curve of maximum abundance by 1-cm water depth classes for depths between 0 and 40 cm for each species, to compute hypothetical bird counts using the following equations:

for G species in water depths 0 – 15 cm, $MAX = \log(WD)$,

for G species in water depths 16 – 40 cm,

$MAX = \log(PWD - [\log(PWD)])$,

for S species in water depths 0 – 5 cm, $MAX = (WD)^3$,

for S species in water depths 6–40 cm, $MAX = ((PWD) - 0.2)^3$,

Table 1 – Number of simulated surveys and total counts by wetland depth classes to compute hypothetical species abundances in four wetlands of varying water depth

Wetland	No. of 1-cm water depth classes covered (0–40 cm)	Times surveyed	Total counts
A	41	3	123
B	25	5	125
C	25	5	125
D	41	3	123
Total			496

where MAX is the maximum abundance, WD is water depth, PWD is the water depth of the previous water depth class after transformation (e.g., for the S species at WD 6, PWD = 4.8; at WD 7, PWD = 4.6; etc.), and log corresponds to the natural logarithm. We subtracted 0.2 or $\log(\text{PWD})$ from the previous water depth class to obtain asymmetric curves and to obtain a decrease in maximum abundance after a peak was reached. These equations allowed us to create hypothetical bird counts that followed our assumptions concerning the relationship between water depth and waterbird abundance: (1) waterbird abundance increases with water depth, up to a point where resource exploitation is maximized, and decreases afterward, and (2) specialist species use a narrower range of water depth than do generalist species.

We produced the above maximum abundance curves for four hypothetical wetlands that differed in their range of water depths during replicated bird counts. Our hypothetical bird abundance estimate corresponded to the number of birds/unit of area since counts were conducted over wetlands that typically vary in size. We used a total of 496 hypothetical bird counts over all wetlands (both species counted), where the average water depth was measured after the bird counts (Table 1). Bird counts were classified by their average water depth (by 1-cm classes), and occurred three times for each 1-cm water depth classes in wetlands A and D, and five times each for wetlands B and C. We computed hypothetical bird abundance using the following equation:

$$\text{bird abundance} = \text{MAX} \times \text{habitat preference factor} \\ \times \text{random number,}$$

where we used MAX associated with the water depth at which the bird count occurred, the habitat preference factor (expressing a hypothetical attractiveness of the resources of a given wetland type to a given species; needed only for the demonstration) was expressed by a multiplicative factor that varied among wetlands and was determined arbitrarily (Table 2), and the random number was a figure between 0 and 1 (up to the third decimal place). Habitat preference factors and ranges in water depths for each species were distributed in such a way that we obtained wetlands similarly preferred but with different ranges of water depths, and wetlands differently preferred with similar ranges of water depths (Table 3). We created such hypothetical distributions to allow separation of effects of water depth from effects of wetland preference on waterbird abundance.

2.2. Relationship between water depth and bird abundance

For each species, we quantified the relationship between bird abundance and water depth using non-parametric regressions (Schimek, 2000). To do so, we classified bird counts by their average water depth for each species, and averaged bird abundance for all bird counts and wetlands by 1-cm depth class; we assumed that the relationship between water depth and bird abundance generally was equivalent throughout all wetlands because it is primarily related to the species morphologic features, such as leg length and body size. Also, we assumed that water depth varied little within water bodies, at any given time where bird counts occurred, and therefore that the average water depth represents a good estimate of the water depth to which bird species are adapted. We acknowledge that using the average water depth probably is not suitable in wetlands where this parameter varies markedly. We chose to use average water depth to simplify our demonstration, and this would need to be adapted where spatial variation in water depth is too high. Non-parametric regression is a compromise between a linear regression of two variables and a series of linear regressions for each pair of consecutive points of these two variables (i.e., local regressions) (Schimek, 2000). Non-parametric regressions use a smoothing parameter (λ) that penalizes slopes of consecutive local regressions that vary too rapidly (Schimek, 2000). If $\lambda = \infty$, then the non-parametric regression produces a constant linear regression fit, whereas at $\lambda = 0$, the non-parametric regression retains all original local

Table 2 – Preferred water depth and habitat preference factor used to compute hypothetical abundances of a specialist (S species) and generalist waterbird species (G species) in four wetlands of varying water depth (WD range)

	Wetland			
	A	B	C	D
S species				
Preferred water depth	5	5	5	5
Habitat preference factor	2	0.1	0.1	0.1
G species				
Preferred water depth	15	15	15	15
Habitat preference factor	10	100	100	100
Observed WD range (cm)	0–40	16–40	0–24	0–40

Table 3 – Mean (least-square means ± S.E.) observed abundances (obs) and relative corrected abundances (corr) of hypothetical generalist (G species) and specialist (S species) species of waterbirds, and mean water depth (MWD) in four hypothetical wetlands

Wetland	MWD (cm)	G species abundance		S species abundance	
		Obs	Corr	Obs	Corr
A	20	3.2 ± 1.6 ^a	-71.8 ± 3.3 ^a	23.3 ± 1.0 ^a	0.6 ± 4.0 ^a
B	28	26.2 ± 1.0 ^b	1.0 ± 3.3 ^b	0.2 ± 1.2 ^b	-84.3 ± 4.0 ^b
C	12	42.0 ± 1.1 ^c	0.6 ± 3.3 ^b	2.2 ± 1.1 ^b	-60.6 ± 4.0 ^c
D	20	33.0 ± 1.0 ^d	2.2 ± 3.3 ^b	1.1 ± 1.1 ^b	-75.3 ± 4.0 ^b

^{abcd} Similar letters denote least-square means that did not differ ($P > 0.05$) within a column.

regressions (Schimek, 2000). The generalized cross-validation criterion (GCV) is used to estimate λ that minimizes the mean square error; the lowest GCV value is associated with the lowest mean square error (Schimek, 2000).

We used PROC LOESS in SAS 8.2 (SAS Institute Inc., 1999) to compute non-parametric regressions between mean bird abundance (by 1-cm depth classes) and water depth. We computed non-parametric regressions for smoothing parameter values at each decimal between 0.1 and 1.0, and chose the smoothing parameter associated with the lowest GCV (SAS Institute Inc., 1999). In PROC LOESS, we requested that 2 degrees of local polynomials be used for each local regression (option DEGREE=2, SAS Institute Inc., 1999) because of our model assumption that bird abundance increases until a maximum is reached, and decreases afterward (i.e., quadratic function).

2.3. Correction of observed abundances for varying water depth

We compared observed abundances with predicted mean bird abundances from non-parametric regressions at corresponding 1-cm water depth classes and computed differences (i.e., analogous to residuals of parametric models). These differences represent abundance corrected for water depth, where there is a common water depth (the fit), and therefore can be used as estimates of the variation in bird abundance unexplained by water depth.

We encountered some problems with negative predicted values; a negative predicted abundance coupled with an absence of birds provides a positive difference. To solve this problem, we replaced negative predicted abundances with 0. Furthermore, we found that negative differences were limited to differences between the fit and 0 birds, which may lead to biased mean differences between wetlands differing in average water depth. For example, at a model prediction of 0.1 birds, the difference with an observed value cannot be lower than -0.1, whereas at a prediction of 2 birds, the maximum negative difference was -2. Therefore, we transformed differences in observed - predicted abundances by a relative measure of their corresponding observed and predicted abundances:

$$\text{relative corrected abundance} = \left(\left[\frac{\text{OBS} - \text{PRED}}{\text{OBS} + \text{PRED}} \right] \times 100 \right),$$

where OBS is the observed abundance, and PRED is the predicted abundance. In cases when both observed and predicted

abundances were 0, we set relative corrected abundances (RCA) to -100% to ensure that we always obtain average abundances of -100% when no birds were present. These calculations allowed us to obtain: (1) relative differences of 0 when predicted and observed abundances were equal at any level of abundances (except when predicted and observed abundances were 0), (2) negative values when predicted abundances exceeded observed abundances (always $\geq -100\%$), and (3) positive values when observed abundances exceeded predicted abundances (always $\leq 100\%$).

RCA estimates are related to the observed:predicted abundance ratio. For example, at observed abundance 0.1 and predicted abundance 0.4, the RCA is -60%, and therefore the observed:predicted abundance ratio is 0.25 (0.1/0.4). At observed abundance 3.0 and predicted abundance 10.0, the RCA is -54%, and the observed:predicted abundance ratio is 0.30 (3/10). An observed:predicted abundance ratio of 0.25 means that 25% of the abundance predicted at the observed water depth was actually counted. Thus, for each RCA, there is a corresponding observed:predicted abundance ratio that is easily interpretable. However, the relationship between the corrected abundance (corr) and the above ratio (ratio) is near exponential ($\text{ratio} = 1.017 \times \exp[2.545\text{corr}]$, $R^2 = 0.983$) when the ratio > 0 and < 10 , but near linear ($0.882 + 1.018\text{corr}$, $R^2 = 0.968$) when ratio < 1 , and best predicted by a polynomial model ($\text{ratio} = 0.996 + 1.911\text{corr} + 1.446\text{corr}^2 + 0.546\text{corr}^3$, $R^2 = 0.999$) in this interval. One could argue that the use of this ratio rather than the RCA would be more straightforward. However, when 0 birds are predicted, the observed: predicted abundance ratio is problematic because of the insolvability of the ratio when the denominator is 0.

To summarize these calculations, the observed abundance describes how many birds were using the wetland surveyed, whereas the RCA describes the extent at which the observed bird abundances followed predictions based on recorded water depths. Thus, the comparison of observed abundances among wetlands indicates whether more birds were using one wetland than another. In contrast, comparison of RCAs among wetlands indicates whether wetlands differ in bird abundances with respect to that expected based upon the average use at recorded water depths.

2.4. Statistical analysis of observed abundances and RCAs

We used separate analysis of variance (ANOVA) to compare wetlands for both RCAs and observed abundances of our two

hypothetical waterbird species among wetlands. ANOVA were conducted using PROC GENMOD, with a Poisson distribution for observed data and a normal distribution for the corrected data (SAS Institute Inc., 1999). We used least-square means to express the average bird abundance in wetlands and tested for difference among wetlands using the diff option of the lsmeans statement of PROC GENMOD (SAS Institute Inc., 1999).

3. Results

3.1. Non-parametric regressions of bird abundance on water depth

As desired, the non-parametric regression fit of G species abundance with water depth (GCV=0.91, smoothing parameter=0.5) indicated that this species used a wide range of water depths (Fig. 1A). The regression model predicted >10 birds at water depths between 1 and 31 cm, and a maximum abundance of about 50 birds at a water depth of 17 cm (Fig. 1A).

The non-parametric regression fit of S species abundance with water depth (GCV=0.67, smoothing parameter=0.2) indicated that this species generally was associated with low water depth (maximum predicted abundance of 53 birds at 5 cm of water) and was more restricted by water depth than was the G species (Fig. 1B). The regression model for this species predicted more than 10 birds between 3 and 15 cm of water, and less than 1 bird for water depths greater than 22 cm (Fig. 1B).

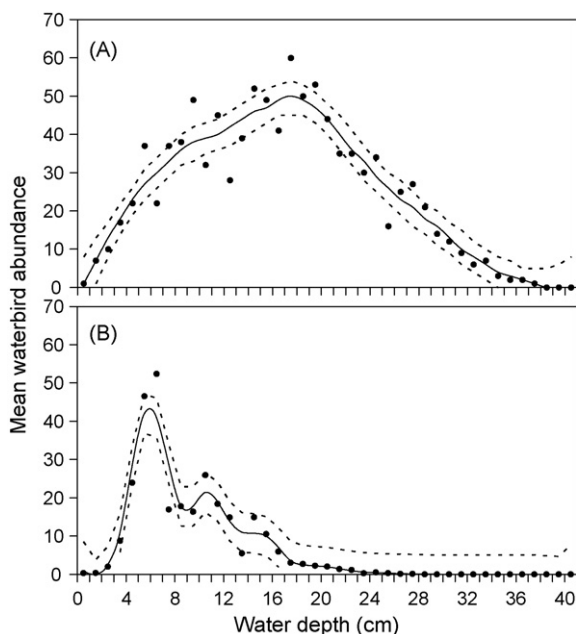


Fig. 1 – Mean observed abundance of a hypothetical generalist waterbird (G species, panel A) and a specialist species (S species, panel B) by 1-cm water depth classes (dots) and non-parametric fit between these two variables (solid line) with associated 95% confidence intervals (dotted lines) as computed from hypothetical surveys in four wetland types (see Section 2 for calculations).

3.2. Comparisons of observed and RCAs among wetlands

The mean observed abundance of the G species varied greatly among wetlands (3.2–42.0 birds) (Table 3). ANOVA and subsequent pairwise comparisons indicated that observed abundances differed among all wetlands (Table 3). In contrast, mean RCAs for the G species in wetlands B–D, were close to 0, which indicates that bird abundances generally were close to abundances expected based on recorded water depth in those wetlands (Table 3). Mean RCA of the G species in wetland A was –71.8, which indicates that approximately six times fewer birds were counted there than that expected based on recorded water depth (associated ratio observed:predicted abundance=0.16). ANOVA and subsequent pairwise comparisons indicated that RCA on wetland A differed from the other wetlands, whereas estimates for wetlands B–D did not differ (Table 3).

The mean observed abundance of the S species varied between 0.2 and 23.3 birds among wetlands (Table 3), and ANOVA and subsequent pairwise comparisons indicated a significant difference among all wetlands. Mean RCA of wetland A approached 0, indicating that bird abundance in this wetland closely followed that expected based solely on recorded water depth. Mean RCA of wetlands B–D ranged between –60.6 and –84.3, indicating that these wetlands supported between 4 and 13 times fewer birds than those expected based on recorded water depth (associated observed:predicted abundance ratios between 0.25 and 0.08). ANOVA and subsequent pairwise comparisons indicated that mean RCAs of S species differed among wetlands, with wetland A supporting higher bird abundances than the three other wetlands (Table 3). Finally, mean RCA was greater in wetland C than in wetlands B and D (Table 3).

4. Discussion

Our analysis of observed and RCAs of the G species was consistent with our prediction that analysis of the latter would best reflect habitat preference. Three hypothetical wetlands of similar preference factor (wetlands B–D) differed in observed abundances just by manipulating water depths at which birds were recorded, whereas their RCAs did not differ. Consequently, our proposed methodology using RCA adequately removed effects of variation in water depth from effects of wetlands on variation in bird abundance for the G species.

Our analysis also indicated that RCAs of the S species differed among hypothetical wetlands of similar preference factor in some cases. The S species used a narrow range of water depths that corresponded best to those recorded in wetland C, whereas the other two wetlands of similar preference (B and C) comprised many counts associated with water depths that the specialist bird avoided. Thus, our methodology may yield differences in RCAs of waterbirds among wetlands of similar preferences, but these results probably are biologically insignificant because of the very low usage of such wetlands. Comparisons of observed and RCAs of the S species indicated that both estimates of abundance provide similar results when differences among wetlands are very large.

Our RCA method adequately separates the effect of water depth from the effect of the wetlands. It therefore provides unbiased estimates of bird abundance relative to water depth, which are useful for comparisons of wetlands with varying water depths. Accordingly, we recommend that users of our methodology present both RCAs and observed abundances to ensure an adequate interpretation of results. Also, because there is no equation associated with non-parametric regressions, we suggest that users include their predicted abundances by water depth classes in their publications. These data could be useful to researchers that want to compare results among studies, or do not have sufficient data to compute their own predicted abundances.

We used a simple case to test our RCA method, but real-life cases (see Bolduc, 2002 page 81 for an example) may require more complicated models to integrate fully all components of the sampling design. For example, replication in space and time may involve both fixed and random effects. Also, multivariate analysis may be better suited for community analysis and count data are not normally distributed, which may require the use of generalized linear models that allow the response probability distribution to be any member of an exponential family of distributions. General additive models (GAM) also may become a more straightforward tool for our type of analyses in the future as they integrate both linear and non-linear modeling. However, most available statistical software packages currently do not provide all the necessary options that are available when using LOESS regression models, such as the integration of a quadratic function. We did try to fit our data into a GAM analysis, but results were not satisfactory for the above reasons. All effects included in a real-life study may be difficult to amalgamate into a single model; thus researchers may need to balance the different aspects of their sampling design against using the model that best describes the system under study. We believe that our RCA method will be helpful in answering future challenges, and users will need to adapt it to their own study situation.

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Appendix A

Steps to complete the relative corrected abundance (RCA) method:

- 1 Establish study objectives, sampling scheme and data collection and analysis methods.
- 2 Data collection
 - a. Bird data, with computed surveyed areas to calculate densities if required.
 - b. Water depth, either at bird locations and/or at random sites depending on study sites and objectives.
- 3 Data analysis
 - a. Compute mean bird abundance by 1-cm water depth class (including zeros) over all counts and habitats.
 - b. Model mean bird abundance by 1-cm water depth vs. water depth using LOESS regression with quadratic function for local regressions. Do for a range of smoothing parameter (e.g., 0.1–1.0), or use automatic selection methods available to choose that associated with lowest GCV value.
 - c. Associate specific predicted abundance with the observed bird data by water depth class.
 - d. Replace negative predicted abundance with 0.
 - e. Compute RCA from observed (OBS) and predicted (PRED) data using the formula: $RCA = ((OBS - PRED) / (OBS + PRED)) \times 100$.
 - f. If both observed and predicted = 0, then replace RCA with –100%.
 - g. Compute statistical comparison of habitats accordingly to step 1.
 - h. Compute associated OBS/PRED ratio of mean responses to help with the interpretation of results.
- 4 Results
 - a. LOESS regressions: report on important statistics (GCV and smoothing parameters), with description of the results, i.e., water depth range, maximum, etc. as computed by the regression. Present table of the predicted abundance by water depth class in appendix for future use by other researchers
 - b. Statistical comparisons of habitats: report on observed as well as corrected data, and on OBS/PRED ratios. Report the usual statistics based on analysis chosen in step 1.

REFERENCES

- Angeler, D.G., Sánchez-Carrillo, S., Rodrigo, M.A., Viedma, O., Alvarez-Cobelas, M., 2005. On the importance of water depth, macrophytes and fish in wetland Picocyanobacteria regulation. *Hydrobiologia* 549, 23–32.
- Baker, M.C., 1979. Morphological correlates of habitat selection in a community of shorebirds (Charadriiformes). *Oikos* 33, 121–126.
- Bancroft, G.T., Gawlik, D.E., Rutchey, K., 2002. Distribution of wading birds relative to vegetation and water depths in the northern Everglades of Florida, USA. *Waterbirds* 25, 265–277.
- Boertmann, D., Riget, F., 2006. Effects of changing water levels on numbers of staging dabbling ducks in a Danish wetland. *Waterbirds* 29, 1–8.
- Bolduc F., 2002. Effects of structural marsh management and salinity on sediments, hydrology, invertebrates, and waterbirds in marsh ponds during winter on the Gulf Coast Chenier Plain. Ph.D. Dissertation. Louisiana State University, Baton Rouge, LA, USA.
<http://etd.lsu.edu/docs/available/etd-0708102-140449/>.

- Bolduc, F., Afton, A.D., 2004a. Relationships between wintering waterbirds and invertebrates, sediments and hydrology of coastal marsh ponds. *Waterbirds* 27, 333–341.
- Bolduc, F., Afton, A.D., 2004b. Hydrologic aspects of marsh ponds during winter on the Gulf Coast Chenier Plain, USA: effects of structural marsh management. *Mar. Ecol. Prog. Ser.* 266, 35–42.
- Cleveland, W.S., Devlin, S.J., Grosse, E., 1988. Regression by local fitting. *J. Econom.* 37, 87–114.
- Colwell, M.A., Taft, O.W., 2000. Waterbird communities in managed wetlands of varying water depth. *Waterbirds* 23, 45–55.
- Connor, K., Gabor, S., 2006. Breeding waterbird wetland habitat availability and response to water-level management in Saint John River floodplain wetlands, New Brunswick. *Hydrobiologia* 567, 169–181.
- Davis, C.A., Smith, L.M., 1998. Ecology and management of migrant shorebirds in the playa lakes region of Texas. *Wildl. Monogr.*, 140.
- DesGranges, J.-L., Ingram, J., Drolet, B., Morin, J., Savage, C., Borcard, D., 2006. Modelling wetland bird response to water level changes in the Lake Ontario, St. Lawrence River hydrosystem. *Environ. Monit. Assess.* 113, 329–365.
- Epstein, M.B., Joyner, R.L., 1988. Waterbirds use of brackish wetlands managed for waterfowl. In: *Proceedings of the Annual Conference of the Southeastern Association of the Fish and Wildlife Agencies*, vol. 42, pp. 476–490.
- Frederick, P.C., McGehee, S.M., 1994. Wading bird use of wastewater treatment wetlands in central Florida. *Colon. Waterbirds* 17, 50–59.
- Hands, H.M., Ryan, M.R., Smith, J.W., 1991. Migrant shorebirds use of marsh, moist-soil, and flooded agricultural habitats. *Wildl. Soc. Bull.* 19, 457–464.
- Hastie, T., Tibshirani, R., 1990. *Generalized Additive Models*. Chapman and Hall, London, UK.
- Holm, T.E., Clausen, P., 2006. Effects of water level management on autumn staging waterbird and macrophyte diversity in three Danish coastal lagoons. *Biodivers. Conserv.* 15, 4399–4423.
- Hoover, J.P., 2006. Water depth influences nest predation for a wetland-dependent bird in fragmented bottomland forests. *Biol. Conserv.* 127, 37–45.
- Isola, C.R., Colwell, M.A., Taft, O.W., Safran, R.J., 2000. Interspecific differences in habitat use of shorebirds and waterfowl foraging in managed wetlands of California's San Joaquin Valley. *Waterbirds* 23, 196–203.
- Kingsford, R.T., Jenkins, K.M., Porter, J.L., 2004. Imposed hydrological stability on lakes in arid Australia and effects on waterbirds. *Ecology* 85, 2478–2492.
- Miller, R.C., Zedler, J.B., 2003. Responses of native and invasive wetland plants to hydroperiod and water depth. *Plant Ecol.* 167, 57–69.
- Mitsch, W.J., Gosselink, J.G., 1993. *Wetlands*, Second edition. Van Nostrand Reinhold, New York, NY, USA.
- Murkin, H.R., van der Valk, A.G., Clark, W.R., 2000. *Prairie Wetland Ecology. The Contribution of the Marsh Ecology Research Program*. Iowa State University Press, Ames, IA, USA.
- Ntiamao-Baidu, Y., Piersma, T., Wiersma, P., Poot, M., Battley, P., Gordon, C., 1998. Water depth selection, daily feeding routines and diets of waterbirds in coastal lagoons in Ghana. *Ibis* 140, 89–103.
- Nudds, T.D., Bowlby, J.N., 1984. Predator-prey size relationships in North American dabbling ducks. *Can. J. Zool.* 62, 2002–2008.
- Özesmi, U., Tan, C.O., Ozesmi, S.L., Robertson, R.J., 2006. Generalizability of artificial neural network models in ecological applications: predicting nest occurrence and breeding success of the red-winged blackbird *Agelaius phoeniceus*. *Ecol. Model.* 195, 94–104.
- Pöysä, H., 1983. Morphology-mediated niche organization in a guild of dabbling ducks. *Ornis Scand.* 14, 317–326.
- Powell, G.N., 1987. Habitat use by wading birds in a subtropical estuary: implications of hydrography. *Auk* 104, 740–749.
- Robertson, D., Massenbauer, T., 2005. Applying hydrological thresholds to wetland management for waterbirds, using bathymetric surveys and GIS. In: Zenger, A., Argent, R.M. (Eds.), *MODSIM 2005 International Congress on Modelling and Simulation. Modelling and Simulation Society of Australia and New Zealand*. Australia, pp. 2407–2413.
- Safran, R.J., Isola, C.R., Colwell, M.A., Williams, O.E., 1997. Benthic invertebrates at foraging locations of nine waterbird species in managed wetlands of the northern San Joaquin Valley, California. *Wetlands* 17, 407–415.
- SAS Institute Inc., 1999. *SAS/STAT User's Guide, Version 8.0*. SAS Institute, Inc., Cary, NC, USA.
- Schimek, M.G., 2000. *Smoothing and Regression: Approaches, Computation, and Application*. John Wiley & Sons, New York, NY, USA.
- Taft, O.W., Colwell, M.A., Isola, C.R., Safran, R.J., 2002. Waterbird responses to experimental drawdown: implications for the multispecies management of wetland mosaics. *J. Appl. Ecol.* 39, 987–1001.
- Vincent, C., Mouillot, D., Lauret, M., Chi, T.D., Troussellier, M., Aliaume, C., 2006. Contribution of exotic species, environmental factors and spatial components to the macrophyte assemblages in a Mediterranean lagoon (Thau lagoon, Southern France). *Ecol. Model.* 193, 119–131.
- Warnock, N., Haig, S.M., Oring, L.W., 1998. Monitoring species richness and abundance of shorebirds in the Western Great Basin. *Condor* 100, 589–600.
- Weber, L.M., Haig, S.M., 1996. Shorebird use of South Carolina managed and natural coastal wetlands. *J. Wildl. Manag.* 60, 73–82.
- Zwarts, L., Wanink, J., 1984. How oystercatchers and curlews successively deplete clams. In: Evans, P.R., Goss-Custard, J.D., Hale, W.G. (Eds.), *Coastal Waders and Wildfowl in Winter*. Cambridge University Press, New York, NY, USA, pp. 69–83.