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NUTRIENT RECYCLING BY EARED GREBES IN THE GREAT SALT LAKE

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ABSTRACT.—Nitrogen (N) and phosphorus (P) cycling in lakes can be impacted by numerous abiotic and biotic factors. Large animals, such as birds and mammals, may recycle nutrients within a system or bring them in from surrounding habitats or different landscapes. Eared Grebes (*Podiceps nigricollis*) congregate in large numbers in the fall on the Great Salt Lake (GSL), Utah, and may have an important role in recycling nutrients from macroinvertebrates back into the water column. We evaluated the role of Eared Grebes in N and P cycling within the GSL by estimating the magnitude of their nutrient recycling capacity. We estimated Eared Grebe population size on the GSL over 5 years at 300,000 to over 4,300,000 birds. We used a previously published food intake model to estimate monthly recycling of N (5 to 300 tonnes) and P (0.4 to 25 tonnes). The maximum estimates of N and P loading by Eared Grebes are about 25% of nutrient recycling in the GSL caused by turnover in the water column. Eared Grebes may speed up nutrient recycling, making nutrients available to primary producers sooner. The contribution of waterbirds to nutrient cycling is important for the entire N and P cycles within the GSL.

RESUMEN.—Los ciclos del nitrógeno (N) y fósforo (P) en los lagos pueden ser afectados por numerosos factores abióticos y bióticos. Los animales grandes, como aves y mamíferos, pueden asimilar nutrientes de hábitats circundantes o de diferentes paisajes, o reciclarlos dentro del sistema. Los individuos de *Podiceps nigricollis* se congregan en grandes números en la caída del Gran Lago Salado (Great Salt Lake [GSL]), en Utah, y podrían tener un papel importante en el reciclaje de nutrientes, por macro-invertebrados, para devolverlos a la columna de agua. Evaluamos el papel de *P. nigricollis* en los ciclos del N y P en el Gran Lago Salado, estimando su capacidad para reciclar nutrientes. Estimamos el tamaño poblacional de *P. nigricollis* en el GSL a lo largo de cinco años, siendo desde 300,000 a más de 4,300,000 individuos. Utilizamos un modelo de ingesta de alimentos publicado previamente para derivar un estimado del reciclaje mensual de N, en un rango de entre 5 y 300 toneladas, y de P, en un rango desde 0.4 a 25 toneladas. Los estimados máximos de N y P transportados por los individuos de *P. nigricollis* son, aproximadamente, alrededor del 25% de nutrientes reciclados en el GSL, derivados de la rotación de la columna de agua. *Podiceps nigricollis* podría acelerar el reciclaje de nutrientes haciendo que éstos estén disponibles para los productores primarios antes de lo que ocurriría si no estuviesen. La contribución de las aves acuáticas al ciclo de nutrientes es muy importante para todo el ciclo del N y P dentro del GSL.

NOTE.—The SI equivalent of 1 tonne is 1000 kg or 1 Mg.

Nutrient cycling by waterbirds may impact nutrient dynamics within water bodies, particularly if the water body is small or waterbird populations are large and dense. Concentrations of birds during breeding (Bildstein et al. 1992), communal roosting (Post et al. 1998), or winter aggregations (Kitchell et al. 1999) may be particularly important nutrient sources for some aquatic ecosystems. Nutrient loading is often considered a transport of nutrients from feeding sites to aquatic ecosystems in the form of excrement (Manny et al. 1994); but birds that forage aquatically may contribute to nutrient cycling in a different form. Aquatic birds may forage and defecate in the same system and provide internal recycling of nutrients (Hahn et al. 2007). This pattern produces more rapid nutrient recycling than would otherwise occur through decomposition.

Nitrogen (N) and phosphorus (P) often limit aquatic productivity, and the positive top-down effect of predators on the abundance of primary producers may have more to do with increased nutrient recycling than decreased herbivory by zooplankton (Vanni et al. 1997). Waterbirds' excrement is high in both N and P, and herbivorous waterbirds such as geese (tribe Anserini) may transport large amounts of these nutrients from terrestrial sources to a wetland (Manny et al. 1994, Post et al. 1998). Carnivorous waterbirds, such as grebes (Podicipedidae) and cormorants (Phalacrocoracidae), typically have a diet higher in N and P than herbivorous birds (Karasov 1990) and therefore may contribute more to nutrient cycling

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within a system than herbivorous birds. Within-lake nutrient recycling by top predators should be incorporated into models of food web dynamics and top-down control of primary productivity to accurately describe within-lake nutrient dynamics (Vanni and Layne 1997).

Eared Grebes (*Podiceps nigricollis*) are carnivorous waterbirds that use saline systems throughout much of their annual lifecycle (Cullen et al. 1999). They are abundant and occur at high densities on North American saline lakes during fall, particularly the Great Salt Lake (GSL), Utah, and Mono Lake, California. An average of 1.5 million birds, more than half of the North American population, use the GSL from September into December (Aldrich and Paul 2002) where they feed on abundant brine shrimp (*Artemia franciscana*). While staging, Eared Grebes molt and become flightless (Jehl 1997). Because Eared Grebes cannot feed in any other water body and are highly reliant on adult brine shrimp for food, they are an ideal model organism for evaluating nutrient recycling in this ecosystem. Eared Grebes may provide a valuable ecosystem service to the GSL's halophile populations by recycling nutrients and providing them in a form usable by phytoplankton sooner and in higher quantities than would otherwise exist during normal death and decay of brine shrimp. Our objective was to estimate the amount of nutrient recycling by Eared Grebes in the GSL during the fall staging period.

METHODS

The GSL ecosystem covers nearly 780,000 ha when at a long-term average lake elevation of 1280 m (Aldrich and Paul 2002). Salinity is variable due to concentrated areas of freshwater inflow and anthropogenic alterations of water exchange. The GSL is an N-limited, hypersaline ecosystem that supports only 3 aquatic invertebrates: brine shrimp and 2 species of brine flies (*Ephydra cinerea* and *Ephydra hians;* Belovsky et al. 2011). We focused on the Eared Grebe and brine shrimp dynamics because the relationship between GSL nutrients, primary production, and brine shrimp dynamics are clearly defined (Belovsky et al. 2011). In contrast, data on brine flies are severely limited and though other bird species forage extensively on brine flies

(Roberts 2013), none are as abundant for as long a time at GSL as Eared Grebes.

Brine shrimp hatch in the spring from overwintering eggs, known as cysts. Hatched brine shrimp (nauplii) progress through a juvenile stage to adults, and their densities peak in mid- to late summer. As water temperatures decrease in the fall, female brine shrimp stop giving birth to live young and begin depositing cysts which form large overwintering masses on the surface of the GSL. Densities of brine shrimp vary spatially in the GSL: their numbers are lowest in Gunnison Bay and in areas with the least saline water (Stephens and Birdsey 2002). The only other primary predator of adult brine shrimp is the California Gull (*Larus californicus*) which inhabits the GSL throughout the spring and summer but has population densities much lower than Eared Grebes and a diet that is more opportunistic and less well defined (Roberts 2013).

We used aerial surveys to estimate population levels of Eared Grebes on the GSL. We conducted stratified random aerial counts during October–January, 2009–2013, to calculate within-year changes in bird numbers and bird use-days. We conducted a stratified random sampling survey where transects were placed 250 m apart, running east to west, throughout each of the 7 strata. We chose transects randomly without replacement and constrained the choice so that 2 adjacent transects were not surveyed in a single month. We flew transects in a fixed-wing airplane at approximately 150 km per hour while one observer counted all birds seen within 250 m of each side of the aircraft. We used the survey package in Program R (R Core Team 2012) to calculate Eared Grebe population size during each survey period. We assumed detection was equal across the survey effort, as all birds were observed on open water during periods of no precipitation and low (<10 km $\cdot$ h^{-1}) wind speeds. Results and sampling design of the survey have been reported previously (Roberts et al. 2013), but we use those data here for estimates of nutrient loading in the GSL.

We used the following food intake model:

$$[X_{bird} = A \times DER/(E \times AM) \times X_{intake}],$$

presented by Hahn et al. (2007), to estimate the daily nutrient loading to the GSL by an individual Eared Grebe (X_{bird}). This model

TABLE 1. Eared Grebe use days (in millions) and estimates of yearly nutrient load of nitrogen (N; tonnes of dry weight) and phosphorus (P; tonnes of dry weight) into the Great Salt Lake, Utah, by Eared Grebes from 2009 to 2013. Bird use-days were calculated using aerial survey estimates and area under the curve from 1 October to 5 January each year.

Year	Bird use days (in millions)	Yearly nutrient load			
		N low	N high	P low	P high
2009	137	181.9	311.3	2.2	35.4
2010	94	125.0	213.9	1.5	24.3
2011	212	281.1	481.0	3.4	54.7
2012	186	247.2	422.9	3.0	48.1
2013	128	169.8	290.6	2.1	33.0

uses a bird's daily energy requirements (DER; $kJ \cdot d^{-1}$), the gross energy content (E; $kJ \cdot g^{-1}$) of the bird's food, and the apparent metabolizable energy coefficient of foods (AM) to calculate what amounts of ingested N and P (X_{intake}; $mg \cdot g^{-1}$) are deposited into an ecosystem. In the model, A is the proportion of a bird's total nutrient release that is deposited in the water compared to other habitats within their daily cycle. For birds that forage and defecate in the same habitat, as is the case here, A = 1.0. Eared Grebe's DER has been calculated previously (391 $kJ \cdot d^{-1}$) for an average-sized Eared Grebe (550 g) using the GSL (Conover and Caudell 2009). Brine shrimp are the primary food eaten by staging Eared Grebes (Roberts and Conover 2013). Caudell and Conover (2006) calculated the E and AM of brine shrimp for Eared Grebes as 21.9 $kJ \cdot g^{-1}$ dry weight and 0.826, respectively. Szyper (1989) determined that N content in brine shrimp from Utah ranges from 90 to 154 $mg \cdot g^{-1}$ dry weight. We used the dry weight range of 1.1 to 17.5 $mg \cdot g^{-1}$ P reported for brine shrimp in Leger et al. (1986). The food intake model produces liberal estimates of total nutrient input as a result of some of its assumptions. For example, the model assumes that the ratio of mass intake to mass excrement is 1:1, producing an estimate 25%–59% higher than a model based on excretion measurements of N and P (Hahn et al. 2007).

We used the range of N and P in brine shrimp to calculate a high and low estimate of X_{bird}. We used the area under the curve method (Irvine et al. 1992) to estimate total Eared Grebe use-days on the GSL for each month and year from aerial survey data and then multiplied use-days by X_{bird} to estimate monthly and yearly nutrient inputs. We employed use-days to scale N and P loading from the individual bird to the monthly and annual population level on the GSL. Eared Grebes reduce their food consumption sometime in mid- or late December in preparation for continued migration further south (Jehl 1988, Roberts and Conover 2013). The exact timing of reduced food intake is unknown and likely varies by year, so we did not reduce estimates of food intake in these models to compensate for reduced intake. Therefore, our estimates of use-days result in larger estimates of N and P inputs than likely occur. We present monthly nutrient inputs per km^2 of GSL surface area, determined from GSL elevation each month (Baskin 2005). The food intake model produces an upper limit estimate of nutrient input (Hahn et al. 2007), so our results are likely higher than the true input but give an order of magnitude estimate of the process.

RESULTS

Eared Grebe monthly population estimates derived from aerial surveys ranged from about 300,000 in December 2012 to over 4,300,000 birds in November 2012. Roberts et al. (2013) provide a range of Eared Grebe abundance estimates and measures of error through 2011. We used the same survey methodology and estimation procedures in 2012 and 2013, and the latter years have similar measurements of error. The lowest yearly population of Eared Grebes on the GSL occurred in 2010. Eared Grebe use-days derived from population estimates ranged from a low of 94 million in 2010 to a high of 212 million in 2011 (Table 1).

Monthly estimates of N loading from Eared Grebes averaged 23.3 $g \cdot km^{-2}$ dry weight (range 0.91–73.5, $n = 5$; Fig. 1). P monthly estimates averaged 1.77 $g \cdot km^{-2}$ dry weight (range 0.01–8.34, $n = 5$). November estimates of N and P deposition by Eared Grebes were
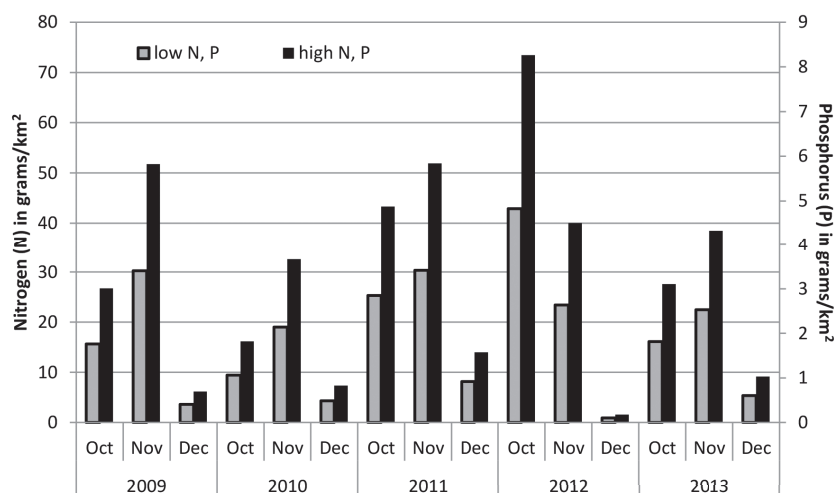
Fig. 1. Monthly estimates of nitrogen (N; g · km^{-2}) and phosphorus (P; grams · km^{-2}) dry weight load to the Great Salt Lake, Utah, by fall-staging Eared Grebes from October through December, 2009 to 2013. Estimates are derived from a food intake model of total daily energy requirements and the resulting N and P excreted from meeting energy demands multiplied by Eared Grebe use-days estimated from aerial surveys. High and low N and P estimates are derived using maximum and minimum measurements from the literature of N in brine shrimp and P in invertebrates.

the highest of any month examined. December Eared Grebe populations were highest in most years of the study; but Eared Grebes migrate throughout December and bird use-days in December were lower, so nutrient deposition was lower than in November (Fig. 1). Total yearly lake-wide estimates of N load ranged from 125 to 481 tonnes, with the peak estimate in 2011 (Table 1). Estimates of yearly P load ranged from 1.5 to 55 tonnes.

DISCUSSION

Eared Grebes may be a significant source of nutrient recycling within the GSL. There are few data on nutrient recycling by birds in other lake systems. In a Netherland lake, nutrient recycling by carnivorous waterbirds resulted in average yearly recycling of 100 tonnes of N and 32 tonnes of P (Hahn et al. 2007). Primary avian nutrient recyclers in the Netherlands were breeding Grey Herons (*Ardea cinerea*) and Great Cormorants (*Phalacrocorax carbo*). Over half of the annual P load by gulls (Laridae) to a northeastern U.S. pond was during the fall migration period (Portnoy 1990), similar to the time frame in the present study.

The GSL is a large water body and a terminal lake. Terminal lakes may become eutrophic

and experience algae blooms when the natural nutrient inputs are supplemented with anthropogenic sources, as seen in one part of the GSL (Wurtsbaugh and Marcarelli 2006). Previous work has shown that yearly nutrient loads in the GSL are not significantly impacted by freshwater inflow sources, though inflow sources are vital to nutrient loading on a decadal time scale (Belovsky et al. 2011). Atmospheric deposition is also not a large yearly contributor of nutrients to this ecosystem (Belovsky et al. 2011). Therefore, various forms of nutrient recycling are likely the primary mechanism for making nutrients available for primary production throughout the year. Nutrient recycling in the GSL likely comes from 3 mechanisms: mixing of water layers; excretion from Eared Grebes, other waterbirds, and invertebrates; and carcass decomposition.

Mixing of water is likely the largest yearly source of nutrients within the GSL. A chemocline often occurs in the GSL causing an anoxic water layer, known as the deep brine layer, to settle in the deepest waters. Mixing occurs among years at low lake elevations and within years when densities between the deep brine layer and upper brine layer are more uniform. Wind events may cause mixing so nutrients that settle in the deep brine layer

become available to phytoplankton in the upper brine layer. An estimate of the N turnover into the upper brine layer can be calculated using previous estimates of deep brine layer ammonia concentrations (5 mg · L^{-1}; Wurtsbaugh and Berry 1990) and percent of the total deep brine layer volume (1.73×10^9 per m^3) that is turned over each year (25%; Jones and Wurtsbaugh 2014). The resulting estimate is about 2200 tonnes of bioavailable N recycled each year from the deep brine layer to the upper brine layer through mixing. Our maximum estimate of Eared Grebe yearly contribution to N recycling is about 25% of the annual mixing estimate. Nutrient excretion by brine flies and brine shrimp on the GSL has not been measured, but estimates have been made for brine shrimp on Mono Lake. Using unpublished estimates of Mono Lake brine shrimp (*Artemia monica*) excretion, Jellison and Melack (1993) found maximum excretion rates of about 25 mmol · m^{-2}d^{-1}. Brine shrimp excretion was nearly always greater than upwelling of nutrients from the lower unmixed layer of Mono Lake (Jellison and Melack 1993). Unfortunately, we do not have similar measurements for brine flies in Mono Lake or the GSL.

Nutrient recycling by Eared Grebes occurs in the fall when nutrients in a free form are at their lowest point in the GSL (Belovsky et al. 2011). Nutrient availability limits phytoplankton growth in the GSL (Belovsky et al. 2011), and food availability limits brine shrimp populations (Wurtsbaugh and Gliwicz 2001, Belovsky et al. 2011). By releasing nutrients, Eared Grebes allow for an earlier start to phytoplankton production in the fall and winter which may benefit the following spring's brine shrimp population. In late summer and early fall, most of the nutrients are locked up in either the deep brine layer or in brine shrimp, and they are not available for primary producers (Belovsky et al. 2011). During summer months, brine shrimp may make nutrients available through their excrement (Belovsky et al. 2011); but during fall when ammonia in the photic zone (top 1 m) is still high, adult brine shrimp populations are low (<1 adult · L^{-1}; Belovsky et al. 2011). Therefore, it is unlikely that brine shrimp excrement is responsible for high levels of nutrients and increases in phytoplankton during the fall in the GSL. On Mono Lake, Eared Grebes account for much of the reduction in brine shrimp in the water column during fall (up to 80%), suggesting that most of the nutrients locked in brine shrimp pass through Eared Grebes during this time (Cooper et al. 1984). Individual Eared Grebes on the GSL consume up to 30,000 brine shrimp a day during fall to meet their daily energy demands (Conover and Caudell 2009). Thus it is plausible for Eared Grebes to rapidly consume large numbers of brine shrimp during the fall and for the nutrients in those individuals to account for large increases in nutrients during fall and subsequent nutrient availability for hatching brine shrimp in the spring.

These results suggest that birds may increase the productivity of lakes by changing the rate and pathways of nutrient cycling (Scherer et al. 1995). Large concentrations of Eared Grebes on the GSL coincide with an increase in phytoplankton abundance on the GSL (Belovsky et al. 2011). In addition to excrement, there is a large input of feathers when Eared Grebes undergo complete molt, and substantial mortality of Eared Grebes occurs during some years (e.g., from avian cholera and botulism). Both events (molt and die-off) potentially increase nutrients in the GSL as feathers and body parts decompose, though these inputs occur at slower rates than inputs from digestion and excrement. Nutrient inputs and outputs within the GSL ecosystem are poorly understood, but avian sources of nutrient recycling should be considered an important part of the cycle.

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