Belovsky et al. (2011) made a remarkable effort to assemble 13 years of limnological data collected by different groups, and describe the dynamics of nutrients, phytoplankton, brine shrimp (*Artemia franciscana*), birds and other ecosystem components in the Great Salt Lake (Utah). Although their work is the first comprehensive effort to summarize long-term ecosystem processes in the lake, and one of the longer time series available for a saline lake, there are several methodological problems, inconsistencies in the data, and difficulties in the statistical analyses that limit its utility for interpreting lake function. Here I review problems in five specific aspects of the paper.

**Incorrect estimates of brine shrimp biomass**

To analyze brine shrimp population dynamics and their interaction with phytoplankton and bird populations, Belovsky et al. (2011; hereafter Belovsky et al.) utilized “adult equivalent” weights based on “live-mass”. Subsequent communications with the authors indicate that the cube of length was actually utilized to get adult equivalent biovolumes, but this was apparently done incorrectly (see below in this paragraph). Consequently, I used the supplemental data for the article and recalculated adult equivalent weights using dry weight that are normally used to estimate the true tissue biomass of zooplankton (Downing and Rigler 1984). For this, the length-dry weight relationship for *Artemia franciscana* of Reeve (1963) was used, and geometric mean lengths were calculated based on the size ranges stated by Belovsky et al. (nauplii, 1–1.5 mm; juveniles 1.5–7 mm). Adults were assumed to average 8 mm. This approach yielded respective dry weight estimates of 1.7, 47 and 480 μg individual\(^{-1}\) for nauplii, juvenile and adult brine shrimp. Consequently, nauplii and juveniles represented only 0.0035 and 0.10 the weight of an adult shrimp, in comparison to the respective 0.13 and 0.63 fractions used by Belovsky et al. Another length-weight relationship for *Artemia monica* (Jones and Stokes Associates 1993) yielded similar equivalent weights to those of Reeve (1963), and the concurrence suggests Reeve’s values are correct. Furthermore, calculating approximate biovolumes based on the cube of the geometric mean weights yields adult equivalent weights nearly identical to those based on the dry weight equation of Reeve (1963). My corrected adult-equivalent densities of brine shrimp were correlated with the estimates derived from Belovsky et al.’s supplemental data (\(r^2 = 0.76\)), but their analysis overestimated densities by a geometric mean factor of 3.1, and by as much as 37-fold when nauplii were dominant in the collections. This error had important ramifications for the analysis of brine shrimp interactions with other trophic levels in many parts of their paper.

**Phytoplankton estimates**

Belovsky et al. reported that chlorophytes usually represented much less than half of the phytoplankton numerical abundance in Gilbert Bay, whereas other authors generally have indicated that the chlorophytes, *Dunaliella* spp., dominate the plankton assemblage at most salinities in the lake (Stephens and Gillespie 1976, Felix and Rushforth 1980, Rushforth and Felix 1982). The non-standard methods used by
Belovsky et al. (2011) for analyzing phytoplankton likely caused significant biases in their estimates of different taxa. They filtered lake samples on 1.2-µM membrane filters and then scraped and rinsed the filters with deionized water, followed by preservation with iodine (Lugol’s solution). Utilizing a mixed phytoplankton culture from the Great Salt Lake growing at 15% salinity I compared their concentration and preservation method with samples preserved with 3% glutaraldehyde. Both samples were counted utilizing the Utermöhl technique (APHA 1998). In the glutaraldehyde-preserved sample the dominant taxon was Dunaliella salina with densities of 3,200 ml⁻¹, whereas in the sample scraped and rinsed with deionized water only a few broken cells of Dunaliella were visible. It is likely that the osmotic pressure caused thin-walled cells like Dunaliella growing at 15% salinity to rupture in the deionized water. I also tested whether scraping of filters with a blade adequately removes phytoplankton that imbed in membrane filters (Standridge 1976), and found that only 43% of the chlorophyll was recovered with their technique. Consequently, their non-standard method likely resulted in biased estimates of the abundance of different taxa in the lake. Future analyses of phytoplankton from the lake would be improved if glutaraldehyde was used as a preservative (APHA 1998) and if standard filter clearing (Crumpton 1987) or Utermöhl settling techniques (APHA 1998) were used. It is also important to note that the 80 species of phytoplankton reported for Gilbert Bay likely included taxa intolerant of the high salinities there, but that were exported from the fresher water Farmington and Bear River Bays (Wurstbaugh et al. 2012). Felix and Rushforth (1979) discuss the problem of including these less-tolerant taxa in the record for the main lake.

**Chlorophyll relationships**

Belovsky et al. (2011) analyzed the relationship between the amount of chlorophyll a in the lake, and the water transparency measured with a Secchi disk over the 13 year record (their Fig. 15a). Chlorophyll values in their paper are given as µg/ml but actually should be in units of µg/L (G. Belovsky, personal communication). Also note that the nitrogen values in Fig. 15d should also be in units of mg/L instead of the mg/ml shown, and that the regression displayed in Fig. 15d is not significant (ANOVA, $F_{1,7} = 2.90, p = 0.13$). As expected, they found a negative relationship between increasing chlorophyll concentrations and decreasing Secchi depth, but the scatter of points was high ($r^2 = 0.42$). Correlations between chlorophyll a concentrations and Secchi depth are normally much better ($r^2 > 0.75$), even for multi-lake data sets (e.g., Carlson 1977). To help understand the reason(s) for the high scatter in the Great Salt Lake relationship I reanalyzed the data, breaking it into periods when data collections were done by Utah State University (USU; 1994–1995), the US Geological Survey (USGS; 1995–2000) and the Great Salt Lake Ecosystem Project (GSLEP; 2000–2006) (P. Brown, personal communication). The results show that all three groups obtained significantly different relationships between chlorophyll a concentrations and the reported water transparencies measured with a Secchi depth (Fig. 1; ANCOVA, $p = 0.0056$). In particular, the USGS data differ the most from the other two groups, showing particularly high Secchi depths at chlorophyll levels above 20 µg L⁻¹. The concurrence of high chlorophyll levels and high Secchi depths only happens when phytoplankton occur in macroscopic colonies such as flakes or balls of cyanobacteria (Edmondson 1980, Carlson and Havens 2005), and these colonial forms do not occur in the Great Salt Lake. Consequently, the discrepancy of the USGS data is perplexing. Review of the USGS reports on which the points were presumably based (Stephens 1997, 1999a, b), and discussions with one author (R. Baskin, personal communication), indicate that although chlorophyll concentrations were measured, Secchi depths were not actually measured by the USGS from 1996 to 2000, and that the 1995–2000 Secchi depth data in Belovsky et al. were likely estimated from a correlation between light extinction coefficients and some Secchi depth measured in 1995. At high chlorophyll levels, the predicted Secchi depths are impossibly high (Carlson and Havens 2005), indicating that the correlation they used to predict Secchi depths was inappropriate.

When the combined data collected by USU and the GSLEP are analyzed separately, the resulting relationship between chlorophyll (Chl, µg L⁻¹) and Secchi depth (S, m) is:

$$S = 3.256\text{Chl}^{-0.445}, r^2 = 0.705. \quad (1)$$
The correlation coefficient in this relationship is better than when the curious USGS data are included, but less than that found in most other lake studies. This could be due to differences in the chlorophyll methodologies used, since comparative calibration analyses were not done when the data collection responsibilities changed from USU to the GSLEP (personal observation). Although, more work should be done to address the discrepancy between the USU and GSLEP methodologies, Eq. 1 provides a more appropriate estimate of the relationship between Secchi depths and chlorophyll concentrations than that given in Fig. 15a of Belovsky et al.

Chlorophyll-Artemia relationships
An important purported finding in the Belovsky et al. paper was a positive correlation between annual (January–March) maximum chlorophyll concentrations in the Great Salt Lake and the subsequent total density of brine shrimp during the following April–October growth period. To construct this regression, several additional data points for previous years (1970, 1971, 1973, and 1985) were added from the literature. However, review of the 1970–1973 publications indicated that no chlorophyll data were presented in them and algal populations were not even studied in 1970 (Wirick 1972, Stephens and Gillespie 1976), and that Artemia densities were only measured for 3 months in 1971. Consequently, it is curious what data are plotted for these years in their Fig. 17a. Additionally, the 1985 point from Wurtsbaugh and Berry (1990) was from a period when lake salinities were ~6%, and when shrimp densities were only 0.01 L\(^{-1}\) instead of the 3.8 shrimp L\(^{-1}\) mistakenly plotted by Belovsky et al. Moreover, the brine shrimp populations in 1985 were controlled not by food levels, but rather by invertebrate predation (Wurtsbaugh 1992) or because brine shrimp cysts sank at low salinities and could not complete their life cycle (Stephens 1990). It seems best to not utilize these four spurious values for the analysis since the origin of the data is uncertain. When the supplemental data of Belovsky et al. (2011) are plotted without these points, there isn’t a significant relationship between maximum annual chlorophyll \(a\) concen-
trations and total brine shrimp densities during the April–October growth period (Fig. 2A; \( p = 0.75 \)).

Additionally, the information in their Fig. 17a and even that shown here in Fig. 2A is not that useful because the *Artemia* densities shown in the graphs are April–October means of all life stages. That is, a single nauplius counted as much as an adult shrimp, even though nauplii weigh only 0.4% the weight of an adult. A more appropriate analysis to test their hypothesis is to plot the mean adult-equivalent *Artemia* biomass densities based on dry weights against the chlorophyll *a* concentration the previous winter (November–March), not just the January–March period. However, this analysis also indicated that there was no relationship between winter chlorophyll concentrations and the subsequent adult-equivalent brine shrimp densities the following summer (Fig. 2B; \( p = 0.45 \)). The relationship between adult-equivalent densities and maximum chlorophyll concentrations in the January–March period that was used by Belovsky et al. was also not significant (\( p = 0.21 \)). This is not surprising, as
analyses of freshwater lakes, marine systems and salt lakes have not utilized winter phytoplankton concentrations to predict summer zooplankton grazer populations (Sommer et al. 1986, Dana et al. 1995, Sommer et al. 2012), because the very short lifetimes (days) of phytoplankton makes their densities on monthly time scales inapplicable. However, as noted by Belovsky et al., it is also difficult to use summer standing crops of phytoplankton to predict brine shrimp populations because of the strong top-down grazing pressure by these grazers (Wurtsbaugh 1992). Measurements of actual primary production, rather than just chlorophyll concentrations, may provide a better approach for predicting whether algal population abundance controls brine shrimp densities.

**Brine shrimp and eared grebe population growth**

Belovsky et al. (2011) reported a strong correlation ($p < 0.001$; their Fig. 17b) between total brine shrimp densities (all stages) per eared grebe (Podiceps nigricollis), and the subsequent per capita growth in the grebe population measured the following year. They suggested that high food levels in the lake led to “greater survival and reproduction”, and consequently higher populations the ensuing year. However, their statistical analysis was flawed, because the X-variable and the Y-variable were not independent because both contain grebe densities as a component of the metric (X, shrimp/grebe; Y, Δ grebes year$^{-1}$). Complete independence of the X and Y variables is a basic tenet for regression analysis (e.g., Zar 1999). Brett (2004) and many others have demonstrated that when a variable is shared between the independent and dependent variables, strong spurious correlations are almost guaranteed, regardless of whether there is an association or not. To demonstrate this problem, I generated a series of 100 years of random brine shrimp densities ($D_t$) within the range they report, and calculated the per capita population growth between years [$G = (D_t - D_{t-1})/D_{t-1}$] in the same manner as Belovsky et al. Similarly, 100 years of random brine shrimp densities were generated, and the brine shrimp per grebe was calculated. These randomly-generated variables yield a highly significant but spurious correlation (Fig. 3; $p < 0.000$). A more appropriate analysis is to directly test if brine shrimp densities were correlated with per capita changes in grebe densities the following year. However, this relationship (Fig. 4) is not significant ($p = 0.72$).

Regardless of the inappropriate regression analysis used by Belovsky et al., the ecological relationship shown in their Fig. 17b is not realistic for three reasons. First, although brine shrimp are the dominant item in the diet, other invertebrate prey form a significant part of grebe diets from July to December when they are at the lake (Conover and Vest 2009, Roberts 2013a). Secondly, when grebes do eat brine shrimp, they utilize only adult shrimp and not the nauplii or small juveniles (Roberts and Conover 2013), so the use of total brine shrimp densities is not even realistic for this food resource. However, the relationship between adult equivalent brine shrimp densities and per capita grebe population growth is also not significant ($p = 0.51$). Thirdly, and equally important, Belovsky et al.’s “significant” regression (Fig. 17b) is driven by two points showing grebe population growth of 4.8 and 5.4 birds bird$^{-1}$ yr$^{-1}$. However, a population growth rate of this magnitude would require 10–11 offspring produced per female yr$^{-1}$, far in excess of the reproductive capacity of this species (Cullen et al. 1999). Consequently, it is improbable that reproduction could have been sufficient to cause these remarkable increases in the population surveyed at the lake. More likely, these very large changes in densities at the Great Salt Lake were due to mortalities in the wintering areas (Jehl 1996, Roberts 2013b). Censusing errors could also have contributed to the large estimated changes in densities since <4% of the area of Gilbert Bay was included in the aerial surveys used by Belovsky et al. (Paul et al. 1999).

**Conclusion**

The Great Salt Lake ecosystem is extremely important for migratory birds, a commercial brine shrimp aquaculture industry, recreation, and for minerals extraction. A recent estimate of the total economic value of these resources exceeded US$ 1.3 billion (Bioeconomics 2012). Consequently, monitoring and other research is needed to understand the dynamics of the largest lake in the western United States. In this regard the Belovsky et al. paper provides an important compilation of much of the limnological collected...
in the lake since the late 1990s. However, because of methodological problems, data inconsistencies, and inappropriate statistical analyses, it must be used cautiously to help understand how this lake or other saline lakes function.

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**Fig. 3.** Simulation showing the spurious relationship obtained when the x and y axes both contain the same variable, and thus are not independent. Here *random densities* of brine shrimp and *random densities* of eared grebe (*Podiceps nigricollis*) abundance were generated. These random data were used to calculate “food availability” (brine shrimp per grebe) in the previous year, and the between year per capita population growth in the population was calculated. Some simulated population growth rates were negative, and thus the value 1 was added to each value to allow plotting the data on a log scale.

**Fig. 4.** Poor correspondence between mean total brine shrimp (*Artemia*) densities in the Great Salt Lake during the previous year, and the per capita growth in the grebe population. The data are derived from the supplemental material of Belovsky et al. (2011).
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