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REPLY

The Great Salt Lake Ecosystem (Utah, USA): long term data and a structural equation approach: Reply

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We welcome this opportunity to publicly respond to Wurtsbaugh's criticisms of the findings of the Utah Division of Wildlife Resources' (UDWR) Great Salt Lake Ecosystem Program (GSLEP), as presented by Belovsky et al. (2011) for the project's first 13 years (1994–2006). GSLEP has involved leading experts on the Great Salt Lake with individuals entering and leaving the team, including Wurtsbaugh (1994–1996). We respond here to his current suite of criticisms (Wurtsbaugh 2014).

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Wurtsbaugh's technical criticisms focus on five points: (1) body size equivalence of brine shrimp life stages; (2) low abundance of Chlorophytes in some years; (3) chlorophyll relationships; (4) his inability to repeat inter-year correlations between shrimp and phytoplankton abundances; (5) correlation between inter-year grebe population changes and shrimp abundances. Interestingly, only the criticism regarding grebe population changes bears on the food web flow charts in Belovsky et al. (2011: Fig. 14), which were the main purpose of the paper.

1. *Body size equivalence of brine shrimp life stages*.—We developed measures of equivalent body sizes for different life stages based on body volume (length cubed) using lengths reported in the literature for Great Salt Lake shrimp (Belovsky et al. 1999). Wurtsbaugh (2014) points out that his body mass values are highly correlated with our body size equivalence values ($r = 0.87$). It is this correlation, not absolute values, that is important for regression analyses, but he is unable to obtain our trophic relationships. The reason is that the monthly values provided in our supplemental data tables are not the values used in the analyses, which was stated in our paper. Rather, we only employed non-zero values from weekly and biweekly sampling when shrimp were present. This leads to different monthly values than in the supplemental data which include many zeroes in spring as the seasonal life cycle starts (shrimp have not yet hatched early in the month), and in fall as the seasonal life cycle ends (shrimp have died-off late in the month).

2. *Low abundance of Chlorophytes in some years*.—Wurtsbaugh criticizes our methods, but our methods follow those established by Wurtsbaugh (1995) in the first two years of the project. Wurtsbaugh's methods were used by Stephens (1998) and others thereafter to maintain continuity. In fact, Wurtsbaugh's description of GSLEP methods are erroneous, since "scraping" and

"de-ionized" water were *not* employed or mentioned in our methods (Belovsky et al. 2011). In addition, Wurtsbaugh's concern over low Chlorophyte abundances is unwarranted. First, he asserts that Chlorophytes dominate the Great Salt Lake phytoplankton based on studies prior to GSLEP. This is what we expected and observed early and late in our study (1994–2006) and recently. It was in intermediate years that Chlorophytes declined and Bacillariophytes (diatoms) increased. These phytoplankton determinations were made by S. Rushforth (Brigham Young University; now at Utah Valley University), the leading expert on Great Salt Lake phytoplankton, for D. Stephens (Stephens 1998). The Chlorophyte decline surprised us and was associated with a decline in brine shrimp populations. However, these changes were corroborated by independent samples collected by other GSLEP members and the brine shrimp industry (T. Bosteels, *personal communication*), and our identifications were verified by samples sent to a commercial lab (PhycoTech, St. Joseph, MI: C. Perschon, *personal observation*). Interestingly, GSLEP and shrimp industry personnel reported that the lake in these years appeared yellow-brown from the air during numerous flights, rather than the typical green color associated with abundant Chlorophytes. Finally, since methods have remained constant throughout GSLEP, we believe that there can be no methodological bias creating the observed Chlorophyte decline during the intermediate years.

3. Chlorophyll relationships.—This is a trivial criticism, as secchi disk measures were never used in examining the lake's food web. Secchi measures were provided at reviewer request to indicate light penetration and we showed a correlation with phytoplankton abundance. We stated that secchi measures varied so much that they are of little predictive value. First, secchi measures are strongly influenced, not only by phytoplankton abundance, but also by abundant shrimp and their cysts that aggregate in "streaks" on the lake's surface and suspend in the water column. Second, secchi measures are affected by a frequent "scum" forming on the lake, and perhaps more critically, by frequent turbidity created by runoff, wind and waves in a shallow lake. Finally, secchi measures are available for years studied by D. Stephens (USGS) that were either obtained by Stephens or UDWR (R. Baskin and D. Naftz, *personal observation*).

Wurtsbaugh claims that there are no chlorophyll measures by him and GSLEP for comparison. However, P. Brown (UDWR, now Great Salt Lake Brine Shrimp Cooperative, whom Wurtsbaugh cites) correlated chlorophyll measures reported in Wurtsbaugh et al. (2012) for 2003–2006 from 3–4 sites in the South Arm of the lake with GSLEP measures from 17 sites that were made within days of each other, and found them to be similar ($r = 0.68$, $N = 23$, $P < 0.0004$: 2011–2012 exchange between Brown, Wurtsbaugh, and Belovsky, *personal observation*).

*4. Chlorophyll-*Artemia *relationships*.—Correlation between annual shrimp number and maximum phytoplankton abundance attempts to explain *inter-annual* variability in shrimp abundance. Our assertion is that maximum phytoplankton abundances may reflect annual potential primary productivity and the potential to support shrimp populations. Nonetheless, as pointed out in #1 above and in our paper, it is not possible to obtain our correlation using the summary data, since monthly averages at the start and end of the annual shrimp life cycle include many zeroes, which we ignored, as shrimp first hatch and die off. Finally, rather than the inter-annual data, we tracked intra-annual changes in shrimp life stage abundances to develop food web flowcharts (Belovsky et al. 2011: Fig. 14) and to assert food limitation.

Wurtsbaugh raises other issues:

a. He is correct that Stephens and Gillespie (1976) did not report chlorophyll, but rather phytoplankton cell counts. However, Stephens (deceased) converted cell counts into chlorophyll for the GSLEP database using his unpublished data.
b. He is correct that his studies in the 1980s are from Farmington Bay. Due to much lower salinity with freshwater inflows and a causeway isolating it, Farmington Bay is dissimilar to the more representative South Arm (Gilbert Bay) that we studied. As we point out, shrimp numbers are much lower and possibly limited by corixid predation in Farmington Bay. However, Wurtsbaugh reported a few observations from the South Arm outside of Farmington Bay and these

observations were included in the GSLEP database (Wurtsbaugh and Berry 1990, Wurtsbaugh 1992).

c. Nonetheless, dropping observations that he questions, a strong correlation still arises when the correct data (see #1 above) are used, and this correlation becomes stronger using data added since 2006. Correlations become even stronger when hyperbolic or log-log functions are used.
d. The shrimp industry employs a relationship between peak chlorophyll and shrimp abundance as a forecasting tool for business planning (T. Bosteels, *personal communication*).

5. Brine shrimp and Eared Grebe populations.—The basis for this criticism is perplexing. While correlation between shrimp per grebe and change in grebe numbers among years is not important to the lake's food web (grebes do not impact shrimp populations; Belovsky et al. 2011: Fig. 14), it is critical for Great Salt Lake conservation efforts for birds, if shrimp numbers affect bird populations.

Wurtsbaugh's concern over lack of independence is valid. However, rewriting the relationship as a simple multiple regression eliminates any non-independence; the correlation is lower, but maintained ($r = 0.85$ vs. 0.90; $P < 0.01$ vs. 0.001), and a bootstrap analysis to examine for independence is moot. Finally, he raises the issue that two years exert excessive influence on the regression. However, in observational studies over time like ours, a few time periods often exert strong influence and these extremes are often sought to identify pattern, i.e., little or no observed variation in observations cannot establish a relationship, even if one exists. Again, the relationship between grebes and shrimp is maintained in the data added since 2006.

Finally, natural history and sampling assertions made by Wurtsbaugh are not supported:

a. Grebes do eat other things than brine shrimp. But the grebe numbers reported by GSLEP are for fall, when grebes are most abundant, molting and concentrated on the South Arm of Great Salt Lake (flightless for more than 6 weeks). Grebe diets can be 90+% brine shrimp at this time (M. Conover, A. Roberts, and M. Frank, *personal communication*, also cited by Wurtsbaugh). The fall dependence of grebes on shrimp and their abundance is why UDWR selected grebes as a benchmark bird.
b. Grebes may predominantly utilize adult shrimp, but the total shrimp population may reflect the productive potential of the shrimp population to provide grebes with food.
c. Wurtsbaugh suggests that UDWR censuses of fall grebes (Paul et al. 1999) are not reliable since <4% of the lake is surveyed. But, in fall, the flightless grebes are largely restricted to certain areas of the South Arm. Therefore, as pointed out by Paul et al. (1999), the census is a stratified sample based on grebe aggregations. After flying the entire South Arm to find aggregations, aggregations were then censused (originally ~13% of South Arm and today >30%: J. Luft and J. Neill, *personal observation*).
d. Contrary to Wurtsbaugh, we do not attribute grebe population changes solely to reproduction. First, in fall, the number of grebes congregating at Great Salt Lake or Mono Lake (almost all grebes are at these sites) may depend on shrimp numbers. In our paper, we show that the shrimp density per grebe that leads to no change in grebe numbers is the same value observed at Mono Lake, when grebes migrate elsewhere. Second, because fall is critical for grebes to molt and deposit fat for migration, and shrimp are the predominant food, this may strongly impact grebe migratory survival (A. Roberts and M. Frank, *personal communication*). Anecdotally, incidents of high grebe mortality may occur in years with low shrimp numbers per grebe in Great Salt Lake (C. Perschon and J. Luft, *personal observation*).

Summary.—One point that Wurtsbaugh raises that we cannot counter is the labeling of chlorophyll graphs, a typo that we did not catch. Ours is a massive long term study that continues, and trying to identify explanations via patterns in year to year observations is daunting. Our paper summarized the first 13 years. We and others (e.g., shrimp industry) continue to observe the patterns identified in our paper, but other observations remain unexplained (such as the periodic decrease in Chlorophytes) and new patterns are emerging over time. Great Salt Lake is important in terms of conservation and economics, and GSLEP findings are used by the State of Utah and industry to successfully manage the lake.

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