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ABSTRACT

The Great Salt Lake has a salinity near 150 g/L and is habitat for over 200 species of migratory birds. The diet of many of these birds is dependent on the food web of carbonaceous biostromes (stromatolites) that cover 260 km^2 of the lake's littoral zone. We investigated the biostrome community to understand their production processes and to assess whether they are a potential vector for bioconcentration of high mercury and selenium levels in the lake. The periphyton community of the biostromes was >99% colonial cyanobacteria. Periphyton chlorophyll levels averaged 900 mg m^{-2} or nine times that of the lake's phytoplankton. Lake-wide estimates of chlorophyll suggest that their production is about 30% of that of the phytoplankton. Brine fly (*Ephydra gracilis*) larval densities on the biostromes increased from 7000 m^{-2} in June to 20000 m^{-2} in December. Pupation and adult emergence halted in October and larvae of various instars overwintered at temperatures <5 °C. Mean total dissolved and dissolved methyl mercury concentrations in water were 5.0 and 1.2 ηg L^{-1}. Total mercury concentrations in the periphyton, fly larvae, pupae, and adults were, respectively, 152, 189, 379 and 659 ηg g^{-1} dry weight, suggesting that bioconcentration is only moderate in the short food web and through fly developmental stages. However, common goldeneye ducks (*Bucephala clangula*) that feed primarily on brine fly larvae at the Great Salt Lake had concentrations near 8000 ηg Hg g^{-1} dry weight in muscle tissue. Data from a previous study indicated that selenium concentrations in periphyton, brine fly larvae and goldeneye liver tissue were high (1700, 1200 and 24,000 ηg g^{-1}, respectively) and Hg:Se molar ratios were <1.0 in all tissues, suggesting that the high mercury concentration in the ducks may be partially detoxified by combining with selenium. The study demonstrated that the high mercury levels in the Great Salt Lake are routed through the biostrome community resulting in invertebrate prey that may provide health risks for birds and humans that consume them.

1. Introduction

The Great Salt Lake, the largest saline lake in North America, is extremely important for migrant birds that forage in its productive waters and along its margins (Aldrich and Paul, 2002). Salinities above 120 g/L in most parts of the lake exclude predacious fish, so that the invertebrates produced in the system can be channeled to the birds. The lake's pelagic zone produces abundant brine shrimp (*Artemia franciscana*; hereafter *Artemia*) but the only other abundant macroinvertebrate in the lake tolerant of high salinity is the brine fly (*E. gracilis*; formerly *E. cinerea*). The brine fly larvae feed primarily on periphyton growing on, and forming the abundant biostromes covering much of the shallow littoral area of the lake (Collins, 1980; Eardley, 1938). Although considerable work has been done on the lake's pelagic food web composed of phytoplankton and *Artemia* (e.g. Stephens and Birdsey, 2002; Wurtsbaugh, 1992; Wurtsbaugh and Gliwicz, 2001), very little is known about the benthic food web in the lake. In saline Mono Lake and Aber Lake the ecology of brine flies are better understood (Herbst, 1988; Herbst, 1990; Herbst and Bradley, 1993), and the brine flies (*E. hians*) in those locations are important prey for several bird species. Collins (1980) studied the population ecology of brine flies associated with biostromes in the Great Salt Lake during the summer, but provided little information on the biostromes themselves, nor about the seasonality of the brine flies. Wurtsbaugh (2009) recently provided some preliminary information on the biostrome food web. However, the ecology of these structures is poorly understood, not only in the Great Salt Lake, but elsewhere. The biostromes food web in the Great Salt Lake is particularly important because it provides abundant brine flies that help fuel the enormous migratory bird populations utilizing the lake (Wurtsbaugh, 2009).

The biostrome food web is important not only as a food resource, but because it may also contribute to high mercury levels observed in some bird species that utilize the lake. The Great Salt Lake was recently found to have some of the highest mercury levels in water documented in the United States (Naftz et al., 2008), and in 2005 the State of Utah placed

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three waterfowl species on a consumption advisory list because of their high mercury levels (Scholl and Ball, 2005). The species with the highest mercury concentration, the common goldeneye duck (*Bucephala clangula*), has a diet consisting of 70% brine fly larvae when it is at the lake (Vest et al., 2009; J. Vest, personal communication). Formation of toxic methyl mercury usually occurs in benthic environments (King et al., 2000) and thus could potentially be associated with the biostromes. Additionally, methylation is strongly associated with sulfate-reducing bacteria in anoxic zones and sulfate levels are extremely high in the Great Salt Lake, thus facilitating methylation (Brandt et al., 2001). However, the expected high primary production by periphyton on biostromes would provide an oxic environment, at least during the day, so strong methylation in this environment would not be expected. Because of the high mercury levels in common goldeneye, and the unique ecology of biostromes, we were consequently interested in understanding the bioconcentration of mercury in the biostrome food web.

The Great Salt Lake and its biota also have high concentrations of selenium (Conover and Vest, 2009a; Conover and Vest, 2009b; Oliver et al., 2009; Vest et al., 2009; Wurtsbaugh, 2009). Because selenium can counteract the toxic effects of mercury (Khan and Wang, 2009) a final objective of our study was to relate the mercury in the biostrome communities to previously reported concentrations of selenium to determine if there might be some antagonistic interactions between the two contaminants.

2. Methods

2.1. Study sites

The Great Salt Lake (Fig. 1) is a 5200 km^2 closed-basin system in Utah, USA (41.04 N, 112.28 W) bordered on its eastern and southeastern shores by the Salt Lake City metropolitan area. The lake has been impacted by industrial and municipal discharges, as well as by transportation causeways that divide the system into four large bays. Gunnison Bay (2520 km^2), located in the northwest of the lake, has salt concentrations over 270 g/L. The biostromes in Gunnison Bay are nearly unstudied. Preliminary observations indicate that they do not have any periphyton associated with them, but there are pink and bright-green microorganisms in different layers, probably representing Archaea and sulfur-reducing microbes. Shallow Farmington Bay (260 km^2; mean depth < 1 m) in the SE has biostromes along the east side of Antelope Island (Wurtsbaugh, unpublished data), but these are not likely growing as severe eutrophication in the bay limits light penetration. We studied Gilbert Bay (2400 km^2), in the central portion of the lake. This bay is separated from Gunnison Bay by a railway causeway. Gilbert Bay typically has surface salinities ranging between 110 g/L and 180 g/L, but salinities have ranged from 60 to 270 g/L over the past 160 years (USGS, 2010. http://ut.water.usgs.gov/greatsaltlake/ Accessed Nov. 2010). Gilbert Bay supports a large population of *Artemia* (Stephens and Gillespie, 1976; Wurtsbaugh, 1988). The mean lake elevation during the study was 1278.6 m (USGS, 2010. http://ut.water.usgs.gov/greatsaltlake/ Accessed Nov. 2010). At this elevation, the respective mean and maximum depths of Gilbert Bay are 4.9 and 9.4 m (Baskin, 2005). The bay is meromictic due to flow of saturated brines from Gunnison Bay through culverts in the railway causeway into the deeper strata of Gilbert Bay (Loving et al., 2002) creating a deep-brine layer (monimolimnion) below approximately 6.7 m. The upper 6.7 m of Gilbert Bay is well-mixed and oxic. The deep-brine layer is anoxic with substantial hydrogen sulfide, and consequently has no macroinvertebrates. Gilbert Bay has high nutrient levels and is mesotrophic (Stephens and Gillespie, 1976; Wurtsbaugh, 1988). With the exception of meromixis due to the railway causeway, Gilbert Bay is the most natural remaining part of the Great Salt Lake with populations of brine shrimp, brine flies and actively growing biostromes.

Biostromes occur along the perimeter of much of the Great Salt Lake (Fig. 1), and at the water surface elevation at the time of the study, occurred at depths from 0 to approximately 3.9 m where there was sufficient light for photosynthesis. Eardley (1938) provided a detailed map of the benthic structure of the Great Salt Lake, although no methods were provided on how this information was collected. The deep brine layer now underlies approximately 44% of Gilbert Bay. In the remaining sediments covered by the oxygenated mixed layer, biostromes, oolitic sand and mud represent 23%, 62%, and 15% of the substrate, respectively (Table 1). Recent work suggests that biostromes may be more extensive than what Eardley suggested (R. Baskin, personal communication). Some of these are laminated and thus can be considered stromatolites, but the composition of few of them has been documented, so we use the more general term "biostrome" here. In Gilbert Bay we have encountered nearly pure cultures of *Aphanothece* sp. in the biostromes. (Halley, 1976) also described the biostromes as being composed of coccoid cyanobacteria characteristic of *Aphanothece* sp. when the salinity was ca. 160 g/L, and (Carozzi, 1962) described them as being formed by *A. packardii* when the salinity was near 270 g/L. Collins

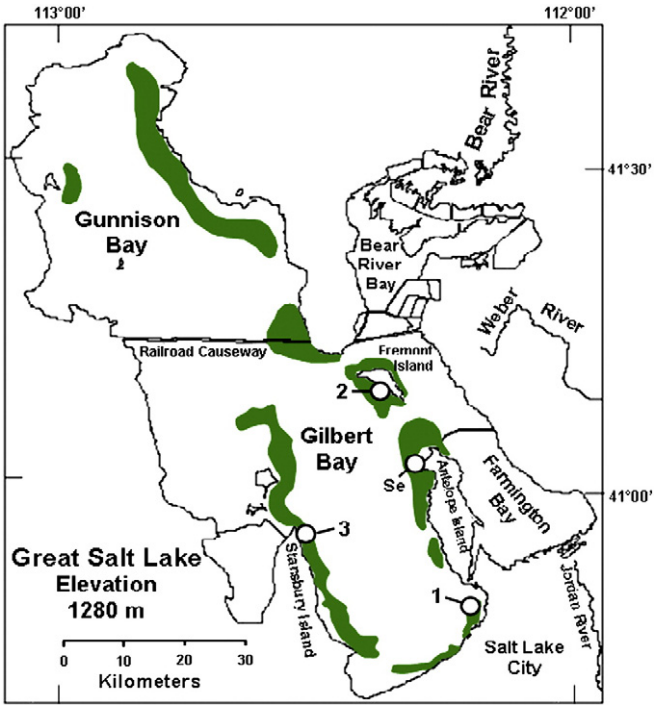

Fig. 1. Sampling stations in Gilbert Bay, Great Salt Lake, and the approximate distribution of biostromes (dark shaded areas; after Collins, 1980; Eardley, 1938). The stations used for mercury sampling were: Sta. 1 — SE Gilbert Bay; Sta. 2 — Fremont Island; Sta. 3 — Stansbury Island. Biostromes at Station 1 were also sampled in 2007 for selenium (Se), as was a station at the northern tip of Antelope Island (Se). Dark shading indicates areas of biostromes.

Table 1
Morphometric characteristics of Gilbert Bay of Great Salt Lake at a lake elevation of 1280.2 m (4200 ft), which is near the mean historical elevation. The data exclude areas of the southern salt ponds and Farmington Bay. Gilbert Bay's area was derived from Baskin (2005). The areas of biostromes, oolitic sand and mud were derived from the proportional areas shown in the map of Collins (1980), with an adjustment to a lake level of 1280.2 m. At that lake elevation the lake's mean depth is 5.55 m.

Region	Area of sediments (km^2)	Volume (m$^3 \times 10^9$)
Gilbert Bay (total)	2057	11.42
Deep-brine layer	912	1.73
Mixed layer	1145	9.69
Biostromes	261 (23%)	
Oolitic sand	712 (62%)	
Mud	172 (15%)	

(1980), however, reported primarily diatoms on the biostromes when the lake had a salinity of 130 g/L. The small 1.4-μm diameter *Aphanothece* cells are embedded in a mucilaginous matrix that is partially calcified. The growing cyanobacteria and likely other microbes change the chemistry of the water, causing carbonates to precipitate and the biostromes to grow (Dupraz and Visscher, 2005). The brine fly *E. gracilis* is the dominant invertebrate on the biostromes, but *Ephydra hians* have also been reported in the lake.

Samples were collected at three locations in 2008 during five periods: 30 May–3 June (hereafter called the June samples); 16–18 July; 2–7 Sept; 20–22 Oct, and; 1–4 Dec. At each location we collected on shallow (0.9–1.6 m) and deep (2.1–3.9 m) biostromes, that were within 1-km of each other. Station 1 was in the SE part of Gilbert Bay (40.805° N, −112.185° W) 5 km north of a large mine (Kennecott Utah Copper) discharge canal and 3 km west of the Goggin Drain that discharges some Jordan River water into Gilbert Bay. Biostromes in the shallow stations here were dome-shaped, approximately 1-m in diameter and 0.2–0.3 m high, but they often grew together forming irregular fields 10–100 m across. Some of the biostromes at the deep location were columns approximately 0.5-m in diameter and 0.7–1.5 m tall. Station 2 (41.145° N, −112.335° W) was adjacent to the SW margin of Fremont Island and biostromes here were similar in configuration to the domed types at Station 1. Station 2 is close to the discharge from polluted Farmington Bay that receives treated sewage and industrial effluents from Salt Lake City and Davis County (Fig. 1). Station 2 is also near the inflow of the lake's primary river via Bear River Bay. Station 3 (40.925° N, −112.495° W) was on the NE side of Stansbury Island, more than 28 km from any of the major freshwater inflows. It is the closest site to the US Magnesium Corporation of America atmospheric emissions, 20 km to the west. The biostromes here formed a continuous hard plate, perhaps 0.4-m thick, except at parts of the deep collection sites where there were some interspersed areas of sand. Halley (1976) and Pedone and Folk (1996) provide additional description of macro- and micro-structure of the biostromes in the Great Salt Lake.

2.2. Water, biostrome collections, chlorophyll and organic matter

Samples to assess dissolved mercury were collected in duplicate at the deep site at each station before other measurements disturbed the area. A SCUBA diver collected water from 2 to 5 cm above the sediment surface using pre-cleaned Teflon tubing which was pumped to the surface using a peristaltic pump and a pre-cleaned (Olson and DeWild, 1999) quartz-fiber filter cartridge. The whole system was flushed with site-specific water at each location. Water was then pumped directly into double bagged, pre-cleaned Teflon® containers and the samples were fixed with Omnitrace® HCL. Replicates were taken at least 5 m apart from each other.

Profiles of water temperature were collected at each site with a YSI Model 85 sensor (Yellow Springs Instruments). There was little stratification and here we report values measured at 0.2 m. Air temperatures were derived from a station at the Salt lake City International Airport located near the SE margin of Farmington Bay. Secchi depth transparencies were measured with a 20-cm black and white disk. Salinities of surface water were measured with a refractometer.

At each station duplicate samples for organic matter, chlorophyll, and total mercury content of live biostromes were collected by SCUBA divers who pried off pieces with a rinsed stainless steel abalone iron. These portions were carefully harvested to prevent turbulent loss of organic matter and care was taken to sample through the total thickness of the organic surface layer. Samples were sealed in pre-cleaned polyethylene bags underwater and immediately placed on ice at the surface.

In the laboratory, biostrome portions were split four ways and the two-dimensional surface areas were determined by photographing each piece along with a ruler and utilizing a computer program to calculate the area. A chlorophyll *a* subsample was frozen and subsequently placed in 30 mL of 95% ethanol, and extracted in the dark for at least 24 h. The chlorophyll solution was then diluted with ethanol and concentrations measured in a Turner 10_AU fluorometer with the non-acidification method (Welshmeyer 1994). Blanks and standards were analyzed at the beginning of each run. In the second sample, organic matter as ash free dry mass (AFDM) was determined by oven drying a subsample at 70 °C to constant weight, and then ashing it at 450 °C for 4–5 h and reweighing. For mercury analysis of the organic material in the biostromes a third subsample from each deep (3 m) site was treated with 1 N Omnitrace® HCl to remove carbonates. This required several hours and the replacement of the acid until all bubbling of CO_2 stopped. Although this treatment should have removed all carbonates, non-carbonate inorganic materials may have remained. The acid-treated fraction was then stored in acid-cleaned polyethylene vials for subsequent total mercury analysis of the remaining periphyton. The total mercury of the whole biostrome was determined from the fourth subsample obtained from the deep sites. This biostrome was rinsed with de-ionized water and frozen. On one occasion we subsampled carbonate material several centimeters below the growth zone of the cyanobacteria so that the mercury content of the carbonate alone could be measured.

2.3. Brine fly collection and analyses

Duplicate larval and pupal brine fly samples were collected at both depths at all sites. The larvae and pupae were sampled on the biostromes by a SCUBA diver using a pump sampler similar to that of Voshell et al. (1992). The 0.053 m^2 sampler consisted of an inverted high density polyethylene carboy with the bottom cut off (Wurtsbaugh and Horne, 1983). A port was cut in the side and a rubber glove attached to it so that a diver could scrub the substrate within the sampler with a brush. A flexible foam strip on the bottom of the carboy helped seal it against the irregular surfaces of the biostromes. Two, 2.3 kg lead weights were attached to the lower part of the bucket to increase stability and to keep the unit on the substrate. To function effectively, the sampler had to be placed on a relatively level substrate. This precluded sampling on the sides of the columnar-shaped biostromes at the deep location of Station 1. Once the sampler was positioned, operators in the boat brought water to the surface with a hand-powered bilge pump (Guzzler Model Vacuum Pump, U.S. Plastics Corp.). The diver then began scouring the substrate with a scrub brush. For each sample, 95 L of water was pumped directly through a 500-μm sieve on deck. This mesh may have allowed some 1st instar larvae to pass through. In a preliminary analysis, an exponential decline model fit to brine fly larvae captured in five different sets of four successive buckets indicated that a 95-L pumped sample captured 97% of the larvae. Brine fly samples were transferred into acid-cleaned 500 mL polyethylene jars, and stored on ice for transport. Brine flies from deep samples remained chilled and were enumerated within 48 h. The duplicate larvae and pupae subsamples (~150 mg) from the deep sites were then frozen for mercury analysis. Samples from the shallow site were fixed with 95% ethanol. These larvae were subsequently counted and measured with a dissecting scope with an ocular micrometer so that length-frequency distributions could be constructed.

At each station a single sample of adult brine flies were collected with a sweep net on the shore nearest the shallow dive site. In the laboratory the flies were rinsed with freshly-deionized water to remove salts, frozen, dried at 70 °C, and subsequently analyzed for total mercury content.

2.4. Mercury and selenium analyses

All mercury analyses were performed at the US Geological Survey Wisconsin District Mercury Research Laboratory in Middleton, Wisconsin. Total Hg (THg) in filtered-water samples was determined using cold vapor atomic fluorescence spectrometry (CVAFS) (Olson and DeWild, 1999). The methyl mercury (MeHg) in the water samples

was determined using distillation/ethylation/gas-phase separation with CVAFS detection (DeWild et al., 2002). Primary standards for THg were obtained commercially and certified against a NIST standard reference material. No reference materials were available for MeHg so standards for MeHg were prepared in the laboratory. Known reference samples were analyzed at the beginning of each analytical run, after every 10 samples and at the end of each run. Laboratory method blanks were prepared by adding $SnCl_2$ to 125 mL of Hg-free water and purging for 20 min to ensure removal of any residual Hg. Method blanks were run periodically during each sample run and used to calculate the daily detection limit (DDL). The accepted value for the DDL is <0.04 ηg L^{-1}. Matrix spikes were analyzed during each run or every 10 samples. Percent recovery of matrix spikes had to fall between 90% and 110% for the sample run to be accepted. Two field replicates and two field blanks were collected and analyzed for THg and MeHg. Field replicate results were in close agreement, with replicates ranging from 3.0% to 5.5% for THg and 2.7% to 15.9% of the routine sample value for MeHg. Field blanks had low THg (0.08 and 0.10 ηg L^{-1}) and MeHg (<0.04 ηg L^{-1}) concentrations.

The THg in biostrome and brine fly samples was extracted and analyzed according to the methods outlined in (Olund et al., 2004). Each sample was extracted by room-temperature acid digestion and oxidation with aqua regia. The samples were then brought up to volume with a 5% BrCl solution to ensure complete oxidation and then heated at 50 °C in an oven overnight. Samples were then analyzed for THg with an automated flow injection system incorporating a cold vapor atomic fluorescence spectrometer. Solid standards from the National Research Council Canada were used (BEST-1 for sediments; TORT-2 or LUTS-1 brine flies). A method detection limit of 0.3 ηg of Hg per digestion bomb was established using multiple analyses of a solid-phase environmental sample.

Mercury concentrations from our study were measured and expressed in units of dry weight, but because wet weights are commonly used for promulgating standards we used ratios of dry weight:wet weight so that we could also express concentrations in wet weight. Periphyton was assumed to be 8% dry weight (Sladecek and Sladeckova, 1963), brine fly larvae pupae and adults were assumed to be 14%, 19% and 23% dry weight, respectively (Herbst, 1986). The assumed dry:wet ratio for goldeneye duck breast and liver tissue was 25% (J. Vest, personal communication). This value was used to convert his mercury data measured in wet weight, to dry weight equivalents. Because of the high variability in determining wet weights of small invertebrates, the mercury values expressed in wet weight units are only approximate.

Results from the mercury analyses were compared from similar collections made in 2006–2007 to measure selenium bioaccumulation in the Great Salt Lake biostrome food web (Wurtsbaugh, 2009). That study used nearly identical methods to those described above but samples were collected only at two stations: Station 1 (as for the Hg study), and a station on the NW end of Antelope Island (Fig. 1). Selenium samples were collected in June and September, 2006, with a small additional set collected in April 2007. Immature brine flies were also collected on mud and sand substrates with a dredge, but few individuals were encountered. The tissue and water samples were analyzed for total selenium by hydride generation–atomic absorption spectrometry with acid-digested samples. The detection limits for selenium in the tissues and water were 0.1 and 0.05 μg Se g^{-1}, respectively.

2.5. Length–weight and dry to wet weight conversions

A length–weight relationship for larvae was established by sorting out groups of similar-sized individuals ranging from 2.0 to 10.5 mm, drying them to constant weight and weighing. The length–weight relationship established was;

$$mg = 0.0318 * \mathrm{mm}^{1.718} \qquad r^2 = 0.913.$$

This relationship was subsequently used to estimate the weights and population biomass of the brine flies on the biostromes.

2.6. Statistical analyses

Statistical analyses were done in SYSTAT version 8.0 (SPSS, Inc.). Statistical outliers identified by SYSTAT were not used in the analyses. In most cases missing values or incomplete factorial designs (e.g. no pupae or adult brine flies during two sampling periods) precluded repeated measure analyses of variances, so some statistical power was lost, and significant differences are consequently conservative.

3. Results

3.1. Environmental conditions, chlorophyll levels and ash-free dry mass

Water temperatures in March were ca. 8 °C, increased to 19 °C by our first sampling in June, and rose to a maximum of 27 °C in July (Fig. 2). By December water temperatures had cooled to near 7 °C. Minimum air temperatures that would influence the survival and breading capability of adult brine flies were exceptionally warm in the spring of 2008, but reached normal temperatures near 14 °C by late May, and climbed to 21 °C in July. By October nighttime temperatures declined to near zero and were negative by December. Secchi disk transparencies varied substantially with the wax and wane of *Artemia* grazers. In the early spring before brine shrimp were abundant transparencies were <0.4 m. The transparency rose to 3.8 m in July and declined to 0.7 m in December when *Artemia* disappeared from the water column and phytoplankton bloomed (see Wurtsbaugh and Gliwicz (2001) for a description of plankton cycles). The mean salinity in Gilbert Bay was 145 g/L during June when the lake was receiving maximum freshwater discharges during spring runoff. The salinity increased to 166 g/L by October and declined to 161 g/L when winter precipitation began.

Chlorophyll concentrations in the biostrome periphyton were high. Mean levels ± s.e. from September–December were 893 ± 48 mg m^{-2}. A 3-way analysis of variance (n = 36) indicated that there were no significant differences in concentrations between stations (p = 0.91), sampling period (p = 0.39) and depth (p = 0.07). A comparison of chlorophyll in the periphyton and in the phytoplankton showed that the biostrome production is very important in the overall economy of the lake (Fig. 3). Although biostromes cover only 18% of the area covered by phytoplankton (Fig. 3A), the concentration of chlorophyll in them was eight times higher than the integrated concentration of phytoplankton chlorophyll (Fig. 3B). The product of the areas times the concentrations provides a measure of the total amount of chlorophyll in each of these compartments, and this calculation indicates that biostrome chlorophyll was more abundant than that of the phytoplankton (Fig. 3C).

The amount of organic material in the biostromes averaged 158 ± 6 mg cm^{-2}. A 3-way analysis of variance (n = 54) of samples

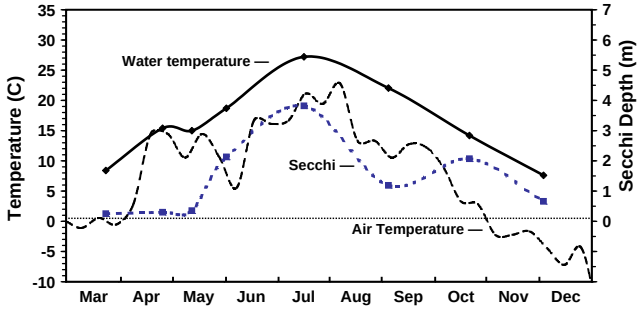

Fig. 2. Minimum nightly air temperatures, and mean water temperature and Secchi depth transparencies in Gilbert Bay, Great Salt Lake, in 2008. Data for March–May were taken by the Utah Division of Wildlife Resources at a mid-lake station.

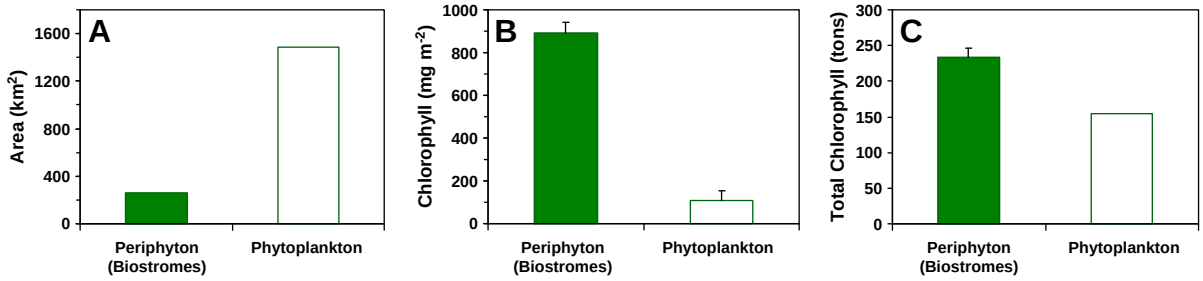

Fig. 3. Comparison of the relative abundance of chlorophyll in the periphyton on biostromes and in the phytoplankton of Gilbert Bay (Great Salt Lake). A. Lake area occupied by biostrome periphyton and that of the phytoplankton. B. Chlorophyll levels on the biostromes and the integrated phytoplankton chlorophyll (0–6.7 m). C. Total chlorophyll (tons) in the Great Salt Lake in the biostromes and phytoplankton. The amount of phytoplankton chlorophyll in Gilbert Bay was based on unpublished values of W.A. Wurtsbaugh collected from 2002 to 2009 ($n=234$; mean 16 mg m^{-3}), and an estimated mixed-layer volume of 9.7×10^9 m^3.

collected from June–December indicated that there were no significant differences between stations ($p=0.13$), sampling period ($p=0.79$) and depth ($p=0.59$). The mean composition of biostrome material for the September sample was 11% organic material, 84% carbonates and 5% inorganic residual left after the combustion and acidification steps.

3.2. Brine fly abundance and biomass

Brine flies were very abundant on the biostromes and they were the only benthic invertebrate encountered, other than occasional *Artemia* that more than likely were in the water column and captured in our bucket sampler. Densities of brine fly larvae were not significantly different at the different stations ($p=0.58$), or at different depths ($p=0.26$), but densities did vary seasonally ($p=0.003$). Larvae were less abundant in the June and July samples, with mean densities between 8000 and 10,000 m^{-2} (Fig. 4). By September samples densities had climbed to over 18,000 m^{-2} and they remained near those levels through early December. Variability was high, and individual sample densities ranged from 2500 to 59,000 m^{-2}. Mean overall brine fly larval density during the study was 16,300 m^{-2}.

Brine fly pupae were considerably less abundant than the larvae (Fig. 4). The pupae densities were not significantly different at different stations ($p=0.49$) or depths ($p=0.09$), but densities were significantly different seasonally ($p=0.000$). Densities were highest in June and July, with means near 1500 m^{-2}. By September densities declined by half and by October and December pupae were negligible or absent. These very low densities coincided with nighttime minimum temperatures near 0 °C or lower. Although we did not quantitatively sample adult flies at the shoreline, they were very abundant from June through September, but by October it was impossible to sample enough for mercury analyses.

Brine fly larval size distributions varied markedly over the sampling period (Fig. 5). Larvae were largest in June, with a single mode centered at 8 mm, and there were no larvae less than 4 mm. By July, however, a new cohort with small larval instars was most abundant, with new modes at 3 and 5 mm, but with a mode remaining at 8 mm. By September the smallest instars were rare, and the most abundant size class was 4–5 mm long. In December the population was also dominated by intermediate size classes.

Brine fly biomass on the biostromes was estimated utilizing the densities, size structure and the length–weight relationship we established. The mean dry weight of the June group of large larvae was 1.4 mg, but the mixed cohorts later in the year had mean weights near 0.7–0.8 mg (Fig. 6). Although larval densities were low in June, the high mean weight resulted in a high biomass near 13 g dry weight m^{-2}. Biomass declined in July, then increased latter in the fall with increases in the densities of larvae. Mean larval biomass on the biostromes from June to December was 14.0 g dry weight m^{-2}.

3.3. Mercury concentrations

Dissolved mercury concentrations over the biostromes in the Great Salt Lake were moderately high (Fig. 7). Total dissolved mercury averaged 5.0 ηg L^{-1} (25 pM) and methyl mercury constituted 25% of the total (1.2 ηg L^{-1}; 6.0 pM). Dissolved mercury concentrations at the different stations were not significantly different ($p=0.252$), but those from different sampling periods were ($p<0.000$). In July total (2.6 ηg L^{-1}) and methyl mercury (0.65 ηg L^{-1}) were significantly lower ($p<0.044$; Bonferroni-adjusted pair wise comparison) than during the other sampling periods.

Mercury concentrations varied substantially between the fractions of the biostromes analyzed. A 3-way ANOVA followed by a post-hoc Bonferroni comparison test indicated that the mercury content in carbonates, intact biostromes, and the acid-treated periphyton material were all significantly different ($p<0.000$), with respective mean concentrations of 22, 69 and 152 ηg g^{-1} dry weight. The mean estimated periphyton concentration based on the assumed dry:wet ratio was 12 ηg g^{-1} wet weight. Because we assumed that brine fly

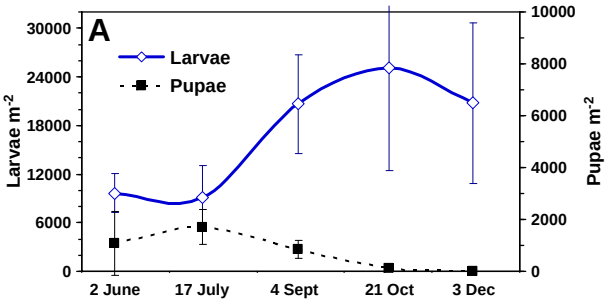

Fig. 4. Mean ± s.e. of brine fly larvae and pupae (right axis) densities at the three biostrome study sites in 2008. Sample dates shown are the median dates of a sampling interval which lasted 2–4 days. Note different scales used for the larvae and pupae.

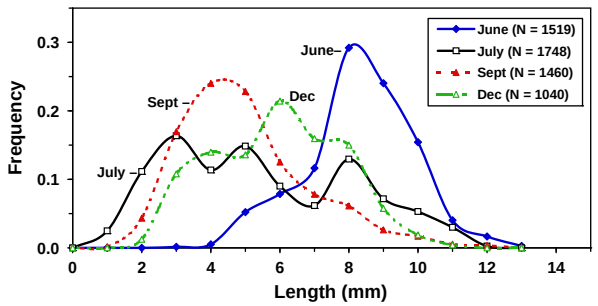

Fig. 5. Size-frequency polygons of larval brine flies on biostromes in the Great Salt Lake during four periods in 2008. The midpoints of the sampling intervals were: 2 June; 17 July; 4 Sept; 21 Oct; 3 Dec.

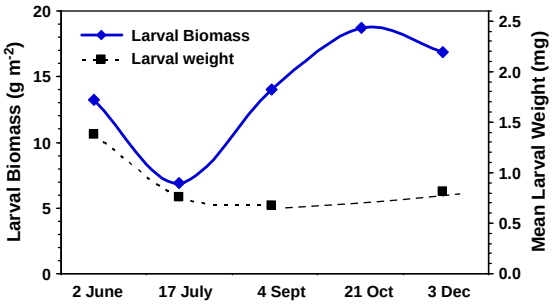

Fig. 6. Mean dry weights of brine fly larvae (right axis), and the biomass (left axis) of larvae on biostromes in the Great Salt Lake. Larval lengths and weights were not estimated in October, so the mean of September and December weights were utilized to estimate larval biomass at that time (open symbol).

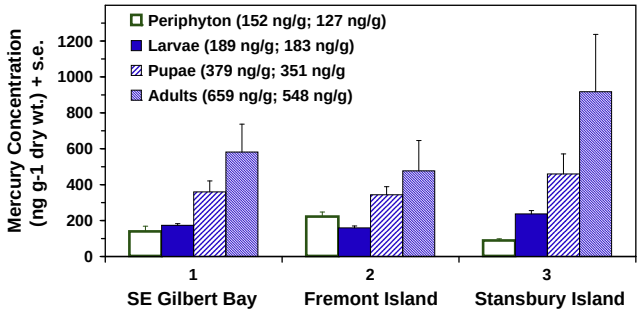

Fig. 8. Mean total mercury concentrations in periphyton and brine fly larvae, pupae and adults associated with biostromes at three stations in the Great Salt Lake. The periphyton values shown here were from samples that were acidified to remove carbonates. Overall arithmetic (left) and geometric mean (right) mercury concentrations are shown in the inset.

larvae fed only on the periphyton, we did a separate 2-way ANOVA on this food component to determine if there were significant spatial or temporal differences. Periphyton at Station 2 (Fremont Island) had significantly higher mercury levels than the other two stations (Fig. 8; $p<0.000$), with a mean concentration of 222 ηg g dry weight^{-1}. Total mercury concentrations of the periphyton in July (65 ηg g dry weight^{-1}) were also significantly lower than the other months ($p<0.032$; June data was not available, however).

Mercury concentrations in the brine flies increased progressively through different growth stages. A paired *t*-test of small (4.6 ± 1.5 mm s.d.) and large brine fly larvae (8.5 ± 1.6 mm s.d.) collected in October and December indicated that the large larvae had significantly ($p=0.02$) higher concentrations (208 ηg g^{-1} dry weight) than the small larvae (179 ηg g^{-1}). Overall mean mercury concentrations during the study based on dry weights were 189 ηg g^{-1} in the larvae, 379 ηg g^{-1} in the pupae, and 659 ηg g^{-1} in the brine fly adults. Respective estimates based on wet weights were 26, 72 and 152 ηg g^{-1}. A 2-way analysis of mercury concentrations in the three brine fly life stages followed by post-hoc tests indicated that these differences were all significant ($p<0.002$). There was also a significant difference among stations ($p=0.030$). In contrast to the periphyton data, mercury concentrations in the brine flies were significantly higher at Station 3 (Stansbury Island) than at the other two stations that did not differ from each other. Tabular values for all of the analyzed mercury samples are given in (Gardberg et al., 2011).

4. Discussion

4.1. Ecological importance of biostromes

Although stromatolites and other biostromes have been studied extensively from a geological perspective with regards to the earth's evolutionary changes (Grotzinger and Knoll, 1999), their importance in modern systems is only beginning to be appreciated (e.g. Dinger et al., 2006; Elser et al., 2006; Paerl et al., 2001; Vasconcelos et al., 2006). Our study demonstrated that the widespread biostromes in the Great Salt Lake contribute significantly to the biological productivity and are important in delivering high levels of mercury in the lake into higher trophic levels.

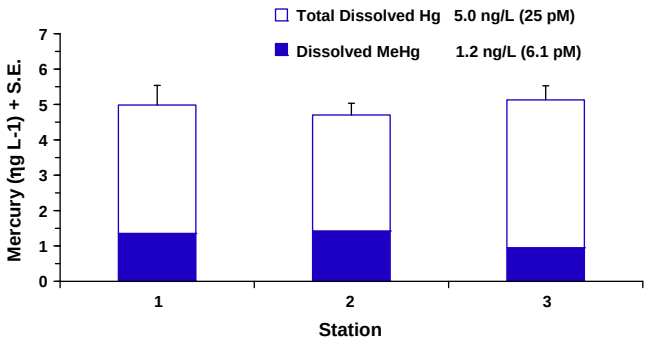

Fig. 7. Dissolved mercury concentrations above biostromes at the three sampling stations in the Great Salt Lake. Methyl mercury accounted for 25% of the total. Mean values for the three stations are shown in the legend.

Although primary production has not been measured on the lake's biostromes, their high chlorophyll levels and large areal extent suggest that they contribute significantly to the lake's organic production. Even though benthic productivity in lakes has not been studied as extensively as that in the pelagic zone, it can often contribute more than 50% of overall productivity, especially in shallow systems (Vadeboncoeur et al., 2008) such as the Great Salt Lake. Kraus-Jensen and Sand-Jensen (1998) report that periphyton primary production per unit of chlorophyll is only about 20% of the rate in phytoplankton. If we apply this factor, it would suggest that primary production in the biostromes is about 30% of that in the lake phytoplankton. Water transparencies in the Great Salt Lake during the summer growing period are usually 2–4 m (Wurtsbaugh and Gliwicz, 2001; Fig. 2), thus allowing sufficient light for photosynthesis to depths of 4–8 m (2 to 3 Secchi depths; Kalff, 2001). When *Artemia* disappear from the water column in winter, grazing is greatly reduced, and phytoplankton proliferates. Water transparencies then decrease to <0.5 m (Wurtsbaugh and Gliwicz, 2001), which would reduce the active growth of biostromes to a depth of 1–1.5 m. The periphyton in the biostromes is thus dependent on active grazing by *Artemia* to allow sufficient light to reach a sufficient part of the lake bottom. The lower depth limit of biostromes (ca. 3.9 m in during our study) might be limited by light penetration, but the availability of carbonate-rich groundwater inflows could also be a contributing factor (Lopez-Garcia et al., 2005; Moore and Burne, 1994). The total depth of the Great Salt Lake varies appreciably with climatic cycles (6 m over the last 140 years), so that the depths where we encountered biostromes are not necessarily reflective of the water depths at which they grew most actively.

The actively growing biostromes in the Great Salt Lake with an abundance of grazing invertebrates is interesting from a paleoecological perspective because it has been argued that the profuse biostromes formed during the Precambrian period 500 million years ago did so because metazoan grazers were absent. The biomass of grazing brine fly larvae on the biostromes in the Great Salt Lake is among the highest reported for benthic invertebrates in lakes (LeCren and Lowe-McConnel, 1980), yet the biostromes were healthy. This suggests that an absence of grazers is not critical for the maintenance of biostromes, as has been suggested by others (Grotzinger, 1990; Moore and Burne, 1994; Pratt, 1982).

4.2. Brine fly population ecology

Brine fly densities and biomass (mean −14 g m^{-2}) on biostromes in the Great Salt Lake, and their overall biomass rival that of *Artemia* in the water column. In the mercury study we only measured brine flies on the biostromes, because a limited study by (Wurtsbaugh, 2009) reported low densities on both sand and mud substrates. Collins (1980) also found low densities of brine fly pupae on sand, but nearly equivalent densities on biostromes and mud substrates, but he did not count larvae on different substrates. Extrapolating our mean brine fly larval densities to biostromes throughout the entire lake yields an estimate of 38 tons of flies (dry weight). If Collins' estimate for brine flies on mud is scaled to the entire lake and added to the biostrome value, we estimate that approximately 62 tons of brine fly larvae are present in the Great Salt Lake. This is 84% of the biomass of *Artemia* in the lake based on calculations by Wurtsbaugh (1992). These estimates are based on only single years of data for both species, and on poorly-documented areas of the different substrates (Collins, 1980; Eardley, 1938), but the calculation nevertheless suggests near parity in the biomass contribution of these two species of invertebrates in the ecosystem. An additional factor that contributes to the importance of brine flies as prey for birds is that the fly larvae are available all year long, whereas during winter *Artemia* juveniles and adults disappear (Wurtsbaugh and Gliwicz, 2001), and the fringing freshwater wetlands of the lake freeze solid.

The annual life cycle of *E. gracilis* appears to be similar to that of the better-studied alkali fly *E. hians* (Herbst, 1988). The length-frequency distributions of brine flies in the Great Salt Lake suggest that there are several cohorts present throughout the year. Pupation and reproduction by adults largely ceased by October when air and water temperatures fell. Herbst (1988) found that *E. hians* pupae could not survive at temperatures of 5 °C, and it seems unlikely that adults could thrive when air temperatures drop below zero. The larval population on the biostromes entered the winter with a diverse size structure (Fig. 5), but in the late spring most of the larvae were large and likely third instars. This suggests that there was slow growth over the winter and more likely in the early spring, with the majority of individuals reaching the third instar by spring, pupating, and starting a new generation. However, the size-frequency distribution in July showed that there were multiple instars present, so clearly reproduction in the spring was not synchronous. Herbst (1988) found a similar situation for the alkali flies in Mono Lake. Collins (1980) suggested that brine flies grow from egg to pupae in 3–4 weeks and spend 2–3 weeks as pupae, and this is similar to growth rates found by Herbst for the alkali fly. This suggests that there could be up to three generations from May to September in the Great Salt Lake. The increasing number of larvae on the biostromes from June to October supports this hypothesis. Unfortunately, we did not sample early in the spring, and our six-week sampling interval was inadequate to clearly resolve detailed population cycles. Consequently, additional year-around analyses will be necessary to better understand the life cycle of the Great Salt Lake brine flies.

4.3. Mercury in the biostrome food web

Mercury concentrations measured in the water and in the biostrome biota were moderately high (Figs. 7 and 8). The total mean mercury concentration in the water (5 ηg L^{-1}) was below the US EPA aquatic life standards of 12 ηg L^{-1} for fresh waters and 25 ηg L^{-1} for salt water (USEPA, 1985), but the mean methyl mercury level of 1.2 ηg L^{-1} was four times the uncontaminated worldwide baseline of 0.3 ηg L^{-1} (Gray and Hines, 2009). Mercury concentrations in brine flies were relatively similar to those of *Artemia* in the lake. Mean concentrations of THg in *Artemia* measured during a parallel study in 2008 (Gardberg et al., 2011) were 59 ηg g^{-1} wet weight, approximately double that estimated for brine fly larvae (26 ηg g^{-1} wet weight) and somewhat lower than concentrations in brine fly pupae (70 ηg g^{-1} wet weight) but lower than that of adult brine flies (152 ηg g^{-1} wet weight). Mean total mercury concentrations in the larvae were only 25% of the lowest observed adverse effect limit (100 ηg g^{-1} MeHg wet weight) for prey of birds proposed by Chan et al. (2003). Large brine fly larvae that are more likely to be eaten by birds had somewhat higher concentrations, but were still below the suggested dietary threshold, even if all of the mercury in them is assumed to be MeHg (see below). Pupae do not appear to be a major dietary item of birds at the Great Salt Lake, but adult flies, with the highest concentration of total mercury 152 ηg g^{-1} wet weight, are commonly eaten by many birds (see below) and do exceed the suggested bird threshold if the mercury in them is primarily methylated.

The reason for the progressively increasing concentration of mercury in the different stages of brine fly is most likely due to lipid loss in the pupae and adults. In a related species (*E. hians*) caloric content decreased from 12.4 to 11.2 to 7.2 cal per individual in larvae, pupae and adults, respectively (Herbst, 1986). This is likely due to metabolism of calorie-rich lipids by the older stages, with an associated concentration of mercury in the remaining tissue.

The significantly higher concentrations of mercury in brine flies collected at Stansbury Island (Station 1) were not expected. Naftz et al. (2009) found that 50% of the fluvial input of mercury to Gilbert Bay entered on the east side of the lake from Farmington Bay, and Sorensen et al. (1988) found mercury concentrations as high as 1500 ηg g^{-1} in the sediments at the south end of Farmington Bay. We consequently expected high concentrations at the station closest to the Farmington Bay discharge to Gilbert Bay (Fremont Island), or at the SE end of Gilbert Bay near the mining discharge of Kennecott Copper Corporation. The higher concentrations we found in the brine flies at the Stansbury Island site are consistent, however, with higher levels of mercury found in water, brine shrimp and eared grebes (*Podiceps nigicollis*; Gray and Hines, 2009) near this site relative to sites on the east side of the lake (Conover and Vest, 2009a). Grebes in the Great Salt Lake eat *Artemia*, as well as brine fly larvae (Gafney, 2008; Conover and Vest 2009b). The reason for the high concentration of mercury in the brine flies and grebes at the Stansbury site is unclear. One hypothesis is that brine fly larvae at this site, being more distant from sources of nutrients, have slower growth rates, and consequently are able to concentrate more mercury than brine flies growing faster (i.e. "growth dilution"; Pickhardt et al., 2002) in areas where nutrients enter Gilbert Bay (near Fremont Island and the southeast side of Gilbert Bay). Alternatively, the higher concentrations may be due to natural deposits of cinnabar (HgS) located in the Stansbury Mountains just 25 km SW of our sample site. There was a discrepancy in our data in that the highest mercury concentrations in biostrome periphyton were found at Station 2 (Fremont Island), whereas the highest concentrations in the brine flies were at Station 3. A possible explanation for this is that our periphyton analyses were biased because that tissue included a small portion of inorganic material that was not removed by the acid treatment. Additional analyses of the spatial distribution of mercury in the biota around the Great Salt Lake are warranted, especially since many birds concentrate in Bear River and Farmington Bays where pollutant sources are potentially much higher.

4.4. Biomagnification of mercury and selenium in the Great Salt Lake food web

Although the diets of birds that forage in the Great Salt Lake have not been studied in detail, it is clear that different species utilize invertebrates from three different food webs: (1) the periphyton-brine fly web on the biostromes; (2) the pelagic food web leading to *Artemia*, and; (3) a playa-based food web with freshwater sheet flow and diverse freshwater invertebrates (Fig. 9). American avocets, eared grebes, and particularly goldeneye ducks rely heavily on larvae and adult brine flies. California gulls and black-necked stilts also feed on *Ephydra*, particularly adult flies. Many other species of birds forage in

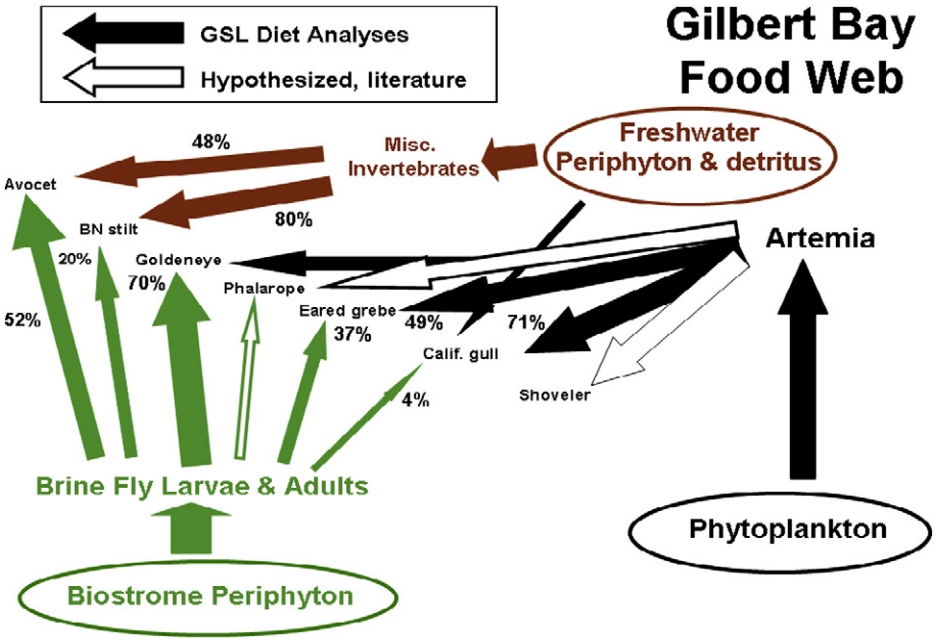

Fig. 9. Food web resources of dominant birds that utilize the Great Salt Lake. Open arrows are hypothesized pathways based on studies in other saline lakes and ponds. The Freshwater Periphyton and Detritus pathway occurs on the mud flats of Gilbert and Farmington Bays. Species codes and samples sizes: Avocets — American avocets (12); BN stilt — Black-necked stilt (4); Goldeneye — common goldeneye ducks (120); Calif. gull — California gull (53); Grebe — Eared grebe (94); Shoveler — northern shoveler duck; Phalarope — Wilson's and red-necked phalaropes. Data from Conover and Vest (2009a), Conover and Vest (2009b), Cavitt (2007), Vest et al. (2009), Gafney (2008).

the Great Salt Lake (Aldrich and Paul, 2002), but whether they utilize brine flies is unknown, as their diets have not been studied.

The biomagnification factors leading to goldeneye ducks were: water → periphyton, 30,000; periphyton → brine fly larvae, 1.2; larvae → goldeneye duck breast tissue, 43× or 269× for liver tissue (based on estimated dry weight Hg concentrations of Vest et al. 2009 and unpublished data of the Utah Division of Water Quality). The high biomagnification of mercury from the water to periphyton was not unexpected (Pickhardt and Fisher, 2007). Additionally, it is likely that some of the mercury taken up by periphyton was derived from pelagic seston particles and *Artemia* fecal matter that settled onto the biostrome surfaces, decomposed on the benthic surface, and enriched the interstitial water of the biostrome, rather than by direct uptake from overlying water. The biomagnification from periphyton into brine fly larvae was quite small (1.2×), whereas the increase from the larvae into the goldeneye duck breast tissue was moderately high (43×). The increase from brine fly larvae to goldeneye liver tissue was very high (269×). The high THg in goldeneye livers (50,800 ηg g^{-1} dry tissue) may be due to the fact that inorganic Hg can bind to proteins and selenium in the liver (Bridges and Zalups, 2005; Khan and Wang, 2009) but not in muscle tissue, thus resulting in elevated concentrations of inorganic mercury in the liver of birds (Scheuhammer et al., 1998). Hepatic demethylation, combined with reactions with selenium, may also concentrate mercury in the livers of birds (Eagles-Smith et al., 2009). We also must caution that the calculated biomagnification factors for the goldeneye are based on the assumption that they obtained their mercury loads only from Great Salt Lake brine flies, but since mercury turnover in liver and muscle can take months, it is possible that the birds obtained mercury along their migration route or in northern breeding grounds.

Detoxification of mercury in bird livers may be facilitated by the relative high selenium concentrations in the Great Salt Lake water and biota (Fig. 10). Selenium levels in the lake are relatively high as a result of selenacious soils in the region, mining activities that release some of the selenium, and the natural characteristic of the lake to concentrate salts. Selenium concentrations were far higher than the mercury levels in the same media: 397 ηg Se L^{-1} in the water, and 1200–1800 ηg Se g^{-1} dry weight in the periphyton and brine fly tissues (Fig. 10). Some have argued that *molar* ratios of total Hg:Se that are less than 1 indicate that mercury is not present in toxic quantities (e.g. Berry and Ralston. 2008). These ratios in the water, periphyton, brine flies and goldeneye duck livers from the Great Salt Lake are all less than 1.0 (Fig. 11). Selenium may also counteract the neurotoxicity of mercury and increase non-toxic mercury content in the brain (Whanger, 2001). Although the molar ratios of Hg:Se are suggestive that selenium may be counteracting mercury toxicity in the Great Salt Lake, analyses of MeHg in invertebrate and bird tissues are needed because not all forms of selenium are antagonistic to mercury toxicity (Yang et al., 2008).

4.5. High mercury levels in the Great Salt Lake

Although mercury levels in the water and biota of the Great Salt Lake are high, the source(s) of the high levels are not understood. Ongoing atmospheric deposition, natural weathering of cinnabar

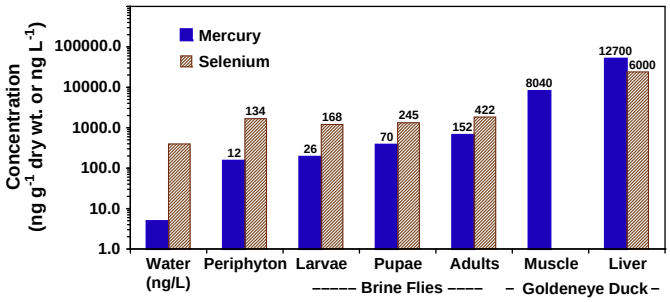

Fig. 10. Concentrations of total mercury and selenium and in the food web associated with biostromes in the Great Salt Lake. Water concentrations are in ηg L^{-1} while histograms for the other components are ηg g^{-1} dry weight. Values shown above the bars are estimated concentrations on a wet-weight basis based on assumed dry:wet weight ratios of: periphyton — 0.08; larvae — 0.14; pupae — 0.19; adults — 0.23; duck muscle and liver — 0.25. Selenium concentrations for the water, periphyton and brine flies were derived from Wurtsbaugh (2009). Mercury concentrations for duck breast muscle are from 2005 samples collected by the Utah Division of Water Quality, and mercury and selenium concentrations in duck livers are from Vest et al. (2009).

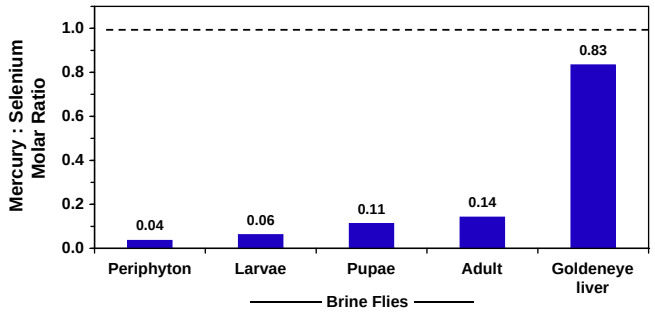

Fig. 11. Molar ratios of mercury to selenium in the food web components associated with biostromes in the Great Salt Lake. The dashed line shows the 1:1 ratio below which mercury is hypothesized to be non-toxic.

deposits in the region and legacy recycling of mercury deposited during gold, silver and mercury mining over the past 150 years have all been suggested (Gardberg et al., 2011; Naftz et al., 2008).

Whatever the source of the mercury, there are several mechanisms that facilitate its retention and methylation so that large amounts concentrate in the biota. The causeway separating Gilbert Bay from the more saline Gunnison Bay allows a deep brine layer (monimolimnion) to form below 6.7 m in Gilbert Bay, and the organic matter from the productive lake decomposes in this layer making it anoxic with reducing conditions. Although the Great Salt Lake is primarily a sodium chloride system like the sea, 7% of its salt is sulfate, and consequently sulfate reduction is extremely high in the monimolimnion and in anoxic sediments (Brandt et al., 2001) around the rest of the lake. Since mercury methylation is often coupled to sulfate reduction (King et al., 2000) the high methyl mercury concentrations, especially in the monimolimnion (10–40 ng L^{-1} Naftz et al., 2008), are understandable. In contrast, we always found oxic conditions in water over the biostromes, suggesting that methylation there may be limited. Nevertheless, steep vertical gradients in redox conditions would be expected within the biostromes, so methylation could occur in deeper layers of them. The lake also has exceedingly high concentrations of dissolved organic matter (DOM > 40 mg C L^{-1}; Leenheer et al., 2004), and this helps maintain mercury in solution, as well as affecting the production and bioaccumulation of MeHg (Aiken et al., 2003; Ravichandran, 2004). Photolytic degradation of methyl mercury to non-toxic forms is also enhanced by humic DOM and inhibited by chlorides (Zhang and Hsu-Kim, 2010). However, because both chlorides and DOM and are very high in the Great Salt Lake, and because the DOM is highly bleached (Aiken and Wurtsbaugh, unpublished data), it is difficult to predict how these competing ligands would interact to influence demethylation. Detailed work will be necessary to unravel the complex chemistry and biotic interactions in this unusual lake.

5. Conclusions

The carbonaceous biostromes in the Great Salt Lake are abundant, covering approximately 260 km^2, or more than 20% of the lake's littoral zone. Total chlorophyll abundance of the dominant cyanobacteria on the biostromes rivals that of the phytoplankton, indicating that the biostrome community is important in the lake's production processes. The only benthic invertebrate found on the biostromes was the brine fly *E. gracilis* with mean densities of 16,300 m^{-2} and biomass similar to that of the *Artemia* in the water column. Published studies of bird diets at the lake and comparisons with other saline lakes indicate that brine flies may be as important as the *Artemia* as a food source and vector for contaminant transfer. However, mercury concentrations in the biostrome biota was less than levels shown to harm birds, and biomagnification of mercury and selenium in the short biostrome food web was low. Adult brine flies, however, had mercury concentrations above recommended thresholds for prey items of birds. Additionally, goldeneye ducks that feed extensively on brine flies had high mercury levels, suggesting either marked biomagnification at that transfer step, or that the birds obtain mercury elsewhere. Mercury:selenium molar ratios were <1 for all components of the biostrome food web, suggesting that even the high mercury levels in the ducks may not be toxic. Additional analyses of methyl mercury are consequently needed to assess whether this contaminant present a problem for birds and humans that utilize these game species.

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