Natural Resources and Environmental Issues

Volume 15 *Saline Lakes Around the World: Unique Systems with Unique Values*

Article 2

2009

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ABSTRACT

Benthic organisms and substrates in Great Salt Lake, Utah, were sampled to measure selenium concentrations of prey organisms of the birds that utilize the lake for nesting and during migrations. The sampling was focused on stromatolite biostromes, as these solid reef-like structures cover approximately 23% of the oxic benthic area of the lake and are the principal habitat for brine fly (*Ephydra cinerea*) larvae and pupae. Samples were taken at depths of 1-5 m along two transects in Gilbert Bay where salinities ranged from 116–126 g l^{-1}. Periphyton on the biostromes had chlorophyll levels of 700 mg m^{-2}, and contained approximately 68% of the chlorophyll in the lake's phytoplankton. Consequently, the biostromes represent a significant component of the lake's primary production. A pumped-bucket sampler effectively sampled brine flies on horizontal surfaces of the biostromes, but not on the sides of the mounded ones encountered in the southern part of the bay. Brine fly larvae and pupae were far more abundant on the biostromes than on the soft substrates, with respective mean densities of 9100 m^{-2}, 530 m^{-2} and 240 m^{-2}, on biostromes, sand and mud. Total brine fly biomass on biostromes averaged 5.9 g m^{-2}, which is about 30% of the biomass present in brine shrimp (*Artemia franciscana*) in the water column. The mean selenium concentration in the combined organic matter-inorganic substrates of biostromes sampled in 2007 was 0.3 ± 0.1 μg g^{-1} dry weight. However, when the inorganic carbonates were removed with acid, the remaining organic matter had selenium concentrations of 1.0 ± 0.1 μg g^{-1} dry weight. Mean Se concentrations in larvae, pupae and adult brine flies were 1.3, 1.5 and 1.8 μg g^{-1} dry weight, respectively, but the differences were not significant. Although there was a 2500X bioconcentration factor between total dissolved Se (mean = 0.40 μg l^{-1}) in the overlying water and in the periphyton of the biostromes, the limited data suggested that there was little biomagnification between the periphyton and the brine flies. A review of the diets of birds utilizing Great Salt Lake and other saline lakes suggests that brine fly produced on biostromes are an important diet component for goldeneye ducks (*Bucephala clangula*), American avocets (*Recurvirostra americana*), black-necked stilts (*Himantopus mexicanus*) and California gulls (*Larus californicus*) and perhaps other birds utilizing the lake. Consequently the benthic food web may be important route for uptake of metal contaminants in these birds in Great Salt Lake. The high selenium concentrations in goldeneye ducks that feed on brine flies suggests that proposed increases in the loading of this contaminant should be reviewed carefully by managers. High mercury levels in goldeneyes suggest that the food web on the lake's biostromes may be an important pathway for other metals into birds.

INTRODUCTION

In lakes and oceans, production processes are often divided between those in the water column and those on the benthic substrates. The food webs of phytoplankton → zooplankton → predators in the water column are better studied than are the periphyton → invertebrate grazer → predator food chains in the benthos. However, a recent review (Vadeboncoeur et al. 2002) documented that in many lakes, food chains based on benthic production are frequently more important for the upper trophic levels than are pelagic food chains. This is particularly true in small or shallow lakes where light penetrates to much of the bottom and consequently fuels primary production by periphyton. For example, in clear, shallow lakes, Vadeboncoeur et al. (2003) found that over 80% of the lake's production came from periphyton, and top predators such as fish and birds are often highly dependent on benthic organisms as food sources (Vadeboncoeur et al. 2002).

In saline lakes, pelagic primary production and food webs are also much better understood than are their benthic counterparts. For example, in Great Salt Lake, Utah, there have been multiple studies of the plankton community (Wirick 1972; Stephens & Gillespie 1976; Stephens 1990; Wurtsbaugh 1988, 1992; Wurtsbaugh & Gliwicz 2001; Marcarelli et al. 2006), but only a single study on the benthic invertebrates (Collins 1980) and none on the primary producers there. The mean depth of Great Salt Lake is near 5 m, and hence a considerable portion of the lake's bottom receives sunlight and can thus support primary production.

Primary production in the sediments of Great Salt Lake has led to the formation of expansive beds of stromatolite biostromes (bioherms) that form when photosynthesis drives up the pH and allows carbonates to precipitate, forming rock-like structures. Only a single study has described the biostromes in the lake. Eardley (1938) provided an assessment of all of the lake's sediment structure, and found that stromatolites covered hundreds of square kilometers, and that they were the only solid

substrate in the lake. The lake may have the most extensive coverage of living stromatolites anywhere in the world, but they are far less known than those in Shark Bay, Australia (Golubic 1992), Cuatro Ciénegas, Mexico (Dinger et al. 2006), or in the Bahamas (Paerl et al. 2001).

The stromatolite biostromes in Great Salt Lake are particularly important as a habitat for brine flies. In the only published study on brine flies in the lake, Collins (1980) found that larval and pupal densities were highest on the calcified biostromes in the lake that provide solid substrates. Mud substrates were secondarily important, and few flies were found on sand substrates. Because brine fly pupae must attach to a solid substrate to undergo metamorphosis, the biostromes may be crucial for their survival in the lake.

The brine flies are likely an important food resource for the extensive bird populations that utilize Great Salt Lake during annual migrations, but it is often assumed that brine shrimp are the dominant prey items. However, in hypersaline ecosystems brine flies are often an important component of bird diets. Herbst (2006) studied bird (including black-necked stilts) use of prey in hypersaline ponds in California and concluded that nearly 90% of all feeding was on brine flies, with the remainder on brine shrimp and corixids. Brine flies (*E. hians*) also have been shown to be an important component of the diet of California gull chicks at Mono Lake, CA (Wrege et al. 2001). Brine flies are also important component diets of eared grebes (*Podiceps nigricollis*) in saline lakes (Jehl 1988) and these birds often concentrate over biostrome areas in Great Salt Lake (personal observation). Another abundant species at Great Salt Lake are red-necked phalaropes (*Phalaropus lobatus*) and Rubega & Inouye (1994) found that brine flies from Mono Lake were a better nutritional source for these birds than were *Artemia*. Few studies on bird diets have been done on Great Salt Lake, but Vest et al. (2008) recently found that larval brine flies were the dominant prey eaten by goldeneye ducks (*Bucephala clangula*), and gulls are often seen feeding on adult flies that accumulate in mass along the shoreline. The limited diet analyses from Great Salt Lake and those from other systems suggest that brine flies may be a very important source of food.

Brine flies may also be an important pathway for the accumulation of contaminants in birds that utilize Great Salt Lake. Benthic food webs may be particularly important for transferring metals to birds and fish, because concentrations are often high in the sediments and because reducing conditions there often mobilize or transform metals into oxic forms (e.g. mercury; Mason 2002). Not all metals respond similarly, however. Selenium, in particular, is frequently made less bioavailable under reducing conditions. Nevertheless, Vest et al. (2008) found high concentrations of both selenium and mercury in the livers of goldeneye ducks that feed heavily on brine flies, and this has led to a consumption advisory to limit mercury intake in humans (Utah DWR 2008).

The objectives of the study were four-fold. The first objective was to test methods for quantitatively sampling the periphyton and brine flies from the biostromes, mud and sand substrates. Most sampling of brine flies has relied on only semi-quantitative kick-net methods (Herbst 1988), or quantitative samples collected by wading in shallow water (Herbst 1990). The second objective was to determine the abundances and biomasses of the periphyton and brine fly community, and to compare them with the primary producers and brine shrimp (*Artemia franciscana*) in the water column. The third objective was to determine the selenium content in the benthic organisms because of concerns that this metal might bioaccumulate in birds at Great Salt Lake and because the Kennecott Utah Copper Corporation had requested to increase its discharge of this metalloid into the lake. The fourth objective was to construct a food web for the birds utilizing recently available data on bird diets from Great Salt Lake, and other literature on bird feeding habits in saline lakes. The benthic study was part of a larger analysis by the Utah Division of Water Quality of selenium in the lake and its potential impacts on birds (CH2MHill 2008).

STUDY AREA

Great Salt Lake is a 5180 km^2 closed-basin system in Utah, USA (41.04 N, 112.28 W) bordered on its eastern and southeastern shores by the greater metropolitan area of Salt Lake City. The lake has been impacted by industrial and municipal discharges, and by transportation causeways that divide the system into three large bays. Gunnison Bay (2520 km^2), located in the northwest of the lake, has salt concentrations between 280 and 300 g l^{-1} (28-30%). Farmington Bay (260 km^2) in the SE, is very shallow with a mean depth < 1 m and highly variable salinities. The benthic food web study described here was focused on 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 typically ranging between 120 and 180 g l^{-1} and supports a large brine shrimp population. The lake elevation during the study was 1279.6 m in June, 2006 (USGS 2007). At this elevation, the respective mean and maximum depths of Gilbert Bay are 5.0 and 9.5 m. In the continental climate, water temperatures in the lake reach 27-28°C in summer and decrease to near 0°C by January (Wurtsbaugh & Gliwicz 2001).

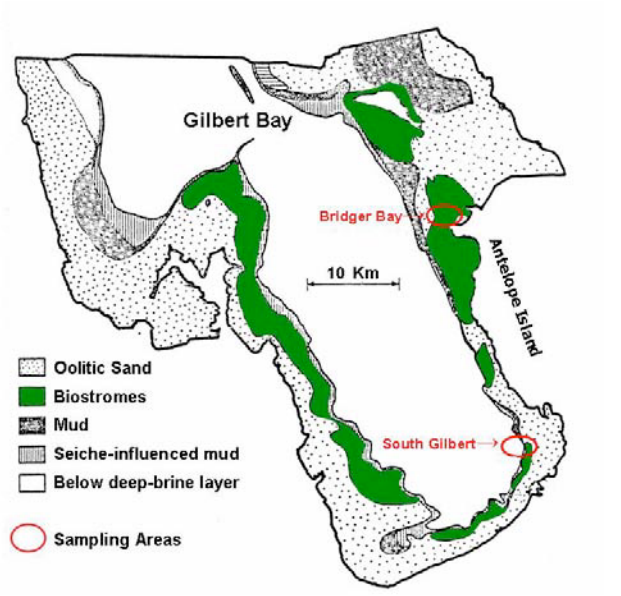

Figure 1–Map of Gilbert Bay showing the two benthic sampling areas. The substrates in the lake are derived from a map in Collins (1980) who used sediment structure data of Eardley (1938).

Gilbert Bay (Figure 1) is meromictic due to infiltration of saturated brines from Gunnison Bay under the railway causeway and into the deeper strata of Gilbert (Loving et al. 2002) creating a deep-brine layer (monimolimnion) below 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. Eardley (1938) provided a detailed map of the benthic structure of Great Salt Lake, although no methods were provided on how this information was collected. The deep brine layer underlies 44% of Gilbert Bay. In the remaining sediments covered by the oxygenated mixed layer, oolitic sand, mud and biostromes represent 62%, 15% and 23% of the substrate, respectively (Table 1).

The biostromes occupy depths of approximately 0.5-3 m in the lake where there is sufficient light for benthic photosynthesis. A single analysis of the microbial composition of the biostromes indicates that the cyanobacterium *Aphanothece* sp. represented over 99% of the cells in the biostromes, but some green algae were present (N. Parker & W.A. Wurtsbaugh, unpublished data). The small 1.4 µm diameter cells are embedded in a mucilaginous matrix that is partially calcified. The growing cyanobacteria change the pH of the water, causing carbonates to precipitate and the biostromes to grow. Treatment with hydrochloric acid dissolves the carbonates, leaving a solid, flexible mucilaginous plate ca. 1 cm thick. Most of the biostromes we have encountered in the lake have a flat plate structure protruding approximately 10-20 cm from surrounding soft sediments. In many places the biostromes have grown together former a nearly continuous plate. However, during the sampling for this study we found that biostromes in water about 3 m deep near the SE end of the lake had considerably different structure, with mounds that protruded ca. 0.8-1.5 m from the bottom, and that were ca. 0.5 m in diameter. These were in dense fields with limited space between mounds, although poor visibility precluded assessing them extensively.

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. Data derived from Baskin (2005). The thickness of the mixed layer was estimated at 6.7 m (22 ft). The areas of stromatolites, 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.

Section	Mean Depth (m)	Area of Sediments (km^2)	Volume ($m^3 \times 10^9$)
Gilbert Bay (total)	5.55	2057	11.42
Deep-Brine Layer		912	1.73
Mixed Layer		1145	9.69
Stromatolites		261	
Oolitic sand		712	
Mud		172	

METHODS

Collection Sites

The primary collections of brine fly pupae and larvae, periphyton, water, and sediment were along two transects in Gilbert Bay (Figure 1) from 14–16 June 2006. The transect for Site 1 began at a depth of 1 m at the SW corner of Bridger Bay on Antelope Island and proceeded westward. Site 2 (Gilbert South) was a N-S transect beginning in the SE end of Gilbert Bay. At each of these sites we sampled at nominal depths of 1, 3 and 5 m. The coordinates and actual depths sampled are shown in Appendix 1. We also collected adult brine flies at three shore locations: rock outcroppings at the SW corner of Bridger Bay, Saltair Beach, and at a beach just north of Kennecott mine tailings on the south shore. Because relatively few sediment samples were collected in 2006, and because some of the analyses were questionable, additional ones were collected at depths of 1-3 m on 28 April 2007. At each site, salinity, oxygen and temperature profiles were measured with an InSitu sonde. Secchi disk measurements were made at each site. On 28 September 2006 we made two additional collections of brine fly larvae and pupae at a depth of 1.9 m at the Bridger Bay sampling site.

Brine Fly & Sediment Collection

Brine fly adults were captured with a fine-meshed butterfly net while running along the beach, or between rocks where brine flies were resting. Netted brine flies were placed in a cooler with dry ice to euthanize and transport them. They were kept frozen at -20°C after return to the laboratory, and then washed with de-ionized water to remove salts, counted, and weighed.

Figure 2–SCUBA diver sampling biostromes in Great Salt Lake with a pump sampler. The inset shows the detail of the bucket and scrub brush used to dislodge brine flies so that they can be pumped to the surface.

Duplicate larval and pupal brine fly samples were collected at each depth. The larvae and pupae were sampled on the biostromes by SCUBA divers using a vacuum pump sampler (Figure 2) similar to that of Voshell et al. (1992). The sampler consisted of an inverted plastic bucket with a port and glove attached to the side of the canister so that a diver could agitate the substrate. A flexible rubber strip on the bottom of the bucket helped seal it against the irregular surfaces of the biostromes. The apparatus sampled an area of 0.075 m^2. Lead weights (4 kg total) were attached to the lower part of the bucket to increase stability and to keep the unit on the substrate. In order to function effectively, the sampler had to be placed on a relatively level and solid substrate. This precluded sampling on the sides of the dome-shaped biostromes in southern Gilbert Bay. Once the sampler was positioned, the diver jerked the attached pump tube so that the operators in the boat could begin bringing 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. Pumping continued until three 20 l buckets were filled on the boat. Subsequent analyzes indicated that this pumped volume removed an average of 92% of the larvae and pupae from the substrate (W.A. Wurtsbaugh, unpublished data). Samples were sieved through a 500-µm sieve and collected in an acid-washed 500 ml polyethylene bottle, and stored on ice for transport to the laboratory. A power analysis of the sampling efficacy of the bucket sampler suggested that respective sample sizes of 5 and 36 would be needed to measure selenium concentrations and larval abundances with an allowable error of 30% (Wurtsbaugh 2008).

To sample organic matter and chlorophyll, the diver broke off a portion of the calcified biostromes. Only edge pieces of flat biostromes, or exfoliating pieces of domed biostromes could be collected, and this could have introduced some bias. Sampled pieces were 100-300 cm^2, and usually about 3 cm thick. Pieces of biostromes of known area were frozen and subsequently placed in 95% ethanol to extract chlorophyll overnight at room temperature. The chlorophyll solution was then diluted with ethanol and concentrations measured in a Turner 10-AU fluorometer with the non-acidification method (Welschmeyer 1994). Blanks and standard were analyzed at the beginning of each run. Biostrome and sediment subsamples were dried at 70°C, weighed and then ashed at 450°C for 6-8 h. Ashed samples were re-wetted using deionized water, dried overnight at 70ºC, and then weighed to obtain ash-free dry mass (AFDM). Subsamples of biostromes were treated with acid to remove carbonates. These samples were submerged in 1 N HCl until all CO_2 bubbling stopped. This required several hours and necessitated replacing the acid up to three times. By removing the carbonates, this procedure allowed us to determine the selenium concentration of the organic component of the stromatolites.

On sand and mud substrates, brine flies and substrate materials were collected with a 0.050 m^2, 24 kg, Ponar grab (Wildco, Inc., Buffalo NY). The samples were brought to the surface and discharged into a plastic tub and then sieved through a 500-µm mesh. In all cases, insufficient brine flies were available from the soft sediment samples for selenium analyses. Separate Ponar grab samples were used to collect sediments for selenium analyses. In some cases the upper few millimeters of sediment were sectioned separately with a plastic spatula to determine if there were vertical differences in selenium content.

In the laboratory, larvae and pupae were counted, washed three times with de-ionized water, then weighed and frozen in polyethylene scintillation vials. Composite samples of larvae (mean, 236 individuals; range 47-500) and pupae (mean, 246 individuals; range 21-500) were analyzed for selenium. The brine fly samples were sent to LET Incorporated (Columbia, MO) for selenium analysis by hydride generation–atomic absorption spectrometry on acid-digested samples. The reporting limit for selenium was 0.1 µg Se g^{-1}.

Water Samples and Statistical Analyses

Water samples were taken first at all dive sites to avoid disturbed sediments. Collection of water samples occurred 2-5 cm above the sediment surface using 60 ml acid washed syringes. Each syringe was rinsed three times with surface water, and once with water from above the sediments prior to collecting the actual sample. Water samples were taken ca. 5 m apart from each other. On the surface, water in the syringes was filtered through Whatman 47 mm GF/F filters (0.80 µm) and placed in 200 ml acid-washed polyethylene bottle. Two ml of concentrated nitric acid were added to fix samples. Samples were sent to Frontier Geoscience, Seattle, WA for total dissolved selenium analysis by hydride generation and atomic fluorescence spectrometry (HG-AFS). Minimum detection limit for total Se was reported as 0.05 µg l^{-1}. The statistical analyzes of selenium concentrations and brine fly densities were done using SYSTAT (Chicago, Illinois).

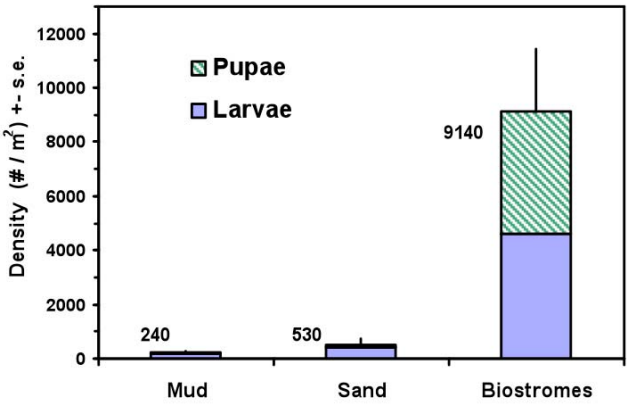

Figure 3–Densities of brine fly (*Ephydra cinerea*) larvae and pupae measured on mud, sand and biostrome substrates in Gilbert Bay of Great Salt Lake during June 2006. Error bars show +1 standard error.

RESULTS

Limnological Conditions

During the 14–16 June 2006 sampling, water temperatures ranged from 20.7°C at the surface to 20.4°C near the bottom and oxygen was at saturation. Surface salinities were 116 g l^{-1} at both sites, increasing to 126 g l^{-1} (12.6%) at 5 m. The Secchi depth (0.72 m) at Bridger Bay was influenced by the algal-laden Farmington Bay water reaching the site, as clearer water was observed farther offshore and in other areas of the lake. In the September sampling at Bridger Bay, water temperatures ranged from 20.0°C at the surface to 16.8°C at 1.8 m, and salinities ranged from 136 g l^{-1} at the surface to 146 g l^{-1} at 1.8 m, indicating an overflow of fresher water from Farmington Bay was influencing the site. When benthic substrates were sampled in April 2007, the Secchi depth was 1.0 m at the Bridger Bay site. Much clearer water was observed in other parts of Gilbert Bay, but transparencies were not measured.

Brine Fly Densities, Biomass, Organic Matter

Brine fly larvae and pupae were very abundant on biostromes but scarce on sand and mud substrates (Figure 3). There was no significant relationship between brine fly densities and depth (linear regression; $p = 0.88$), so data from all depths are pooled for presentation. Total brine fly densities on biostromes averaged 9140 m^{-2} and reached over 1.6 x 10^4 m^{-2} in three samples. Larval brine flies on biostromes were significantly (2-way ANOVA; $p = 0.015$) more abundant (7060 m^{-2}) in Bridger Bay than at the Gilbert South site (1470 m^{-2}), but there was no significant difference for pupae ($p = 0.226$; mean = 4600). Combined larval and pupal densities on mud and sand were 240 m^{-2} and 530 m^{-2}, respectively, but pupae were very rare on these substrates. Both larvae and pupae were significantly more abundant on biostromes than on the combined category of sand/mud (t-test; $p = 0.003$). Total brine fly biomass on biostromes sampled in June averaged 5.9 g m^{-2}, but only 0.2 g m^{-2} on sand/mud substrates. Larval and pupal brine fly densities at Bridger Bay in September 2006 were 3160 ± 670, and 410 ± 132 m^{-2}, respectively.

Organic matter content was high in the biostromes, but low in the sand and mud substrates (Figure 4). The organic matter content of sand substrates averaged 3% and that in mud was 12%. The organic matter of intact biostrome material was 30%, but when the carbonates were removed by acidification, the remaining material had an average organic matter content of 72% (Figure 4). Chlorophyll *a* concentrations on the biostromes were high, averaging 700 ± 210 mg m^{-2}. Chlorophyll was not measured on the sand/mud substrates.

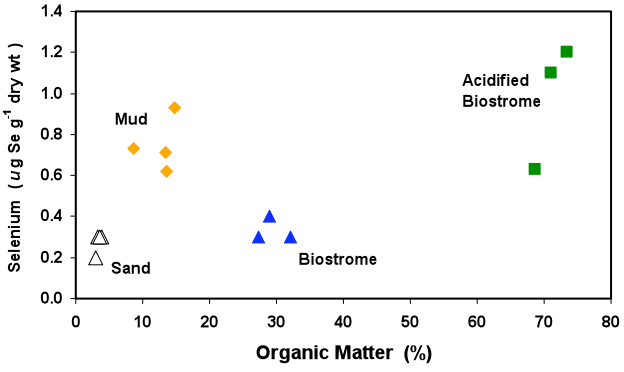

Figure 4–Relationship between organic matter in benthic substrates and their selenium content in replicate samples collected near Bridger Bay in 2007. Biostromes were analyzed either intact (Biostrome), or after acidification to remove carbonates (Acidified Biostrome).

Selenium Concentrations

The concentrations of selenium in water and the benthic organisms were moderate but showed little indication that there is biomagnification (Figure 5). Mean total dissolved selenium concentrations in the water were low (0.40 µg Se l^{-1}) and did not differ significantly between the Bridger Bay and the Gilbert South sites ($p = 0.117$). Variability in selenium concentrations in the water was very low with a range of 0.37-0.43 µg Se l^{-1}. The mean Se concentration in microbial community on the biostromes was 1.0 µg g^{-1} (980 µg kg^{-1}). This represents a 2500-fold bioaccumulation factor between the water phase and the microbes. The selenium concentrations in the sand (mean 0.3 µg g^{-1}), mud (0.8 µg g^{-1}) and non-acidified biostrome material (0.3 µg g^{-1}) were lower than concentrations measured in the primarily organic material (1.0 µg g^{-1}) from the acidified biostromes (Figure 4).

The mean concentrations of Se in brine flies increased from larvae to pupae to the adults, but these differences were not significant ($p > 0.15$). Mean Se content for all three stages of flies average 1.5 µg g^{-1}. A two-way ANOVA (site x brine fly stage) indicated that the brine flies in Bridger Bay had significantly higher concentrations of selenium than did those in Gilbert South ($p < 0.000$) with a mean difference of 1.6 vs. 1.3 µg Se g^{-1}.

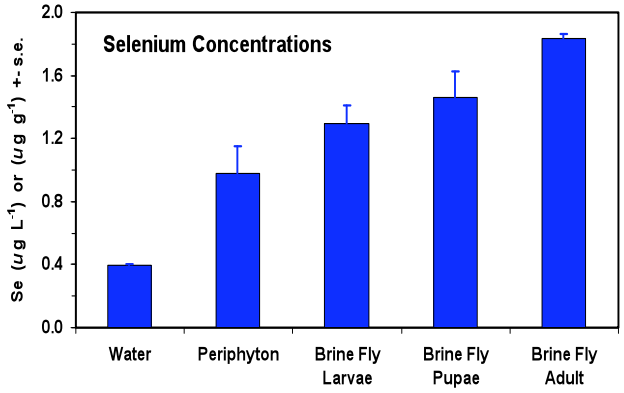

Figure 5–Selenium concentrations in water, periphyton (cyanobacteria + other microbes) and three stages of brine flies in Great Salt Lake. The value for periphyton was from biostrome samples collected in 2007 that were acidified to remove carbonates, leaving primarily organic matter. The selenium concentration for water is in units of µg l^{-1} while that for the periphyton and brine flies is in units of µg g^{-1} dry weight. A Bonforroni-adjusted multiple comparison of the periphyton and brine fly stages indicated that only periphyton and adult brine flies had significantly different selenium concentrations ($p = 0.022$). Error bars show +1 standard error.

DISCUSSION

Food Web Dynamics and Selenium Bioaccumulation

The data collected on the biostromes indicates that they are an important component of the food web in Gilbert Bay, and they may consequently have an important influence of the bioaccumulation of metals such as selenium and mercury. A relative comparison of periphyton on biostromes and the phytoplankton can be done as an approximation of how much production may come from these two sources. Primary production data are not available for the biostromes, so chlorophyll levels in the two can be compared. Biostromes are estimated to underlie an area of 261 km^2 in Gilbert Bay, which is only about 18% of the area where phytoplankton occurs (Figure 6A). However, areal chlorophyll levels are about 380% higher on the biostromes than in the integrated phytoplankton from the 6.7 m thick mixed layer (Figure 6B). Multiplying the areal coverage of the two habitat types by the chlorophyll concentrations indicates the total amount of chlorophyll in the two habitats. This calculation suggests that the cyanobacteria and algae on the biostromes is about 70% of that in the water column (Figure 6C). Note that this calculation does not include the contribution of chlorophyll on the expansive mud and sand substrates in the littoral zone of the lake. Although the cyanobacteria on (and in) the biostromes may not be as accessible to the brine flies as phytoplankton cells are to grazing *Artemia*, this preliminary analysis indicates that the abundant biostromes are an important component of the food web in the lake. This analysis is consistent with recent views on the importance of benthic areas for primary production and the production of invertebrates in lakes (Vadeboncoeur et al. 2002).

The brine flies on the biostromes also represent a significant component of the invertebrates in the lake and contain a large amount of the bioavailable selenium for birds (Figure 7). The biomass of brine flies we measured in June was about 30% of that in *Artemia* (Figure 7A). The seasonality of brine flies is not well known, but Collins (1980) found comparable densities of pupae on biostromes from June through August, suggesting that our measurements in June are at least indicative of the summer period. Selenium concentrations in brine flies were somewhat higher than in *Artemia* (1.5 vs. 1.2 µg g^{-1}; Figure 7B), contrary to what others have found Great Salt Lake (Adams 2005 unpublished) or elsewhere (Herbst 2006). The resulting estimate of total selenium in the benthic invertebrates suggests that brine flies contain about 38% of the total selenium that is contained in *Artemia.* These comparisons, although based on relatively few samples, indicate that brine flies could be a significant source of selenium for birds in the Great Salt Lake.

In contrast to the biostromes, the sand and mud substrates we sampled had relatively few brine flies associated with them. This is consistent with the findings of Collins (1980), although he did estimate that perhaps 18% of brine fly production could occur on the expansive mud and sand sediments. The soft sediments in much of the lake may produce little periphyton for the brine flies. It is likely that the sands in shallow waters shift so much that algae cannot become well-established. Conversely, in deeper water, periphyton may have insufficient light for photosynthesis. The photic zone at the time of our survey was estimated to be only about 2 m deep (two Secchi depths), so photosynthesis would be restricted below this depth. Our survey sites, however, were located relatively close to discharges of nutrient-laden water (Farmington Bay and the Goggin Drain) from metropolitan Salt Lake City, and the resulting phytoplankton growth in these areas may shade-out periphyton. Secchi depths in the lake often increase to > 3.5 m (i.e. 7 m photic zone) when intense grazing by *Artemia* removes phytoplankton (Wurtsbaugh & Gliwicz 2002), so benthic photosynthesis may often occur throughout the littoral zone sediments. The limitation of stromatolites to depths < 3.5 m (Eardley 1938) suggests, however, that intense benthic photosynthesis may be limited to this zone. A thorough study of benthic primary production will be necessary before we fully understand this process in Great Salt Lake.

The benthic food web is a likely route for selenium transport into birds, because a large portion of the estimated 20 metric tons of selenium in the lake (water + upper 2 cm of sediments) is in the bioactive benthic zone (Table 2). A comparison of data collected by Johnson et al. (2008) and that reported here yields an approximate estimate that 67% of the selenium is in the top 2 cm of the sediments and biostromes in the lake while only 8% is in suspending particulate matter (seston) available for *Artemia* to graze on, and 25% is dissolved in the water (Table 2). Biostromes contain an estimated 4% (upper 2 cm) of the selenium. A large portion of the selenium (46%) is estimated to be in the anoxic sediments below the deep brine layer. It is important to consider that the selenium in the organic material of the biostromes is potentially available to the invertebrates, whereas that beneath the deep brine layer will cycle very slowly to the oxic zone of the lake (Johnson et al. 2008) where invertebrates could take it up. The oxic sand and mud substrates, with an estimated selenium content of 17% of the lake total, could potentially be important for the transfer of selenium to invertebrates. However, the very low numbers of brine flies found on the sand and mud suggests that even the organic selenium in soft sediments would not be utilized to any significant degree. This comparison between the different lake zones is based on a small number of benthic samples from the oxic zone, and several assumptions, so it is clear that more research is needed in order to construct a true estimate of selenium in the different compartments.

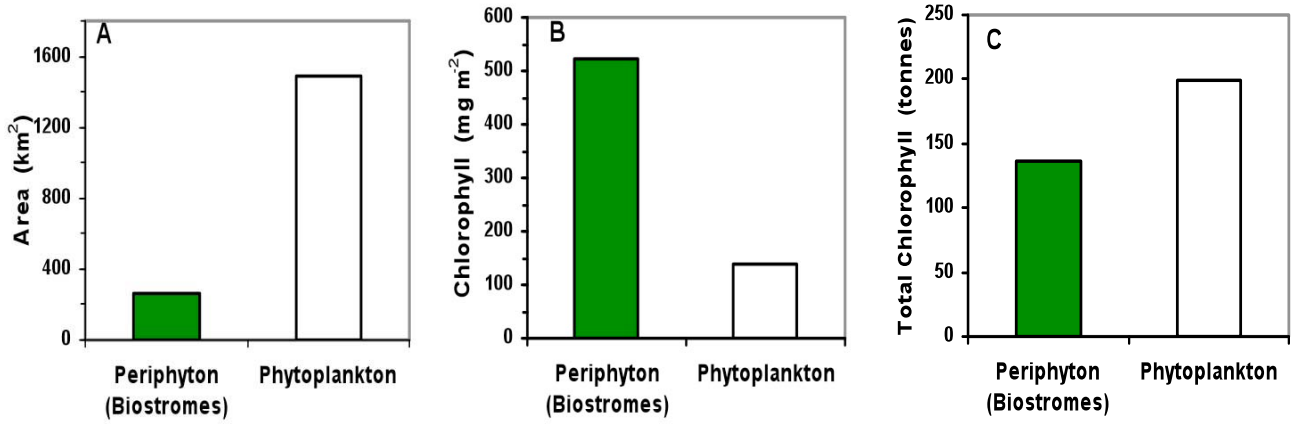

Figure 6–A. Comparison of the area covered by periphyton on biostromes (solid fill) and that of the epilimnion of Gilbert Bay where phytoplankton can grow (open). B. Concentrations of chlorophyll on biostromes (solid fill) and that in phytoplankton in the water column (open). C. Total chlorophyll estimates (metric tones) for Gilbert Bay in periphyton attached to biostromes, and that in the phytoplankton. The latter was based on chlorophyll in Gilbert Bay calculated from data from 2002–2005 of W.A. Wurtsbaugh, and an estimated epilimnetic volume of 9 x 7 10^9 m^3.

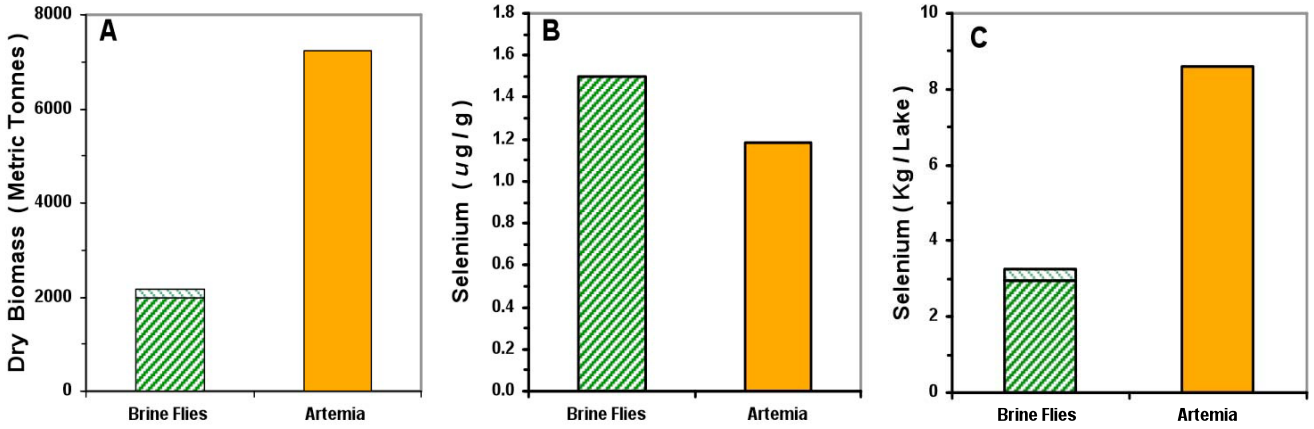

Figure 7A–Comparison of the amount of biomass in brine flies and that in *Artemia*. The brine fly data are from June 2006, and represents the sum of larvae and pupae. The dark green diagonal shading shows brine flies on biostrome substrates. The light green shading represents brine flies on soft sediments. B. Mean selenium concentrations in brine fly larvae and pupae and that in adult *Artemia* (Marden 2008). Selenium concentrations were 2–4X lower in juvenile *Artemia*, but the data from adults was used because: (1) they are likely the main prey of birds, and; (2) under most circumstance they would dominate the biomass. C. Estimated total amount of selenium in brine fly larvae and pupae on biostromes (dark green shading), on soft sediments (light green shading), and in *Artemia*. The *Artemia* data are based on an April-December mean dry biomass of 0.75 mg l^{-1} (data of Brad Marden). Estimates of brine fly biomass and selenium concentrations are based on limited samples.

If the mean estimated selenium content in the biostrome organic material collected in 2007 is correct (1.0 µg Se g^{-1}) there appears to be little or no biomagnification up the benthic food web (Figure 5). The selenium content of organic material from biostromes measured in 2006 (Appendix 1) was higher (mean, 1.7 µg Se g^{-1}), so if this value were used it would suggest a negative biomagnification factor. There was, however, a 2500-fold bioconcentration from the dissolved phase (0.4 µg Se l^{-1} = 0.4 ng Se g^{-1} of water) into the periphyton. This bio-concentration factor is likely an overestimate, because much of the selenium reaching the periphyton biofilm does so by sedimentation of particles (Johnson et al. 2008). The mineralization of these particles likely would yield much higher dissolved selenium concentrations in the interstitial water surrounding the microbes than that in the water centimeters above the biostromes. Nevertheless, most of the accumulation of selenium into organic matter must occur between the water and microbes, because the brine fly larvae do not increase concentrations further. This is similar to the results of Brix et al. (2004), who also did not find significant biomagnification of selenium by *Artemia*, and by the relatively low concentration factors reported for selenium by Chapman et al. (1968). Grosell (2008) also found relatively low uptake of selenium by brine shrimp at high salinities, and suggested that this might be due to competitive exclusion of Se uptake by the high sulfate levels in Great Salt Lake. The slight increase in selenium concentrations from larvae to pupae to adults that we found may be the result of modifications in fat content or other constituents, since feeding does not occur after the brine flies pupate. It is also possible that exoskeletons of pupae are low in selenium, so that molting into the adult stage would increase the selenium concentrations in the flies.

With the limited sampling reported here it is difficult to assess the spatial variations in selenium that may be present in the benthic zone of the lake. We did not anticipate finding higher selenium concentrations at the brine flies from the Bridger Bay site than at the Gilbert South site. The latter is near the discharge points of Kennecott Utah Copper Corporation and the Goggin drain where 55% of the selenium load enters the lake (Naftz et al. 2008), and where Cavitt (2008) found high selenium in shoreline organisms. In contrast, the Farmington Bay discharge near the Bridger Bay site contributes only 13% of the selenium load, and concentrations of the effluent from Farmington Bay are only 56% of those from the Goggin drain (Naftz et al. 2008). The higher concentrations of selenium in the brine flies at Bridger Bay may be attributable to the very high organic content of the effluent from Farmington Bay, which is highly eutrophic (Wurtsbaugh & Marcarelli 2006). Rosetta & Knight (1995) found that brine flies bioaccumulated selenium much faster from a dissolved organic compound than they did from selenate or selenite. Indeed, most uptake of selenium by benthic invertebrates is thought to be via incorporation of organic selenium (Presser & Luoma 2006).

Table 2–Estimates of selenium in different areas of the lake. That in the water column was based on the selenium concentrations reported by Johnson et al. (2008). Sediment estimates assume only a 2 cm thick bioactive layer, and a solids component of 33% (W. Johnson unpublished data) and a density of dry sediment and stromatolites of 1.5 g cm^{-3}. Selenium concentrations in the anoxic sediments are from Johnson et al. (2008), whereas the oxic sediment concentrations are from the 2007 data reported here. The Se concentration for the biostromes is for non-acidified samples.

	Se Concentration		Area/Volume	Se (Metric Tons)	Percent
Water column (total)	0.56	µg l^{-1}	11.4 x 10^9 m^3	6.4	33%
Water column (dissolved)	0.42	µg l^{-1}	11.4 x 10^9 m^3	4.8	25%
Water column (particulate)	0.14	µg l^{-1}	11.4 x 10^9 m^3	1.6	8%
Sediments (total)			2057 km^2	13.1	67%
Sediments (anoxic)	1.0	µg g^{-1}	912 km^2	9.0	46%
Sands (oxic)	0.3	µg g^{-1}	712 km^2	2.0	10%
Muds (oxic)	0.8	µg g^{-1}	172 km^2	1.3	7%
Biostromes	0.3	µg g^{-1}	261 km^2	0.9	4%
Total				19.5	

The selenium content of brine flies is important because birds in Great Salt Lake feed on them extensively (Figure 8). Cavitt (2008) found that brine fly larvae comprised 20-100% of the diet (by volume) of American avocets (*Recurvirostra americana*) sampled at different sites prior to or during nesting at Great Salt Lake. The highest proportion of larvae in the diets occurred at Antelope Island where biostromes and dense brine fly populations occur close to shore. The lowest proportion of brine fly larvae in the avocet diets occurred in Ogden Bay where the mud flats are distant from biostromes and where fresher water allows other prey to be abundant. A small sample of black-necked stilts (*Himantopus mexicanus*) at the Ogden Bay site also suggested that brine fly larvae could be an important diet item for them. *Artemia* were absent from the diets of both of these birds. In contrast, Conover et al. (2008) found that the diets of California gulls (*Larus californicus*) were composed of 45-83% *Artemia* at his three study sites, and brine flies represented a maximum of 25% of the diet. Diet sample sizes were small for the birds, so these are only approximate proportions, and they represent only the short early or pre-nesting period when selenium in prey items can be passed to eggs. Brine flies are also important component diets of eared grebes (*Podiceps nigricollis*) in saline lakes (Jehl 1988). Additionally, red-necked phalaropes (*Phalaropus lobatus*) at Mono Lake feeding on brine flies maintained their weight, whereas those feeding only on *Artemia* lost weight (Rubega & Inouye 1994). The high fat levels and energy content of the Mono Lake brine flies makes them a good prey item for birds, but Caudell and Conover (2006) found that brine flies from Great Salt Lake had lower caloric densities than did *Artemia*. The dominant brine fly in Great Salt Lake (*E. cinerea*) is also considerably smaller than the *E. hians* at Mono Lake, so it is possible that the flies in Great Salt Lake may not be utilized as extensively by birds as are the brine flies in Mono Lake.

Selenium concentrations in birds that feed extensively on brine flies are moderately high and may potentially cause physiological impairment. The diet of common goldeneye ducks is composed of approximately 70% brine fly larvae and pupae (Vest et al. 2008; J. Vest, personal communication). Mean selenium concentrations in the livers of these birds increased from < 3 to nearly 10 µg g^{-1} during their winter residence at Great Salt Lake (Vest et al. 2008). Selenium concentrations of 3 µg g^{-1} and 10 µg g^{-1} are respective thresholds for reproductive and health-impairment in mallards (Heinz 1996; Heinz et al. 1989). Goldeneye do not breed at Great Salt Lake and since selenium is lost quickly from the body, the high concentrations of this metal would not likely impair reproduction in the spring. The relative sensitivity of goldeneye and mallards to selenium is not known, so it is uncertain whether the high concentrations of this toxicant in the birds late in the year could be impairing their health. Goldeneye also accumulate very high concentrations of

mercury while residing at Great Salt Lake, suggesting that brine fly larvae and pupae may be a pathway for the uptake of this metal. American avocets in the lake have moderately high concentrations of selenium in their blood and livers (Cavitt 2008), and there was a negative correlation between selenium concentrations in the liver and the mass of the bird. Reproductive success of the birds, however, was high and apparently not impaired by their moderately high selenium concentrations in their tissues. Additionally, the concentrations of selenium in brine flies in our study (mean, 1.5 μg g^{-1}), and the similar concentrations found at most study sites by Cavitt (2008), were below thresholds reported by Lemley (1996) to cause impairment if eaten by birds. Additional physiological and diet data for the birds, as well as more thorough analysis of seasonal changes in the metal concentrations in their prey are warranted to explain these discrepancies.

In conclusion, this study demonstrated that biostromes and their associated brine fly grazers are an important component of the food web in Great Salt Lake. In contrast, the open mud and sand substrates appear to produce few brine flies, but more work in different parts of the lake is needed to confirm this. The brine flies produced on the biostromes are an important component of the diet of some birds that may be impacted by selenium, and for a number of other species that utilize the lake. Although these conclusions appear sound, our results were based on relatively few samples collected primarily in the spring. Additional research is needed to better characterize the seasonal and spatial variability in the benthic habitats in Great Salt Lake. Whereas *Artemia* and their phytoplankton food resources in the lake have been studied extensively over the past decades, very little work has been done to understand the brine flies and their biostrome habitats. Increasing eutrophication of Gilbert Bay may alter light penetration and influence the relative contribution of benthic and pelagic algae to the food web. Specific projects that need to be considered include: (1) detailed mapping of the benthic characteristics in the lake, and in particular, the distribution of different types of biostromes in the lake; (2) analysis of the spatial and temporal distribution of brine flies over an annual cycle, and (3) additional analyses of linkages between the periphyton, brine flies and the birds that feed on them.

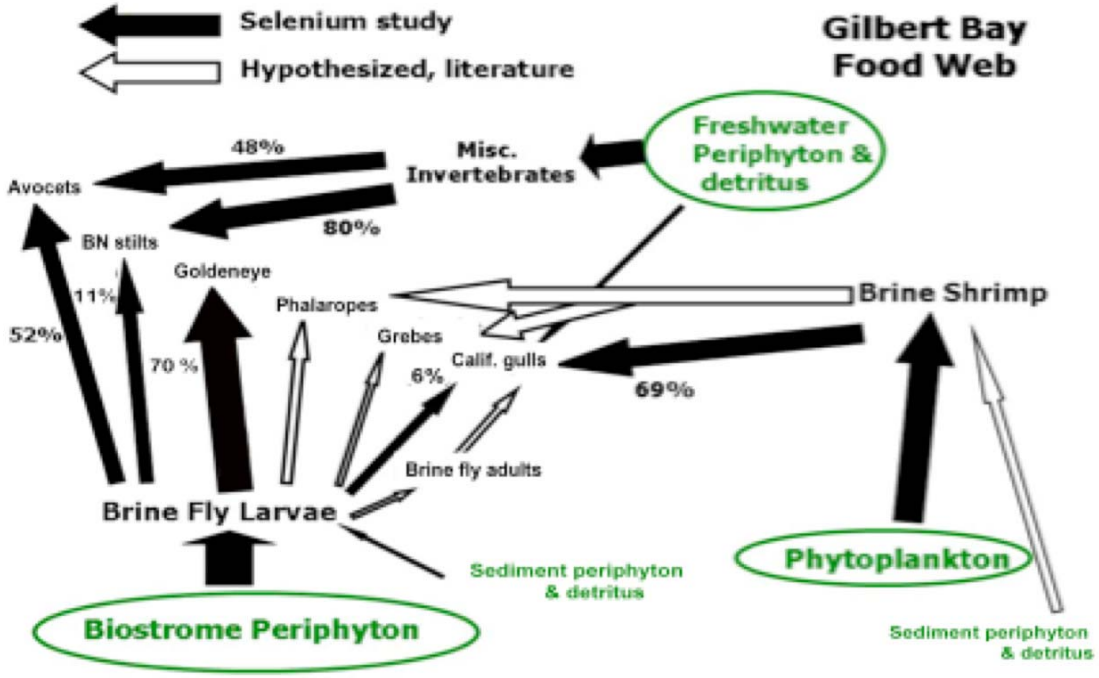

Figure 8–The food web in Gilbert Bay with an emphasis on pathways leading to birds that utilize the lake. The width of the arrows indicates the importance of a pathway. Solid arrows show data taken during the 2006–2007 selenium study (Conover et al. 2008; Cavitt et al. 2008; Vest et al. 2008). Open arrows 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 stilts–Black-necked stilt (4); Goldeneye–Goldeneye ducks (> 100); Calif. gulls–California gulls (53); Grebes–Eared grebes. Note the small sample sizes for some species.

ACKNOWLEDGEMENTS

J. Kris Bell, Sonja Raub, Leyland del Re, and Joel Moore assisted in sampling and data processing. Ian Washbourne, Sonja Raub, and Justin Robison collected samples with SCUBA. David Naftz, William Johnson and Brad Marden shared unpublished data and provided constructive advice on the project. Theresa Presser, Anne Fairbrother, Harry Ohlendorf, Earl Byron and Caleb Izdepski provided useful reviews of the manuscript or an earlier draft report. Funding for the study was provided by the Utah Division of Water Quality and the North Davis Sewer District.

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Appendix 1–Selenium and ash-free dry mass content (AFDM) of benthic substrates at two sites in Gilbert Bay of Great Salt Lake. Some dredge samples included the upper 50 mm of material, but some samples were sectioned to determine if Se content varies with depth. The visual estimate made by SCUBA divers of the percentage of biostrome, sand and mud is given. Some samples were acidified to remove carbonates. The data from 2007 are considered more reliable.

Site	Sample Date	Lat-itude	Long-itude	Depth (m)	Substrate Type	Sediment strata (mm)	% Bio-strome	% Sand	% Mud	Acidified	AFDM %	µg Se/g dry wt
Bridger Bay	16-Jun-06	41.036	12.323	3.9	Mud	0-50	2	98	0	Y	2%	9.80
Bridger Bay	16-Jun-06	41.034	112.325	5.0	Mud	0-50	2	10	88	Y	6%	3.10
Bridger Bay	16-Jun-06	41.034	112.325	5.0	Mud	0-3	2	10	88	Y	7%	3.30
Bridger Bay	16-Jun-06	41.034	112.325	5.0	Mud	0-50	2	10	88	Y	10%	1.40
Bridger Bay	14-Jun-06	41.043	112.276	1.0	Biostrome		95	5	0	N		0.40
Bridger Bay	14-Jun-06	41.043	112.276	1.0	Biostrome		95	5	0	Y	56%	2.10
Bridger Bay	14-Jun-06	41.043	112.276	1.0	Biostrome		95	5	0	Y		0.90
Bridger Bay	14-Jun-06	41.043	112.276	3.0	Biostrome		95	5	0	N		0.60
Bridger Bay	14-Jun-06	41.043	112.276	3.0	Biostrome		95	5	0	Y	61%	2.20
Bridger Bay	14-Jun-06	41.043	112.276	3.0	Biostrome		95	5	0	Y		1.30
Gilbert South	15-Jun-06	40.802	112.163	2.7	Biostrome		100	0	0	N	58%	3.10
Gilbert South	15-Jun-06	40.802	112.163	2.7	Biostrome		90	10	0	N	59%	-
Gilbert South	15-Jun-06	40.810	112.183	3.2	Biostrome		90	10	0	N	52%	0.40
Gilbert South	15-Jun-06	40.810	112.183	3.2	Biostrome		40	60	0	Y	60%	1.30
Bridger Bay	28-Apr-07	41.041	112.279	2.5	Mud	3-40	0	0	100	N	15%	0.90
Bridger Bay	28-Apr-07	41.041	112.279	2.5	Mud	0-3	0	5	95	N	14%	0.60
Bridger Bay	28-Apr-07	41.043	112.276	3.0	Mud	3-30	0	0	100	N	9%	0.70
Bridger Bay	28-Apr-07	41.043	112.276	3.0	Mud	0-3	0	0	100	N	14%	0.70
Bridger Bay	28-Apr-07	41.043	112.271	1.0	Sand	3-50	0	100	0	N	3%	0.20
Bridger Bay	28-Apr-07	41.043	112.274	1.0	Sand	3-50	0	100	0	N	4%	0.30
Bridger Bay	28-Apr-07	41.043	112.274	1.0	Sand	0-3	0	100	0	N	4%	0.30
Bridger Bay	28-Apr-07	41.043	112.271	1.0	Sand	0-3	0	100	0	N	3%	0.30
Bridger Bay	28-Apr-07	41.043	112.275	1.0	Biostrome		100	0	0	N	32%	0.3
Bridger Bay	28-Apr-07	41.041	112.279	2.1	Biostrome		100	0	0	N	27%	0.3
Bridger Bay	28-Apr-07	41.043	112.276	3.0	Biostrome		100	0	0	N	29%	0.4
Bridger Bay	28-Apr-07	41.043	112.275	1.0	Biostrome		100	0	0	Y	69%	0.6
Bridger Bay	28-Apr-07	41.041	112.279	2.1	Biostrome		100	0	0	Y	71%	1.1
Bridger Bay	28-Apr-07	41.043	112.276	3.0	Biostrome		100	0	0	Y	73%	1.2