THE DIATOM ASSEMBLAGES OF THE SALT PLAINS NATIONAL WILDLIFE REFUGE AND DIATOM ALLOMETRY IN THE SOUTHWESTERN UNITED STATES

By

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PREFACE

The first three chapters of this thesis investigate the diatom diversity of the Salt Plains National Wildlife Refuge (SPNWR), Alfalfa County, Oklahoma. These are followed by a chapter investigating the allometric relationship between diatom biovolume and abundance in four samples from the Southwestern United States. The SPNWR is a unique and relatively unstudied type of habitat. This work should provide useful baseline data for future studies as well as comparison to similar habitats. This thesis may serve to guide future work in aspects of diatom ecology and taxonomy at the SPNWR.

The last chapter covering diatom allometry does not relate to my work at the SPNWR, but it is useful as a preliminary topic that has not yet been uninvestigated. Allometric relationships are often used to suggest that there are "universal scaling laws" that determine anatomical, physiological and ecological traits of all organisms. After finding no literature supporting this relationship for diatoms, I conducted a preliminary investigation of this topic. Additional research could shed new light on the applicability of allometric theory.

ACKNOWLEDGEMENTS

This work was made possible by the assistance of many people. Firstly I would like to acknowledge my advisor Dr. William J. Henley for the opportunity to be a member of his laboratory, and the freedom he allowed me in my research. The experience I gained working in his lab as an undergraduate, then as a graduate student has greatly impacted my interests and my future. Secondly, I would like to thank Dr. Michael W. Palmer for his continued assistance and encouragement in my studies. I would also like to thank Mike for broadening my research interests into new and exciting areas of ecology.

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My research would not have been possible without the cooperation of the U.S. Fish and Wildlife Service, and the staff of the Salt Plains National Wildlife Refuge. Also I would like to thank everyone that assisted me with my research in the laboratory and in the field, especially Dr. Andrea E. Kirkwood and Jessica Milner.

Researching diatoms has proven to be a challenging task, and I would like to thank all of the Diatomists that have helped and encouraged me along the way. Spending time in the summers at the Iowa Lakeside Lab, working with Mark Edlund and Sarah Spalulding has greatly increased my knowledge of diatom systematics and ecology. I would like also to thank the Phycological Society of America for receipt of the Hoshaw

Travel Award and a Croasdale Fellowship for participating in the Ecology and Systematics of Diatoms at the Iowa Lakeside Lab. Finally I would like to thank my friends and family for their patient and encouraging enthusiasm throughout my time at Oklahoma State University.

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CHAPTER 1

DIATOM GENUS DIVERSITY AND COMMUNITY COMPOSITION IN RELATION TO SALINITY AT THE SALT PLAINS NATIONAL WILDLIFE REFUGE, ALFALFA COUNTY OKLAHOMA

ABSTRACT

Despite the common geographic occurrence of inland (athalassic) saline habitats, their biota has not been extensively studied. Diatoms have been estimated to contribute as much as 25% to the earth's primary production (Werner 1977). However, in hypersaline systems the proportion of *in situ* carbon fixation by diatoms is likely to be higher. I used substrate samples taken from the Salt Plains National Wildlife Refuge, an athalassic hypersaline ecosystem, to investigate the relationship between diatom genus diversity, composition and salinity. These samples range in salinity from 14 to 306 ppt and contain 21 genera. Six genera (*Cymbella, Mastogloia, Psamodictyon, Amphora, Navicula* and *Nitzschia*) comprise 97% of the diatoms counted in all samples. Diatom genus diversity shows an inverse relationship with salinity while genus richness shows no clear relationship with salinity. Hence, loss in diversity is the result of dominance by fewer taxa at higher salinities. The relative abundance of the genus *Navicula* is positively correlated with salinity, with it dominating the highest salinity sites. I used a canonical correspondence analysis (CCA) to explore the relationship between salinity and relative abundance of diatom genera. The primary variables influencing diatom genus composition at the Salt Plains were found to be the variability of salinity within a site and the overall magnitude of salinity.

INTRODUCTION

Biological diversity in nature is a complex phenomenon that can not easily be explained by a single process or theory (Huston 1994, Palmer 1994). Understanding diversity comes through an understanding of biological and environmental interactions that combine to produce it. General patterns in diversity can be explained by factors such as habitat heterogeneity (MacArthur and MacArthur 1961), latitude (Currie 1991), and disturbance (Connell 1978).

Diatom assemblages respond to environmental conditions such as pH (Round 1990, Siver 1999), water temperature (Wolfe 2003), water depth (Kingston et al. 1983), nutrients (Underwood et al. 1998, Siver 1999, Underwood and Provot 2000, Soininen et al. 2004) and salinity (Blinn 1993, Cumming et al. 1995, Nubel et al. 1999). Most studies on the effects of salinity on diatoms have focused on sites with salinities near or below that of seawater. Few studies exist on hypersaline habitats (Sylvestre et al. 2001), and even fewer are available for athalassic, (inland) hypersaline systems. The Salt Plains National Wildlife Refuge (SPNWR) of Oklahoma offers an opportunity to study diatom diversity in a natural inland hypersaline habitat.

An understanding of how diatom diversity and composition relates to salinity could give insights into the evolutionary pathways between freshwater, marine and hypersaline environments. I have observed diatoms occupying sites on the Salt Plains ranging from freshwater up to saturated brine (0->300 ppt). In order to better understand how diatoms respond to salinity I have begun an investigation of the diatom assemblages of the SPNWR. In this study I had two main objectives: to determine how the diatom

assemblages respond to the high and variable conditions in salinity at the SPNWR, and to propose some mechanism that might drive the observed patterns of diversity.

METHODS

STUDY SITES

The SPNWR covers an area of 65 km^2 in the northwestern part of Alfalfa County, Oklahoma. For the most part the salt flats are devoid of vascular plants except a riparian zone dominated by the invasive *Tamarix chinensis*. These riparian zones are the only reliable source of water on the salt flats that rarely exceeds the salinity of seawater (35 ppt). Unlike most inland saline aquatic habitats which accumulate salts due to their position in a drainage basin, Permian brine deposits underlie the area of the SPNWR. Normally conditions are dry, and high evaporation rates leave the sandy surface encrusted with NaCl crystals as saturated groundwater percolates up through the soil. These surface salt deposits are temporarily washed away during flood events but reform in a matter of days. As floods recede they leave behind isolated pools of fresh water that soon become saturated with salts and eventually dry up. Consequently, algal biomass and diversity are generally low (Major et al. 2005).

In the summer of 2004 I sampled benthic diatoms from a diversity of habitats across the Salt Plains. The sites fall into four main categories based on salinity and physical conditions: Large permanent pool (LPP), small permanent pool (SPP), ephemeral brine pool (EBP) and a permanently flowing stream Clay Creek (CC). Figure 1 shows the location of the four sites across the salt flats and the location of the SPNWR within Oklahoma. LPP is located at the northern end of the salt flats where a large

permanent pool meets the flats. Because of its large size and depth this pool persisted for at least five years. It had an average salinity of 43.3 ppt for the period between May and August 2004, and a maximum depth of 1 m. Primary productivity at this site is assumed to be high relative to that of other sites on the flats based on the presence of extensive benthic algal mats and the growth of aquatic macrophytes such as *Potamogeton pectinatus.* During heavy rain events the pool forms a network of small streams that flow out onto the flats and eventually into a larger permanent stream to the northeast. As the network of streams recedes towards the main pool it leaves behind smaller pools that form in low-lying areas. Depending on the amount of evaporation, these pools once detached from the main pool begin to increase in salinity. At the first sampling date I chose sites at the edge of the main pool that eventually became isolated and began to increase in their salinity.

Clay Creek (CC) is a permanent sand bed stream that transects the salt flats and flows into a reservoir to the east. Constant drainage through the creek causes salinities to remain low throughout the year, averaging 21 ppt for May through August 2004. Flooding of the creek is not uncommon during rainy periods. Depending on the intensity of rains and due to the flat topography of the region, CC can cover a significant portion of the salt flats and effectively wash away surface salt accumulations. As floods recede, pools are left along the course of the ephemeral drainage system. These pools start as fresh water, but begin to increase in salinity as evaporation occurs.

Through time as surface water evaporates most pools begin to dry up completely; however, some pools are sufficiently low that they are recharged by groundwater. Pools located next to the creek have a significantly higher salinity than the flowing water

however, due to the buffering of the stream they do not reach salt saturated conditions as do the more distant pools. This close hydrological connection of these small permanent pools (SPP) creates unique conditions of high but stable salinity; averaging 88 ppt during the sampling period. The ephemeral brine pools (EBP) exhibit greatly variable high salinities averaging 259 ppt during the sampling period, and ranging from freshwater immediately after a rain to saturation in as short as several days, depending on the evaporation rate.

SAMPLING AND ANALYSIS

I collected sediment samples throughout the summer of 2004; I limit the samples used for this study to those collected between May 18 and June 3, 2004. This roughly two-week period allowed for our sites to fluctuate from low salinity conditions after a rainy period in early May to higher salinities when conditions were drier in June. Therefore, each site has a set of samples that represent low salinity conditions and a set that represent high salinity conditions. Our sampling methods were designed such that I were certain to have representatives from the broadest range of salinities as possible, while representing the diversity of site types found across the landscape. In some cases our sampling was limited due to lack of suitable sites. For example, there are many sites along CC suitable for sampling, but the occurrence of permanent and ephemeral pools is limited.

In this investigation I include a total of 22 samples for our analyses. The CC, LPP, and EBP sites are represented by six samples each, three for the first sampling date and three for the second. The SPP site is represented by four samples, as I only found two

small permanent pools near the creeks. Samples from CC represent three locations along the creek. EBP samples correspond to three separate pools along an ephemeral drainage. LPP samples represent one sample from each end of the large pool and one in the middle.

At each of the four sites I collected 50 ml of surface sediments using a turkey baster. I also recorded GPS coordinates, marked each site with a stake, and measured salinity using a handheld refractometer. Samples were then fixed using 3% formalin and stored at 40°C. Samples of diatoms were cleaned according to the procedure of Battarbee et al. (2001) and permanently mounted on microscope slides using Naphrax. On each slide I counted a minimum of 500 valves along a transect and identified them to genus. Taxonomy follows Krammer and Lange-Bertalot (1999a, b, 2004a, b). In samples from EBP diatom abundances were so low that several transects had to be counted to attain 500 valve counts. Abundances of genera were used to calculate Simpson diversity, which reflects both abundance and evenness of taxa present. The equation for the Simpson's index is $D=1/\Sigma(n/N)^2$, where n is the total number of individuals of a particular taxon present in a sample, and N is the total number of individuals of all taxa in a sample.

Diatom diversity and assemblage structure were analyzed using linear least squares regression, Canonical correspondence analysis (CCA) and partial Canonical correspondence analysis (pCCA). I used both simple linear regression and multiple regression to explore the relationship between Simpson's diversity, log of salinity (ppt) and log of salinity (ppt) standard deviation. I also used simple linear regression to compare the arcsin root transformed relative abundance of *Navicula* with log salinity ppt. CCA is an ordination method which provides a means for directly investigating the relationship between community data and associated environmental variables (ter Braak

1988). pCCA provides the ability to test the significance of environmental variables while using others as covariables (Lepš and Šmilauer 2003) . Data for each of the 22 samples in the CCA and pCCA included genus relative abundance, the log of salinity (ppt), and standard deviation of log of salinity (ppt). I used the computer program CANOCO 4.5 for Windows (ter Braak and Šmilauer 2002) to perform the CCA and pCCA.

RESULTS

SALINITY FLUCTUATION AT SITES

The salinity of samples used in this study ranged from 14 ppt at CC to 306 ppt at the EBP. In order to represent the temporal and spatial variability in salinity that can occur at each site I used salinity measurements taken from the middle of May until the end of July to calculate the standard deviation. Standard deviations are calculated using all samples taken at a site for the whole sampling period. I felt that this measure of variability was more biologically meaningful than using only standard deviation for the two dates of samples used in this study. Figure 2 shows trends in daily averages of salinity for each site for roughly a three-month period from May 14- July 31, 2004. Of the three sites the LPP shows the least variation in salinity while the EBP are the most variable.

DIATOM GENUS DIVERSITY

From the four sites a total of 21 diatom genera were identified from 22 samples. Of these, six genera (*Navicula, Nitzschia, Amphora, Mastogloia, Psamodictyon,* and *Cymbella)* had relative abundances above 1% for all samples combined, and together

composed 97% of diatoms counted. Table 1 gives a summary of the relative abundances of the 21 genera for each site along with genus richness and relative abundance combining all sites. Of the six most abundant genera *Navicula, Nitzshia*, and *Amphora* are found at all sites, *Psamodictyon* at SPP, CC and EBP, *Cymbella* at both LPP and EBP ,while *Mastogloia* occurred only at LPP. The EBP, SPP and CC sites have similar assemblages, sharing all genera that occur in at least 1% abundance at one of these three sites. The LPP shares all but three of its genera with the other three sites. The genera *Mastogloia*, *Rhopalodia*, and *Tabularia* occur only at the LPP. Genus richness shows no significant relationship with salinity for all sites (Figure 3. p=0.296).

The results of two independent linear regressions indicate that both the log of salinity and the log of salinity standard deviation are both significantly negatively correlated with Simpson's diversity ($p<0.01$). However, the results of a multiple regression show that in relation to Simpson's diversity these two measures of salinity are redundant. Because of the problem of multicolinearity with our two independent variables, I chose to use the more direct measure of salinity, the log of salinity (ppt) for further regressions. Simpson's diversity is significantly negatively related to the log of salinity (ppt) (Figure 4. p<0.0.01). Simpson diversity was highest at CC while EBP had the lowest.

The genus *Navicula* dominates the assemblages at the EBP, SPP, and CC sites with 77%, 64%, and 41% relative abundance for each site respectively. The high relative abundance of *Navicula* for these sites corresponds to low evenness. *Navicula* reaches its lowest relative abundance with 7% at the LPP. The arcsin root transformed relative

abundance of *Navicula* was found to have a significant positive correlation with salinity as shown in Figure 5 ($p<0.01$).

ASSEMBLAGE STRUCTURE

All CCA axes were significant after Monte Carlo tests with 499 permutations. I was able to interpret only the first two axes. Salinity standard deviation and salinity magnitude correlate with these first two axes. The first axis is related to site specific variables, and correlates with variability in salinity. The second axis correlates to the magnitude of salinity. Using pCCA I tested the independence of the two variables; both log salinity and standard deviation of log of salinity were significant ($p<0.05$) in explaining variability in diatom assemblages at the Salt Plains.

Figure 6 shows a CCA biplot with samples and environmental variables. The first CCA axis correlates well with the standard deviation of log of salinity and separates out the four sites into groups of samples. CCA axis 2 is correlated with log of salinity. Samples for EBP show that it has the most variable and highest salinity. CC samples have the lowest salinities, with little variation in salinity. LPP samples show that it is the most stable of the four sites. Figure 7 is a CCA biplot showing genera and environmental variables. Only genera with a relative abundance higher than 1% for any site are shown. The separation of such diatoms as *Mastogloia* and *Cymbella* from *Navicula*, *Achnanthes* and *Cyclotella* indicate the strong effect of variability of salinity on composition of diatom genera. The effect of salinity can bee seen by the separation of *Navicula* and *Entomoneis*.

DISCUSSION

Salinity is an important predictor of diatom genus diversity at the SPNWR. Diatom genus diversity has an inverse relationship with salinity at the sites used in this study. This supports the findings of other studies concerning diatom diversity and salinity (Nubel et al. 1999, Clavero et al. 2000). This decline in diversity seems to be the result of dominance by fewer taxa rather than a loss of richness. One explanation for this pattern could be that although diatom taxa are found at high salinity sites they may be metabolically inactive. Therefore, these taxa are contributing to the *richness* of a sample in which the salinity conditions inhibit their *growth*. Therefore, taxa such as *Entomoneis*, *Psamodictyon*, *Nitzschia*, and *Amphora* that are all common in CC are not able to become established at EBP and SPP due to the rapidly changing and high salinities. However, *Navicula* grows optimally at high variable salinities and is therefore dominant at EBP and SPP.

Though salinity magnitude and variability seem to explain a large portion of the variation in diatom genus diversity and assemblage composition, other factors are also likely to be important. Salinity standard deviation appears to be a site specific variable; variability is dependent on location. Therefore, observed patterns in diversity may be responding to other site specific variables such as water chemistry or water body characteristics that might covary with salinity standard deviation. The most striking example of where this may be true is the site LPP. Here the assemblage is dominated by a genus, *Mastogloia* who is not found at the other sites. The diatoms *Rhopalodia* and *Tabularia* also indicate that this site is unique.

Potential limitations to the study include the use of genus in place of species diversity which could obscure the patterns as some genera are represented by multiple species and some by one. For example *Mastogloia* at the LPP is represented by one species, *M. pumila* and the *Navicula* at the EBP is largely composed of *Navicula cf. cincta* however, there are more than twenty species of *Navicula* at CC. Also a larger number of samples and types of sites would greatly improve our ability to make interpretations.

Conditions at the SPNWR are highly variable through space and time, but general patterns in diatom diversity can still be seen in relation to salinity. This study shows that much of the variation in diatom diversity can be explained by salinity. Also evident are differences in assemblage composition between sites, which can be attributed primarily to the magnitude and variability of salinity. In order to better understand what effect salinity has on diatom diversity at the SPNWR, future work will include a larger number and diversity of sample sites and the use of species level identification. This is the subject of chapter 2.

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Tables

Table 1. List of genera and relative abundances for each site and relative abundance for all samples combined

Genus	CC	LPP	EBP	SPP	Combined
Nitzschia	29.13	15.35	13.18	5.17	15.71
Navicula	40.98	7.26	77.35	64.35	47.48
Amphora	20.70	14.57	5.66	24.96	16.47
Cyclotella	0.96	0.22	1.37	0.10	0.66
Psamodictyon	4.39	-	0.52	2.97	1.97
Tryblionella	0.10	0.03	0.33	0.05	0.13
Bacillaria	0.22	-	0.20	-	0.10
Encyonema	-	-	0.07	-	0.02
Achnanthes	1.31	0.16	0.52	0.53	0.63
Calonies	0.03	-	0.07	0.05	0.04
Surirella	0.61	-	0.55	0.10	0.31
Fallacia	0.19	-	-	-	0.05
Entomonies	1.12	0.06	0.03	0.24	0.36
Gyrosigma	0.10	-	-	0.05	0.04
Chaetoceras	0.13	0.29	0.03	1.39	0.46
Thalassiosira	0.03	-	0.03	-	0.02
Hantzschia	-	-	0.07	0.05	0.03
Mastogloia	-	55.25	-	-	13.81
Cymbella	-	6.39	0.03	-	1.61
Rhopalodia	-	0.29	-	-	0.07
Tabalaria	-	0.13	-	-	0.03
Genus Richness	15	12	16	13	21

Figure Legends

Figure 1. Map showing aerial photo of the Salt Plains National Wildlife Refuge with the four sites indicated by arrows. An inset locates the Salt Plains National Wildlife Refuge within Oklahoma. SPP=small permanent pool, LPP=large permanent pool, FPS=Clay Creek, and EBP=ephemeral brine pool

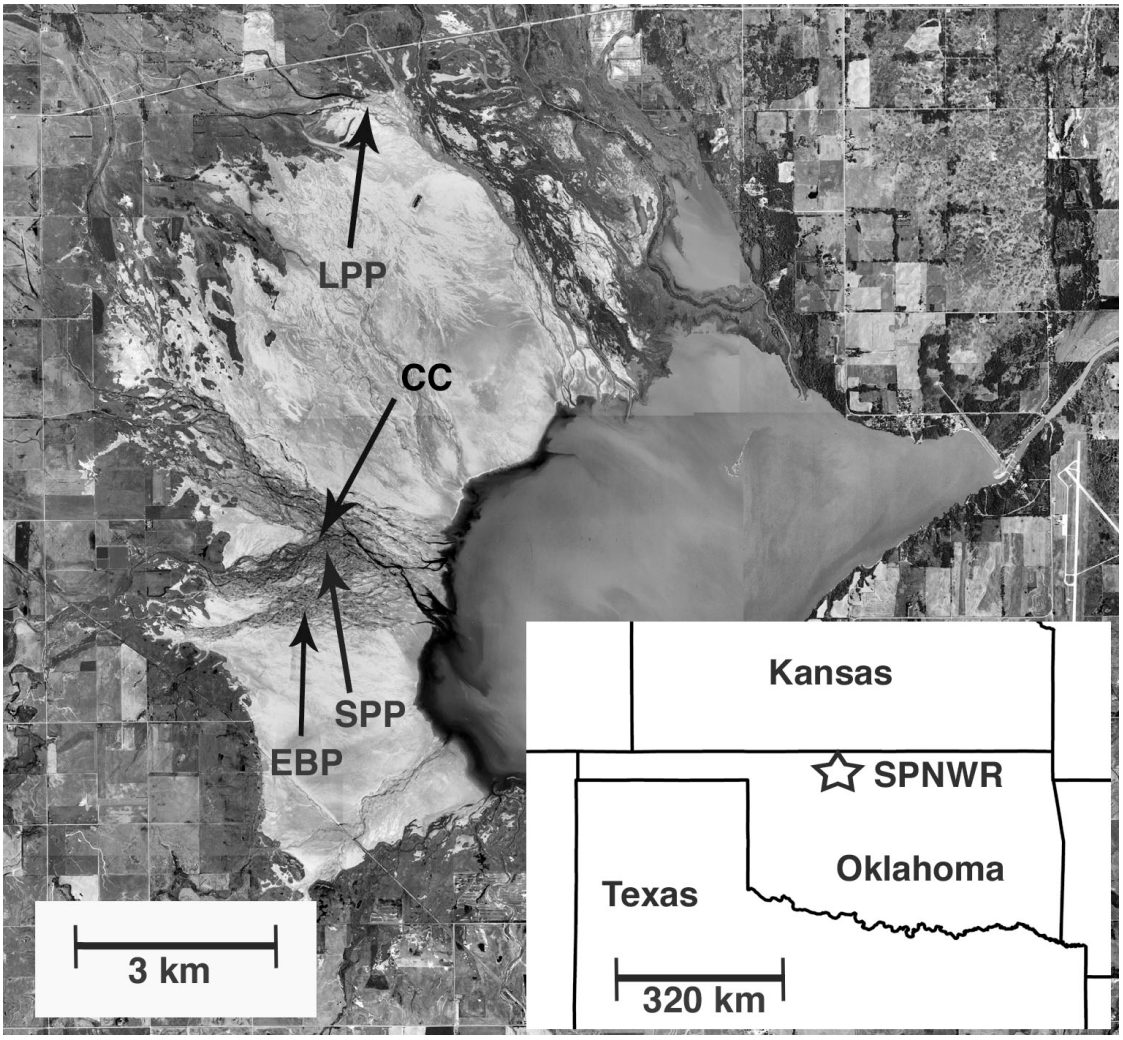


Figure 2. Change in salinity through time from of the four study sites for May 14 – July 31, 2004. EBP=ephemeral brine pool, SPP=small permanent pool, LPP=large permanent pool and CC=Clay Creek

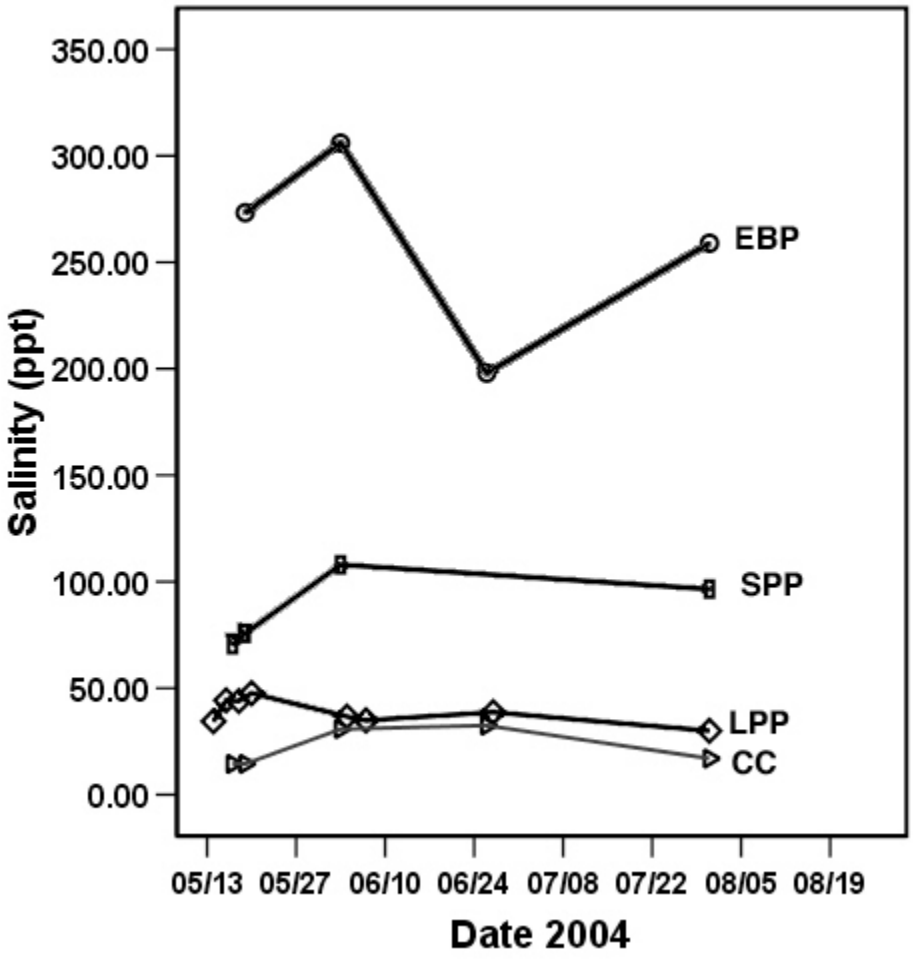


Figure 3. Relationship between log of salinity and diatom genus richness for all sites combined ($p<0.01$, $R^2=0.0495$). Triangles=Clay Creek, Circles=ephemeral brine pool, Rectangles=small permanent pool, Diamonds=large permanent pool

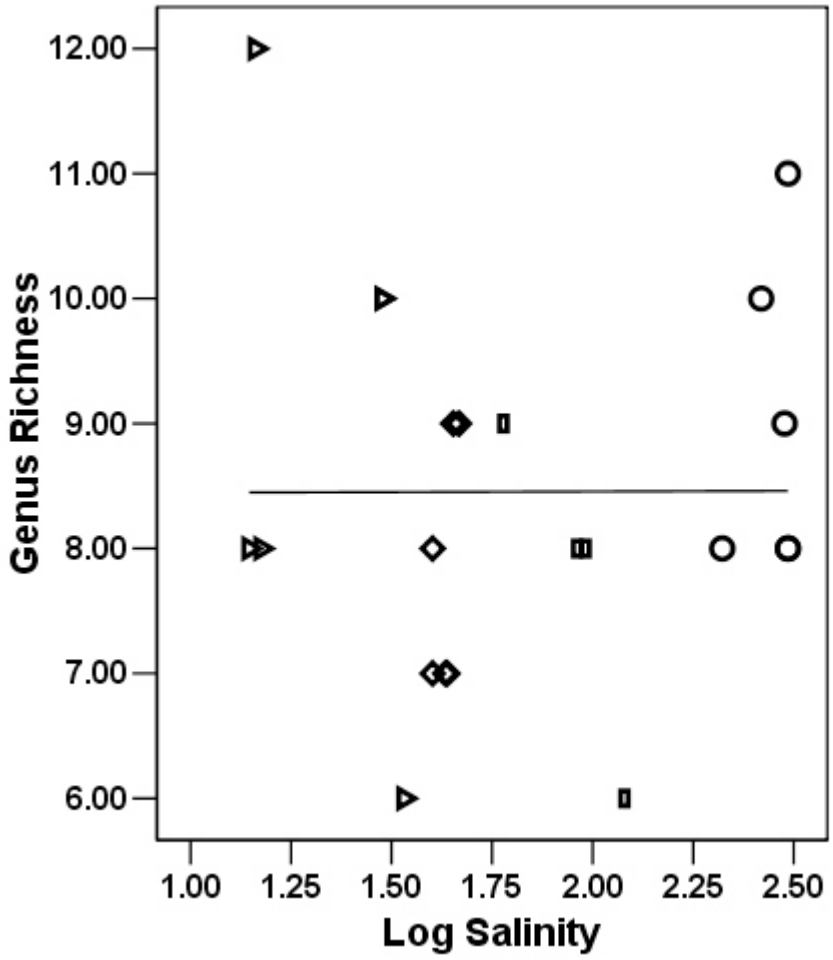


Figure 4. Relationship between natural log of salinity and diatom genus diversity using the Simpson's index ($p<0.01$, $R^2=0.316$) for all samples combined. Triangles=Clay Creek, Circles=ephemeral brine pool, Rectangles=small permanent pool, Diamonds=large permanent pool

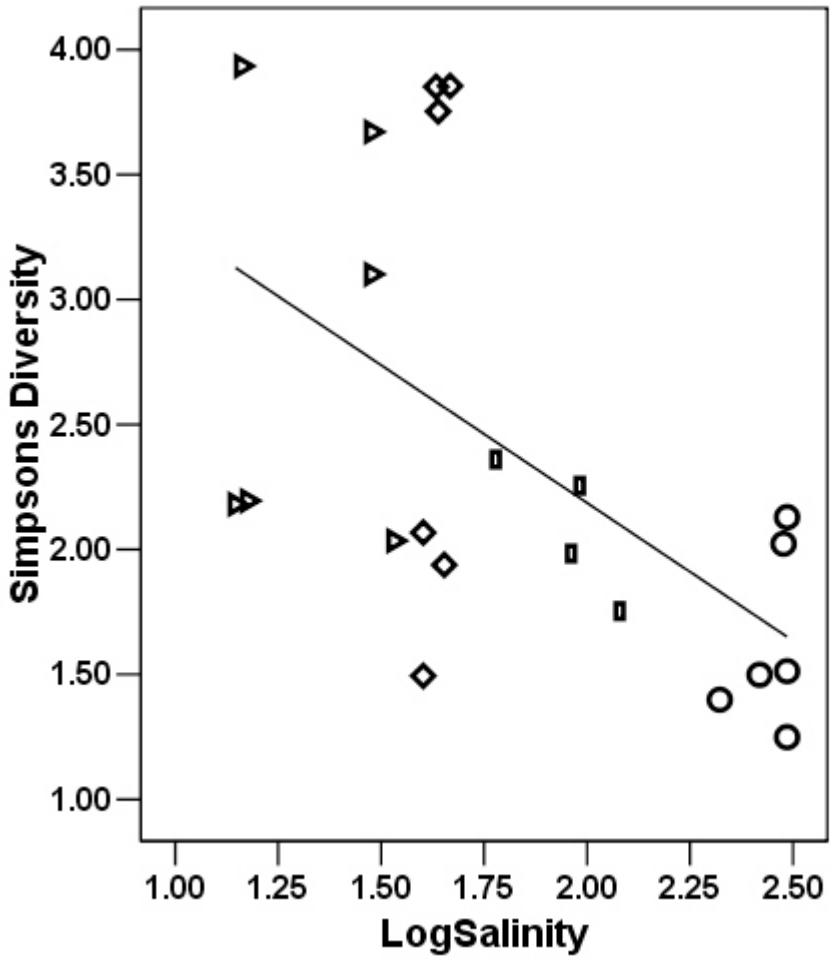


Figure 5. Relationship between log of salinity and arcsin root transformed relative abundance of *Navicula* for all samples combined ($p<0.01$, $R^2=0.418$). Triangles=Clay Creek, Circles=ephemeral brine pool, Rectangles=small permanent pool, Diamonds=large permanent pool

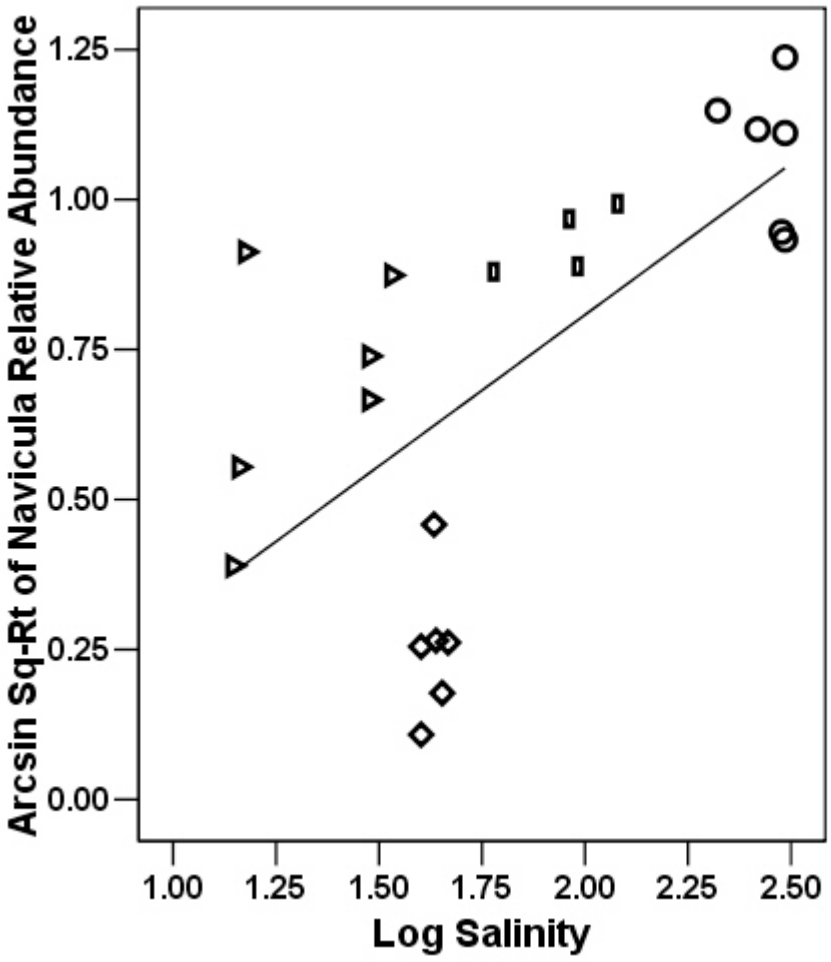


Figure 6. CCA sample scores biplot for all 22 samples. (Triangles=Clay Creek, Circles=ephemeral brine pool, Rectangles=small permanent pool, Diamonds=large permanent pool, Sal SD=log salinity standard deviation, log salinity=Log salinity (ppt))

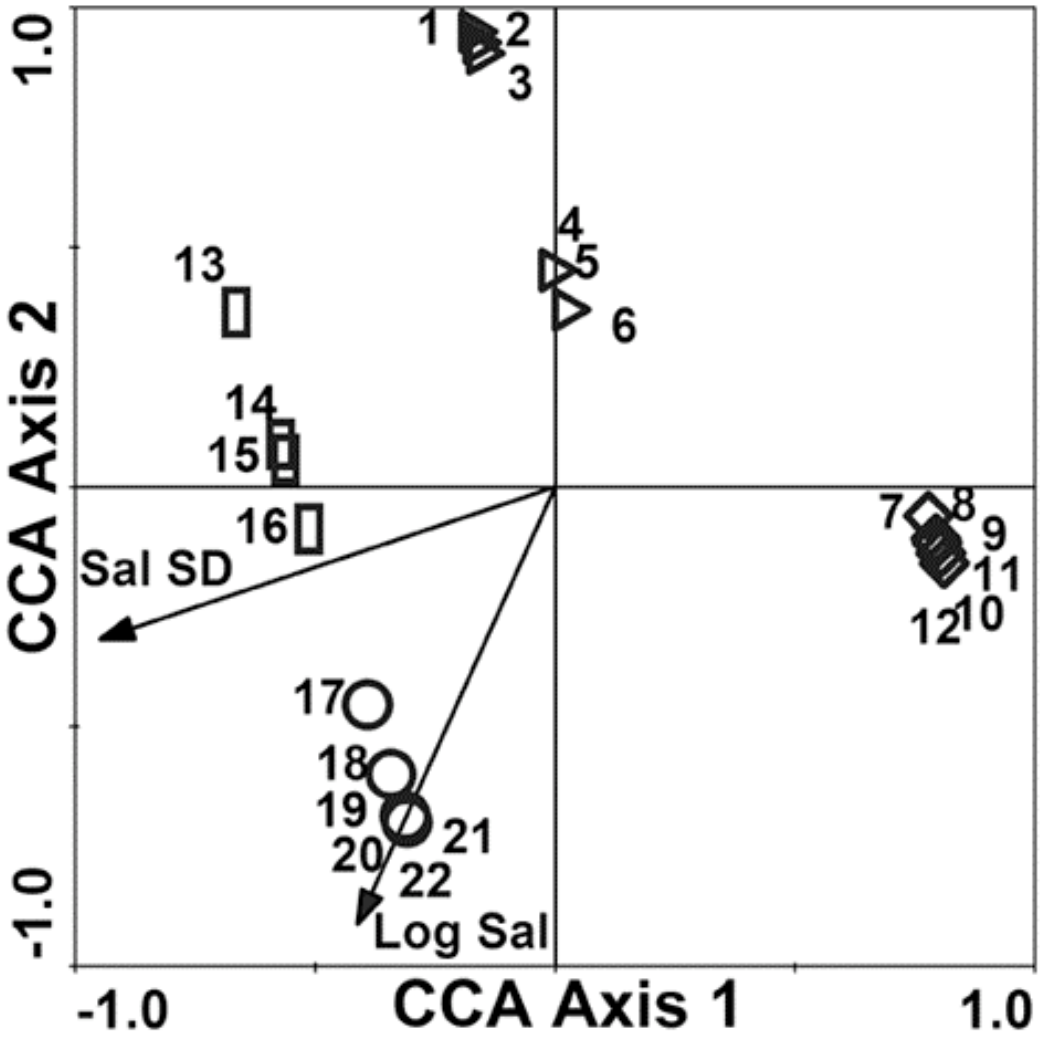
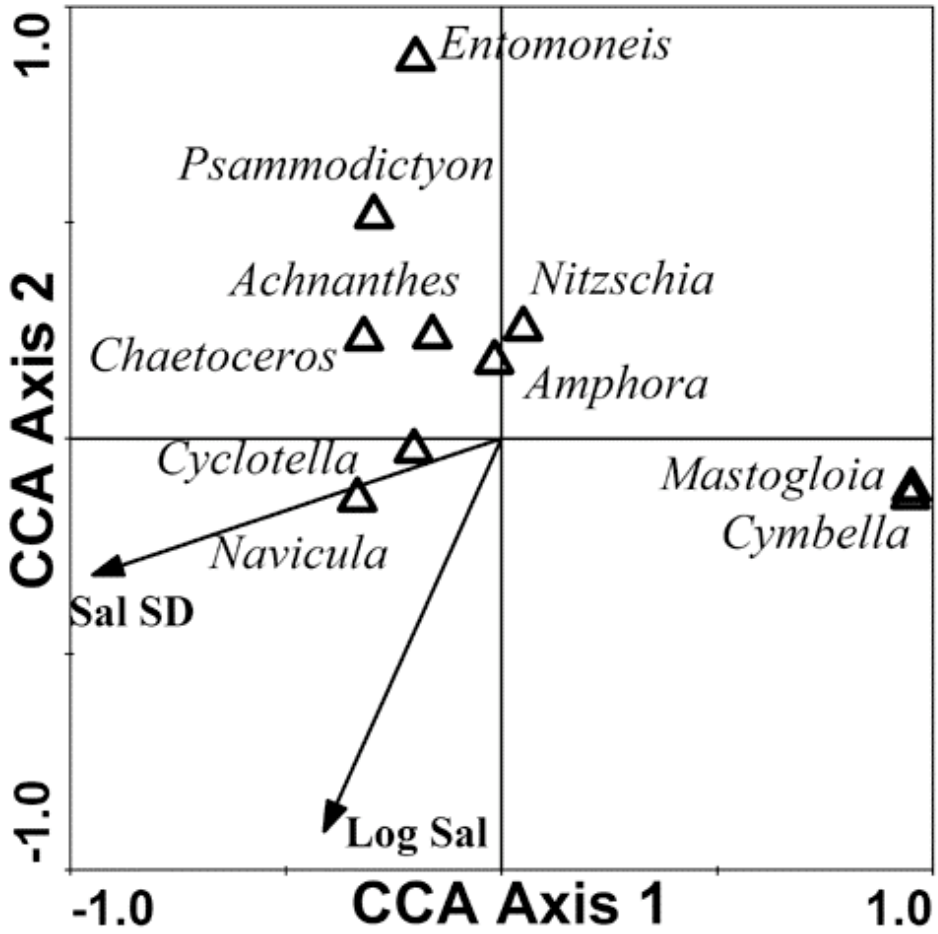


Figure 7. CCA biplots for all 22 samples showing species scores. (Triangles=Clay Creek, Circles=ephemeral brine pool, Rectangles=small permanent pool, Diamonds=large permanent pool, Sal SD=log salinity standard deviation, Log salinity=log salinity (ppt))



CHAPTER 2

DIATOM SPECIES DIVERSITY AND COMMUNITY COMPOSITION IN RELATION TO SALINITY AT THE SALT PLAINS NATIONAL WILDLIFE REFUGE, ALFALFA COUNTY, OKLAHOMA

ABSTRACT

The Salt Plains National Wildlife Refuge (SPNWR) is a unique type of athalassic hypersaline habitat located in western Oklahoma. Salinity is highly variable both spatially and temporally, varying from freshwater up to saturated brine (0-300 ppt). Four main types of habitats can be distinguished at the SPNWR based on their salinity magnitude and variability. I have identified a total of 107 species from twenty samples taken from these habitats. Diatom species richness, evenness and Shannon's diversity show no significant relationship with salinity. These observations suggest that several species have the ability to grow at the highly saline and variable conditions at the SPNWR. However these patterns may also be impacted by factors such as flooding, whereby individuals are deposited in unsuitable habitats. Analysis of diatom assemblages using CCA shows that site specific variables such as salinity variability and salinity magnitude account for most of the changes in assemblage composition. The SPNWR is a site that provides a high diversity of saline aquatic habitats both spatially and temporally. The presence of diatoms tolerant of such extreme saline conditions suggests that they have special osmoregulatory adaptations to such environments.

INTRODUCTION

Living organisms and the communities they compose are dynamic. Organisms are affected by the abiotic and biotic environment in which they live. By their presence organisms also affect the abiotic and biotic environment. However, despite this complexity in biological communities we are to observe general patterns that describe their structure and function, ultimately leading to a better understanding of the ecosystems of which they are a part (Huston 1994).

Saline aquatic habitats can be broadly categorized as either thalassic or athalassic. Further classification of these habitats has been based on the total concentration of salts and the biological communities which inhabit them. However, such classification systems are often inadequate to describe all saline habitats. Herbst (2001) recognized four categories of habitats based on their stability and strength of the salinity gradient. Indeed it seems that some saline habitats have such spatial and temporal variability as to fit in several categories of specific systems depending on when and where they are observed.

Several studies exist which investigate the relationship between diatom assemblages and salinity (Cumming et al. 1995, Herbst and Blinn 1998). Blinn (1993) revealed that ionic concentrations were related to diatom diversity in athalassic saline habitats across North America. Furthermore he showed that highest diversity occurred in sites with ionic concentrations greater than and ionic composition similar to that of seawater. Sylvestre et al (2001) show that fluctuation in salinity was one of the main factors controlling diatom assemblages in a hypersaline lagoon. Therefore it seems that salinity magnitude and variability are important factors shaping diatom assemblages in saline habitats.

The Salt Plains National Wildlife Refuge in north central Oklahoma is a dynamic athalassic saline habitat. Aquatic habitats at the SPNWR range from freshwater to hypersaline and vary spatially and temporally. Salts are composed mainly of NaCl. About 1/3 of the area of the SPNWR is covered with barren slat flats, with vegetation restricted to a thin zone along stream systems. These streams provide one of the few sources of water that rarely exceeds the salinity of seawater. Periodic flooding of these streams creates ephemeral drainage networks that after receding, form a series of small pools. These small pools are commonly found to have salinity up to saturation. Large pools with fairly stable salinities near that of seawater are also present. Viable diatoms have been found to occur at any site where sufficient water is available and salinity occasionally drops to a permissive concentration for cell growth. This paper describes diatom species diversity and community composition as they relate to salinity at the SPNWR.

METHODS

STUDY SITES

To begin an initial investigation of the diatoms of the SPNWR I collected substrate from the SPNWR in May-August 2004. An effort was made to collect samples that represent the diversity of aquatic habitat types and range in salinity. Aquatic sites in the study area span the range in salinity from freshwater to saturated brine (0-300 ppt). These sites are maintained by periodic flooding of the salt flats. During rains sufficient to produce local seasonal flooding (~5 cm in one day), many sites are inundated with freshwater which washes salt accumulations away. Although heavy rainfall can reduce surface salinities, moderate rain can increase salinity by concentrating surface salt deposits into low lying areas. After the temporarily reduced salinities following a flood,

surface waters begin to increase in salinity at a rate dependent on total evaporation. During dry periods subsurface brine percolates up through Quanternary sand and deposits NaCl on the surface. The flats thus rarely, if ever, dry completely, and have a moisture content of approximately 13-19% by weight (Major et al. 2005; Kirkwood et al. *in press*).

Throughout the sampling season I recognized four categories of sites; large permanent pools (LPP), small permanent pools (SPP), ephemeral brine pools (EBP) and flowing perennial streams (FPS). Sites were placed in each category to reflect similarities in overall salinity (ppt), temporal salinity variability, and the permanence of each site (Potter et al. 2006). These four categories of aquatic habitats at the SPNWR are maintained by surface fluvial processes as well as groundwater flow. Figure 8 shows the relative locations of each of the four site types at the SPNWR.

I found only one site that fit into the category of LPP. The LPP was located on the northwest corner of the salt flats, just south of the Salt Fork of the Arkansas river. This pool was about 1.5 km in length, with and average depth of ~0.5 m. The conditions of this site are characterized by having moderate and stable salinities. The pool is surrounded by grassland on all sides except for the eastern end, which are salt flats. The salt flats in this area are covered with extensive microbial mat communities up to 1 cm in thickness. Although the soil surrounding the pool becomes encrusted with salts, the pool itself has never been observed to exceed 50 ppt. The permanence and relatively low salinity of this site is assumed to be related to its proximity to the Salt Fork river, which dilutes the salinity of the ground water in the region. This pool has never been observed to go dry, and during periods of heavy rain, may gently flow into the Salt Fork river.

SPP sites generally form near streams in areas that are scoured during flood events, creating long depressions filled with water. The feature unique to SPP sites is there somewhat stable but high salinities. The salinity of these pools is higher and fluctuates more than that of the LPP, but does not reach saturated conditions, or does so rarely. The stability in salinities is attributed to their close hydrological connection with the streams where they have formed. The salinities at these FPS sites are typically low (< 30 ppt), and stable. During floods these streams can inundate a significant area of the salt flats.

Ephemeral brine pool (EBP) sites occur in the floodplain of the creeks but at a greater distance than the SPP sites. EBP sites are characterized by strong variability in salinity from freshwater up to saturated brine. I have observed ephemeral brine pool sites to go from freshwater to saturated brine in a period of two weeks after a flood. EBP sites are often formed in low lying areas of ephemeral drainages which flow only during flood events. Some EBP sites are located in areas that have been scoured below the level of the water table, allowing them to persist through long dry periods. EBPs especially those connected to the water table, characteristically accumulate salt crusts that can reach 3 cm in thickness.

Sampling and analysis

I used a turkey baster to collect the top centimeter of sediment along with 50 ml of water. Sample processing was modified from Battarbee *et al*. (2001). Before preservation with formalin, salinities were measured dwerectly from each sample using a handheld refractometer. Samples were prepared for microscopy by oxidizing a portion of

the sediment and mounting the cleaned material onto microscope slides. Oxidation was carried out by heating the sample with 30 ml of 30% H_2O_2, then adding 15 ml HCl. Heating of the mixture was continued until sample became clear and there was no sign of frothing. The cleaned mixture was then centrifuged and rinsed with deionized water for 6 cycles or until the mixture was neutral in pH. The resulting cleaned sample was then shaken, diluted and dried on coverslips in a setting free of air currents to ensure uniform distribution of sediment and diatom frustules. The coverslips were then mounted to slides using the mountant Naphrax. In the case of large amounts of fine sediments or diatom valves, the cleaned sample was further diluted until a desirable amount for counts was present on the coverslip.

Diatom counts were carried out along transects on coverslips until a minimum of 300 valves were counted and identified. In samples taken at EBP sites several transects were often necessary to get the 300 valve count. Identifications were made following Krammer and Lange-Bertalot (1999a, b, 2004a, b), Patrick and Reimer (1966 and 1975), and Round et al. (1990). I based taxonomic identifications on morphological features visible in the light microscope. Valve outline, striae density and pattern, nature of the raphe, length and width were the main morphological characters used. In many cases I could not find species descriptions matching with diatoms I encountered. In some situations the species was close to known taxa, in which case I used cf to indicate closest matching taxon. In other cases diatoms were sufficiently different from described taxa that I simply labeled them by species number as a distinct unnamed species. This procedure of fine-grained taxonomy is advocated as a more accurate measure of diatom

species diversity (Mann 1999, Kociolek and Spaulding 2000, Kociolek and Stoermer 2001).

Due to time limitations a subset from all samples taken were used in this study. I selected sub-samples to be used by grouping all samples into one of the four site categories LPP, SPP, EBP and FPS. I then randomized samples within each of these groups using a spreadsheet program. I chose the top ranking sample from each category to begin the investigation of samples. Since I was interested in the effects of salinity I chose four subsequent samples in each category based on their ability to represent the range in salinity of each category. I investigated a total of 20 samples, with five representing each site category.

I performed several analyses to investigate the relationships between diatom species diversity with salinity. Diatom species diversity was measured using richness, evenness and Shannon's diversity. Although Shannon's diversity is a measure of both richness and evenness I deemed it useful because of its commonness in the literature. Potential explanatory variables included day of year, and ln salinity (ppt). I used multiple linear regressions on each measure of diversity using both explanatory variables. Simple linear regressions were then used to investigate the relationship between salinity and the three measures of diversity.

I investigated the composition of diatom assemblages using several Canonical correspondence analysis (CCA). CCA is an ordination method which directly links community data and associated environmental variables (ter Braak 1988). I used ln salinity (ppt) as a continuous environmental variable. I also used the four site categories LPP, SPP, EBP and FPS as dummy variables. Species data were entered as relative

abundance values for each sample. CCA was performed in the program Canoco for Windows version 4.5 (ter Braak and Šmilauer 2002).

RESULTS

DIATOM SPECIES DIVERSITY

From the 20 samples used in this investigation I identified 107 species and varieties. Table 2 summarizes the relative abundances of the 107 species for each site type and all sites combined. The three most species-rich genera were *Navicula* with 30, *Nitzschia* with 26 and *Amphora* with 14 species. Of the 107 species found, 22 had relative abundances of at least 1% for all samples combined and accounted for about 82% of all diatoms counted.

Table 3 summarizes diversity and salinity values for the four habitat types. The highest species richness was found at the FPS sites, with a total of 80 taxa recorded. Of these 80 taxa present at FPS, EBP shared 72%, SPP shared 78% and LPP shared 73%. Of all species encountered 12 were found at all sites, while 36 were found at only one site. The LPP site had the lowest richness with a total of 26 species recorded. The results of three independent linear regressions show that species richness (Figure 9), evenness (Figure 10) and Shannon's diversity (Figure 11) were not significantly related to salinity for all samples (p's>0.05). Multiple regressions using the diversity measures with salinity and day of year also show no significant relationship ($p>0.05$; not shown).

ASSEMBLAGE STRUCTURE

All CCA axes were significant after Monte Carlo tests with 499 permutations. Here I interpret only the first two axes. Figure 12 shows the CCA biplot for the 20

samples used in the study and environmental variables. Salinity correlates negatively with both axis one (r=-0.35) and axis 2 (=r-0.46). CCA axis-1separates each site type and seems to represent some site specific variables, grouping FPS, SPP and EBP close together on the left side of the diagram and LPP to the far right. Axis two orders sites based on salinity with the lowest salinity site FPS at the top and the saltiest site EBP at the bottom.

Figure 13 is a CCA diagram showing diatom species and environmental variables. CCA axis one groups species by sites at which they most commonly occur. Species on the far right such as *Rhopalodia musculus* and *Mastogloia pumilla* are dominant members of the LPP assemblage. Species located in the center of the diagram such as *Navicula minima*, *Navicula bulnehmii*, and *Cyclotella meneghiniana* are common to all sites. Species found on the left side of the diagram are those that are dominant at either FPS, SPP or EBP. The species found on the left of the diagram are further separated by axis two. Species typically found in high abundance in FPS samples such as *Navicula salinarium* and *Psamodictyon constrictum* are found in the upper left of Figure 4. Species on the lower left of the diagram such as *Navicula digitoradiata* and *Navicula cincta* are found in highest abundance at the EBP and SPP sites.

DISCUSSION

Diatoms occur at the SPNWR at salinities ranging from near freshwater up to saturated brine (3-300ppt). Although many studies suggest a negative relationship between diatom species diversity and salinity, my SPNWR data show that salinity has no significant effect on diatom species richness, evenness or Shannon's diversity.

In previous work on diatom genus diversity at the SPNWR Potter et al. (2006) showed that while genus richness has no relationship, Simpson's diversity was negatively correlated with salinity. The observed drop in Simpson's diversity was due to a loss of evenness of genera in saltier samples. This drop in evenness does not occur with diatom species.

High salinity sites at the SPNWR are dominated by the species of the genus *Navicula*. However this dominance is shared by several *Navicula* species, resulting in high evenness proportionate to species richness. Therefore, several species of the genus *Navicula* such as *Navicula cincta* and *Navicula digitoradiata* are well adapted to the high and variable salinity at the EBP and SPP, sharing dominance at these sites. This suggests that these species have special osmoregulatory adaptations to rapidly changing salinity.

The LPP site, which is of moderate salinity is dominated by a single species, *Mastogloia pumila*. This dominance by a single species results in low diversity values for LPP, a site that if salinity were controlling diversity, would be expected to have higher values compared to the EBP and SPP. Therefore, sites with moderate and stable salinity do not have significantly different diversity values than sites with high and variable salinity.

The high species richness of the EBP, SPP and FPS, may be a result of periodic deposition of species from distant sites. These species likely do not prefer the saline conditions where they are found. The FPS provides a good example of how this may be true. Of the 80 species found at the site, only 20 reach a combined relative abundance above 1%. Thus, most species are in low abundance, reflecting that the conditions are sub-optimal for their growth. Many of the rare species found at FPS are reported as

freshwater taxa, while the more abundant ones are typical brackish water taxa. It is likely that many of the freshwater taxa wash in from upstream sites with lower salinities during heavy runoff.

Samples from the EBP and SPP sites show a similar pattern. Species found in EBP and SPP samples are a subset of the more abundant ones present in the FPS. It is likely that there is constant recruitment from the FPS during the periodic floods, depositing species into the EBP and SPP sites. The rapid increase in salinity after the flood restricts the growth of many of these species, while the several *Navicula* species tolerant of high salt conditions are able to grow.

The recognition of habitat types based on salinity magnitude and variability within the SPNWR seems to be supported by species composition of diatom assemblages.

Athalassic saline habitats are common across western North America, however these habitats display site specific characteristics that distinguish them. The SPNWR in Oklahoma displays a high degree of spatial and temporal variability in salinity conditions. The ability to rapidly acclimate to extreme changes in salinity in such an isolated habitat may have lead to the evolution of unique diatom taxa with restricted geographic distributions. An investigation the diatom floras of such isolated saline habitats could reveal patterns of diatom biogeography as well as shed light on the evolutionary significance of their adaptations to athalassic hypersaline habitats.

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Table 2. Summary of diatom species along with relative abundances for each site

	Species	Code	FPS	EBP	SPP	LPP
Navicula	*salinarium*	Navisali	13.72	1.80	2.87	0.00
Nitzschia	sp. 2	Nitz2	13.32	2.13	4.67	0.00
Navicula	sp. 2	Navi2	7.06	0.66	0.00	0.00
Psamodictyon	*constrictum*	Psamcons	6.26	0.73	1.33	0.00
Amphora	sp. 6	Amph6	5.33	0.80	7.27	2.19
Nitzschia	*reversa*	Nitzreve	5.26	0.00	0.07	0.00
Amphora	*coffeaeformis*	Amphcoff	4.26	0.47	0.13	2.00
Navicula	*cryptocephala*	Navicryp	3.73	0.40	0.20	0.06
Amphora	*acutiuscula*	Amphacut	3.46	0.20	2.93	22.79
Nitzschia	sp. 1	Nitz1	3.20	0.00	0.80	0.00
Nitzschia	*fonticola*	Nitzfont	2.73	0.80	0.33	0.00
Nitzschia	*palea*	Nitzpale	2.60	2.53	6.53	0.00
Amphora	sp. 2	Amph2	2.53	0.00	0.47	0.00
Navicula	*cincta*	Navicinc	2.26	28.32	32.07	2.00
Amphora	sp. 12	Amph12	2.26	0.07	0.00	0.00
Amphora	sp. 5	Amph5	1.86	0.00	0.13	4.20
Surirella	*striatula*	Suristri	1.60	0.00	0.33	0.00
Amphora	sp. 3	Amph3	1.33	2.13	0.07	0.84
Navicula	*bulnheimii*	Navibuln	1.00	0.07	1.27	1.10
Nitzschia	*microcephala*	Nitzmicr	1.00	0.07	0.13	0.00
Amphora	sp. 1	Amph1	0.93	0.00	1.13	0.13
Navicula	sp. 7	Navi7	0.87	0.20	0.27	0.00
Navicula	*eidrigiana*	Navieidr	0.87	0.00	0.13	0.00
Nitzschia	*pura*	Nitzpura	0.80	0.00	0.00	0.00
Cyclotella	*meneghiniana*	Cyclmene	0.73	1.60	0.00	0.84
Navicula	sp. 4	Navi4	0.67	1.06	1.00	0.00
Achnanthes	sp. 1	Achn1	0.60	1.06	0.40	0.52
Nitzschia	*bacilliformis*	Nitzbaci	0.53	0.00	0.00	0.32
Navicula	*spicula*	Navispic	0.47	0.00	1.00	0.19
Navicula	sp. 8	Navi8	0.47	0.00	0.00	0.00
Navicula	*minima*	Navimini	0.40	0.40	0.80	0.90
Entomoneis	*paludosa subsalina*	Entopalu	0.40	0.07	0.07	0.06
Achnanthes	*biasoleattiana*	Achnbias	0.40	0.00	1.40	0.00
Hippodonta	*hungarica*	Hipohung	0.33	1.40	0.13	0.00
Navicula	sp. 6	Navi6	0.33	0.47	0.07	0.00
Caloneis	*molaris*	Calomola	0.33	0.13	0.20	0.06
Navicula	sp. 10	Navi10	0.33	0.00	0.07	0.00
Nitzschia	*thermaloides*	Nitzther	0.33	0.00	0.00	0.00
Nitzschia	sp. 6	Nitz6	0.33	0.00	0.00	0.00
Entomoneis	sp. 1	Ento1	0.33	0.00	0.00	0.00

Table 2. continued

	Species	Code	FPS	EBP	SPP	LPP
Nitzschia	*frustulum*	Nitzfrus	0.27	0.13	0.53	1.10
Amphora	sp. 9	Amph9	0.27	0.00	0.00	0.00
Nitzschia	sp. 3	Nitz3	0.27	0.00	0.00	0.00
Amphora	sp. 7	Amph7	0.20	0.80	0.00	0.00
Nitzschia	*hungarica*	Nitzhung	0.20	0.66	0.00	0.00
Nitzschia	*bergii*	Nitzberg	0.20	0.07	0.00	10.91
Achnanthes	*levanderi*	Achnleva	0.20	0.00	0.00	0.00
Nitzschia	sp. 7	Nitz7	0.20	0.00	0.00	0.00
Navicula	sp. 5	Navi5	0.20	0.00	0.00	0.00
Surirella	sp. 2	Suri2	0.20	0.00	0.00	0.00
Centric	sp. 1	Cent1	0.20	0.00	0.00	0.00
Gyrosigma	*nodiferum*	Gyronodi	0.13	0.07	0.00	0.00
Plagiotropis	*arizonica*	Plagariz	0.13	0.07	0.00	0.00
Cocconeis	*disculus*	Coccdisc	0.13	0.00	0.47	0.00
Diatoma	*vulgaris*	Diatvulg	0.13	0.00	0.07	0.00
Navicula	sp.18	Navi18	0.13	0.00	0.07	0.00
Achnanthes	*lemmermannii*	Achnlemm	0.13	0.00	0.00	0.00
Navicula	sp. 3	Navi3	0.13	0.00	0.00	0.00
Navicula	*digitoradiata*	Navidigi	0.07	29.92	8.40	0.00
Navicula	*salinicola*	Navisali	0.07	8.84	1.40	0.00
Bacillaria	*paradoxa*	Bacipara	0.07	0.53	0.07	0.00
Nitzschia	sp. 8	Nitz8	0.07	0.53	0.00	0.00
Fallacia	*pygmaea*	Fallpygm	0.07	0.13	0.07	0.00
Caloneis	*amphisbaena*	Caloamph	0.07	0.13	0.00	0.00
Surirella	*angusta*	Suriangu	0.07	0.07	0.07	0.00
Nitzschia	*commutata*	Nitzcomm	0.07	0.07	0.00	0.00
Surirella	*brebissonii*	Suribreb	0.07	0.07	0.00	0.00
Amphora	*perpusilla*	Amphperp	0.07	0.00	0.33	0.00
Navicula	sp. 9	Navi9	0.07	0.00	0.33	0.00
Surirella	sp. 1	Suri1	0.07	0.00	0.27	0.00
Chaetoceros	*spore*	Chaespor	0.07	0.00	0.20	0.32
Nitzschia	*scalpelliformis*	Nitzscal	0.07	0.00	0.13	0.00
Navicula	*radiosa*	Naviradi	0.07	0.00	0.00	0.00
Amphora	*pediculus*	Amphped	0.07	0.00	0.00	0.00
Nitzschia	*laevis*	Nitzlaev	0.07	0.00	0.00	0.00
Navicula	*eplanata*	Naviepla	0.07	0.00	0.00	0.00
Navicula	*circumtexta*	Navicirc	0.07	0.00	0.00	0.00
Navicula	sp.17	Navi17	0.07	0.00	0.00	0.00
Surirella	sp. 3	Suri3	0.07	0.00	0.00	0.00
Cyclotella	sp. 1	Cyclo1	0.07	0.00	0.00	0.00

Table 2. continued

	Species	Code	FPS	EBP	SPP	LPP
Navicula	*cinminuta*	Navicinm	0.00	3.79	2.87	0.00
Navicula	*gregaria*	Navigreg	0.00	2.93	0.67	0.00
Nitzschia	*pusilla*	Nitzpusi	0.00	0.66	0.00	0.00
Amphora	sp. 11	Amph11	0.00	0.66	0.00	0.65
Luticola	*cohnii*	Luticohn	0.00	0.60	0.00	0.00
Navicula	sp. 19	Navi19	0.00	0.47	7.00	0.00
Nitzschia	*compressa*	Nitzcomp	0.00	0.33	3.27	0.00
Gomphonema	*parvulum*	Gompparv	0.00	0.20	0.00	0.00
Surirella	*ovalis*	Gompparv	0.00	0.20	0.00	0.00
Navicula	sp.15	Navi15	0.00	0.13	2.93	0.00
Luticola	*mutica undulata*	Lutimuti	0.00	0.13	0.00	0.00
Diploneis	*puella*	Diplpull	0.00	0.07	0.00	0.00
Opephora	*martyi*	Opepmart	0.00	0.07	0.00	0.00
Nitzschia	*lanceola minuta*	Nitzlanc	0.00	0.07	0.00	0.00
Nitzschia	*clausii*	Nitzclau	0.00	0.07	0.00	0.00
Navicula	sp*. 20*	Naviques	0.00	0.00	0.67	1.42
Navicula	sp. 11	Navi11	0.00	0.00	0.47	0.00
Nitzschia	*modesta*	Nitzmode	0.00	0.00	0.40	0.00
Achnanthes	sp. 2	Achn2	0.00	0.00	0.40	0.00
Amphora	sp. 10	Amph10	0.00	0.00	0.33	0.00
Cocconeis	*placentula*	Coccplac	0.00	0.00	0.20	0.00
Rhopalodia	*musculus*	Rhopmusc	0.00	0.00	0.07	2.39
Nitzschia	*filiformis*	Nitzfili	0.00	0.00	0.07	0.00
Cymbella	*pusilla*	Cymbpusi	0.00	0.00	0.00	3.81
Mastogloia	*pumila*	Mastpumi	0.00	0.00	0.00	40.80
Nitzschia	sp. fragment	Nitzfrag	0.00	0.00	0.00	0.06
Navicula	*cf9*	Navicf9	0.00	0.00	0.00	0.32

Table 3. Mean salinity (ppt), richness, Shannon's diversity and evenness values for the four site types

	Site			
	FPS	EBP	SPP	LPP
Salinity	16.1 ± 9.64	191.6 ± 110	71.5 ± 23.29	42.6 ± 6.8
Richness	29.8 ± 9.2	19.8 ± 8.07	21.4 ± 5.86	12.8 ± 2.59
Shannon	2.56 ± 0.18	1.84 ± 0.68	1.94 ± 0.67	1.34 ± 0.53
Evenness	0.76 ± 0.02	0.62 ± 0.17	0.63 ± 0.18	0.52 ± 0.17

Figure Legends

Figure 8. Aerial photo showing areas where each site type typically occurs at the SPNWR. The inset shows the location of the SPNWR within Oklahoma. LPP=large permanent pool, FPS=flowing perennial stream, SPP=small permanent pool, EBP=ephemeral brine pool

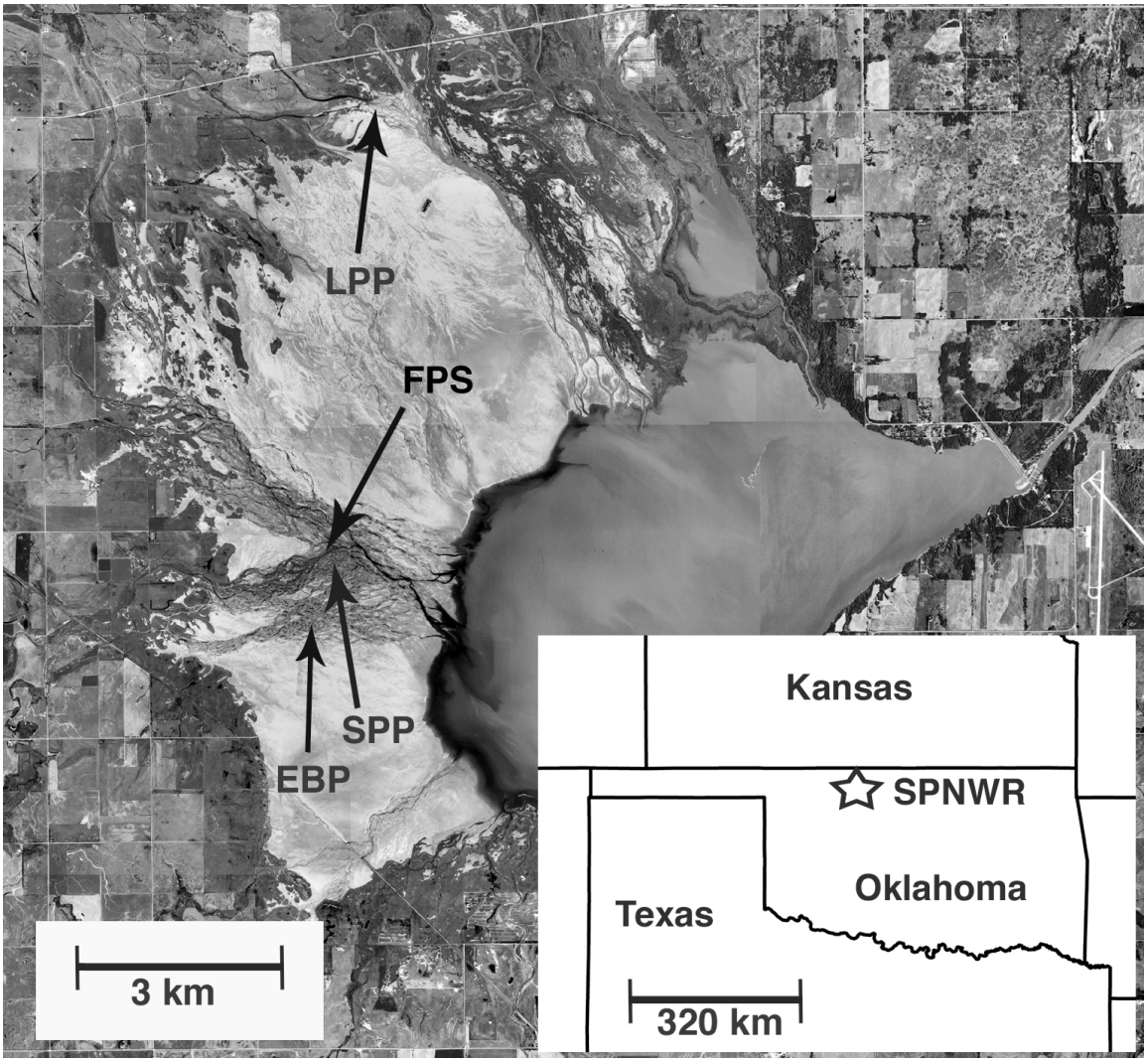


Figure 9. Relationship between diatom species richness and log salinity (ppt) for all samples

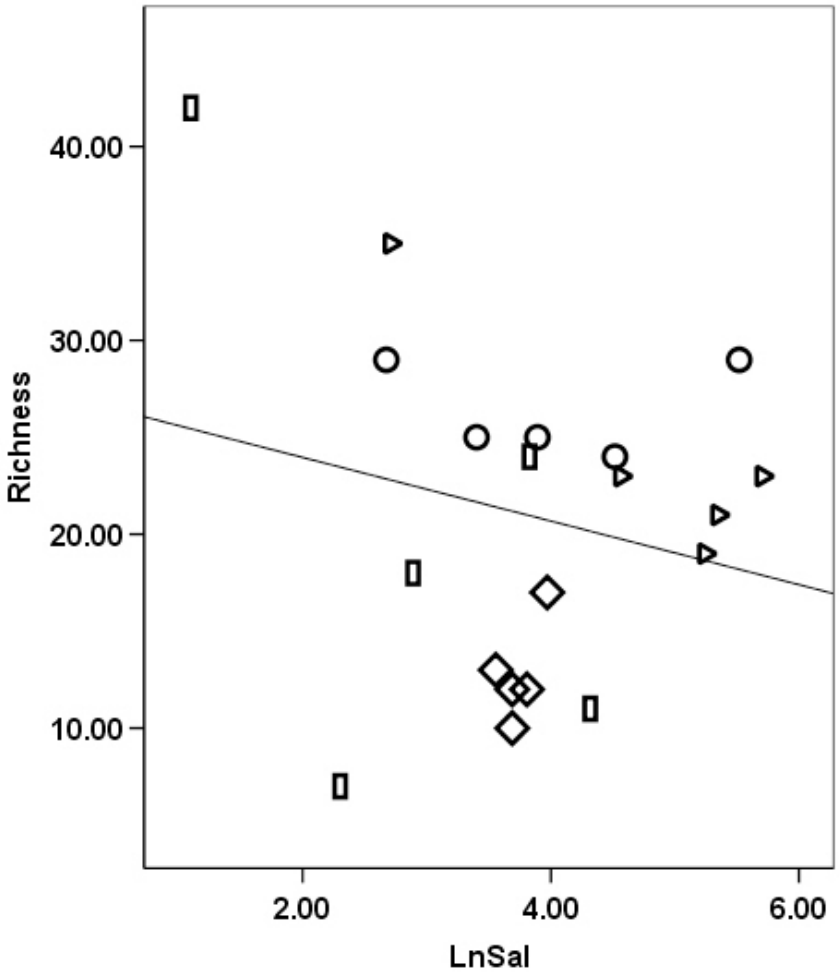


Figure 10. Relationship between diatom species evenness and log salinity (ppt) for all samples

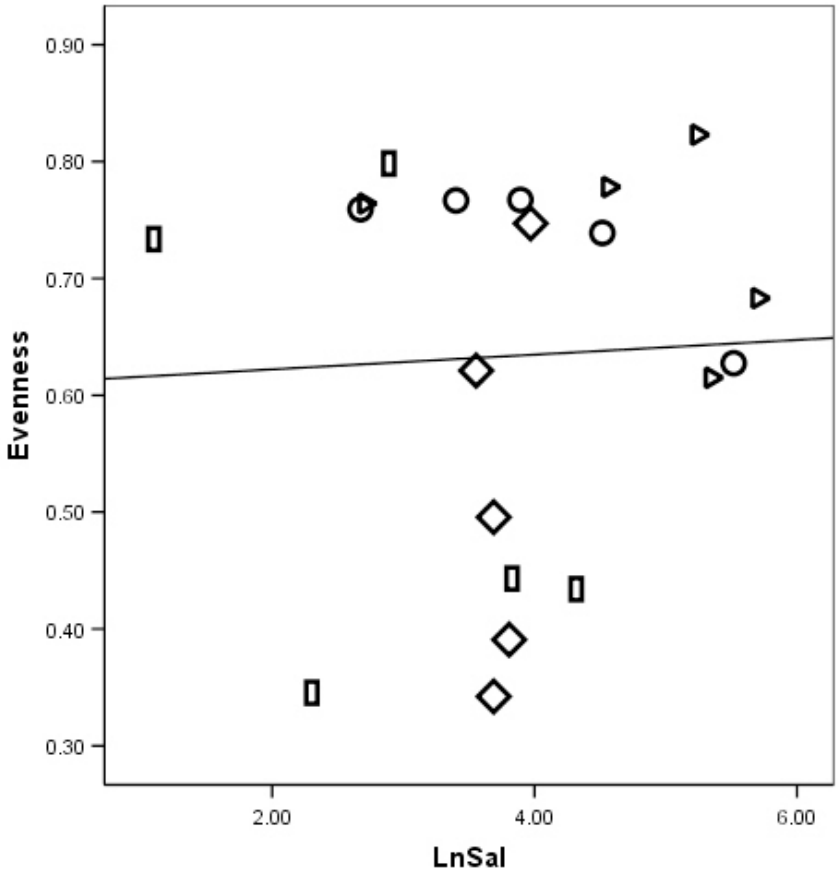


Figure 11. Relationship between Shannon's diversity of diatom species and log salinity (ppt) for all samples

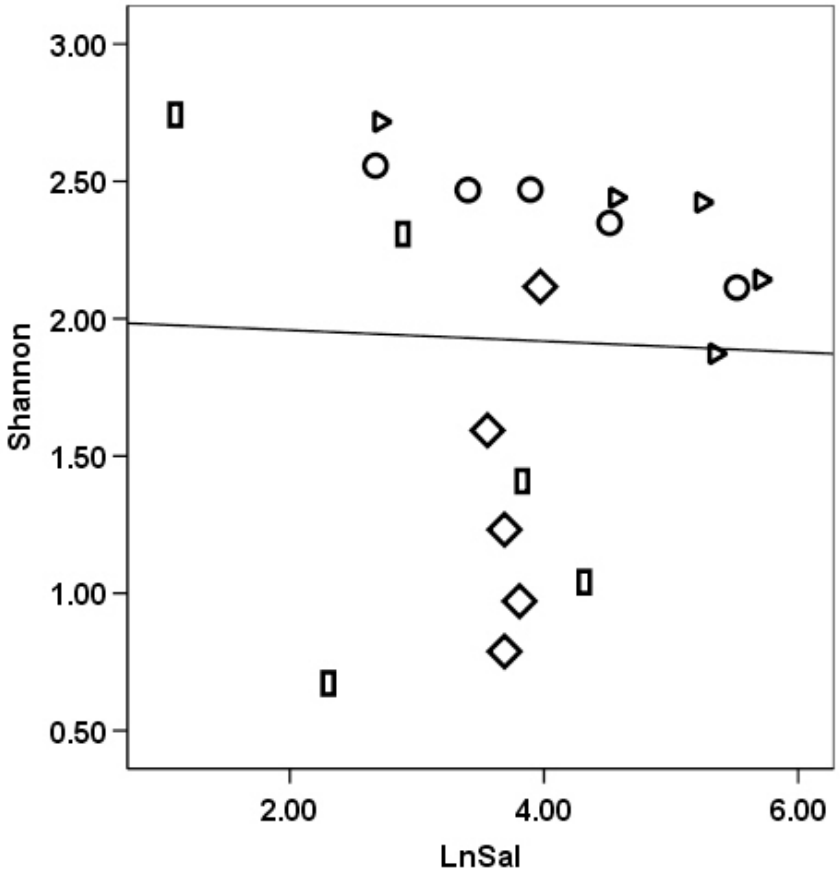


Figure 12. CCA biplot showing samples grouping by habitat type and salinity (ppt)

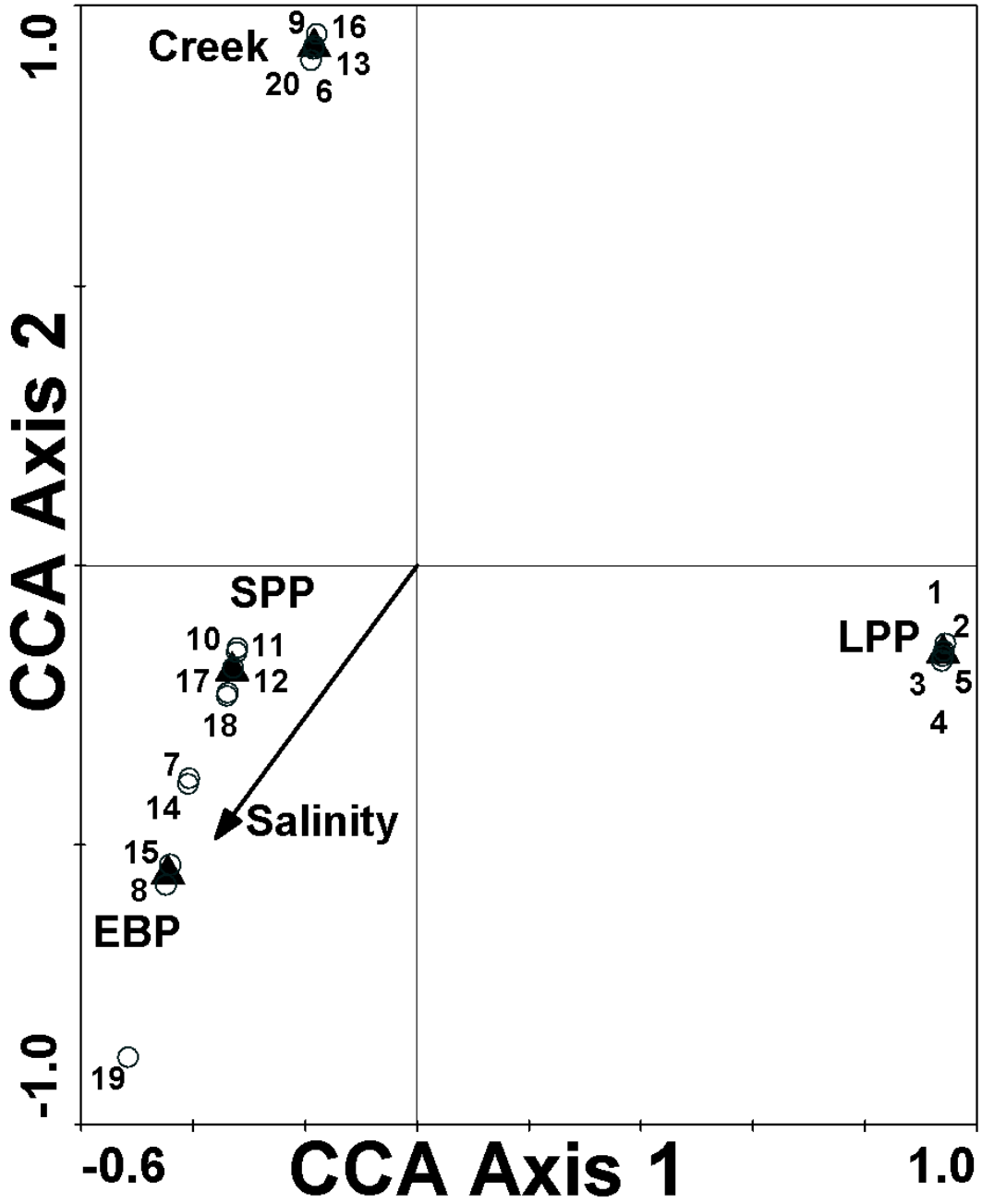
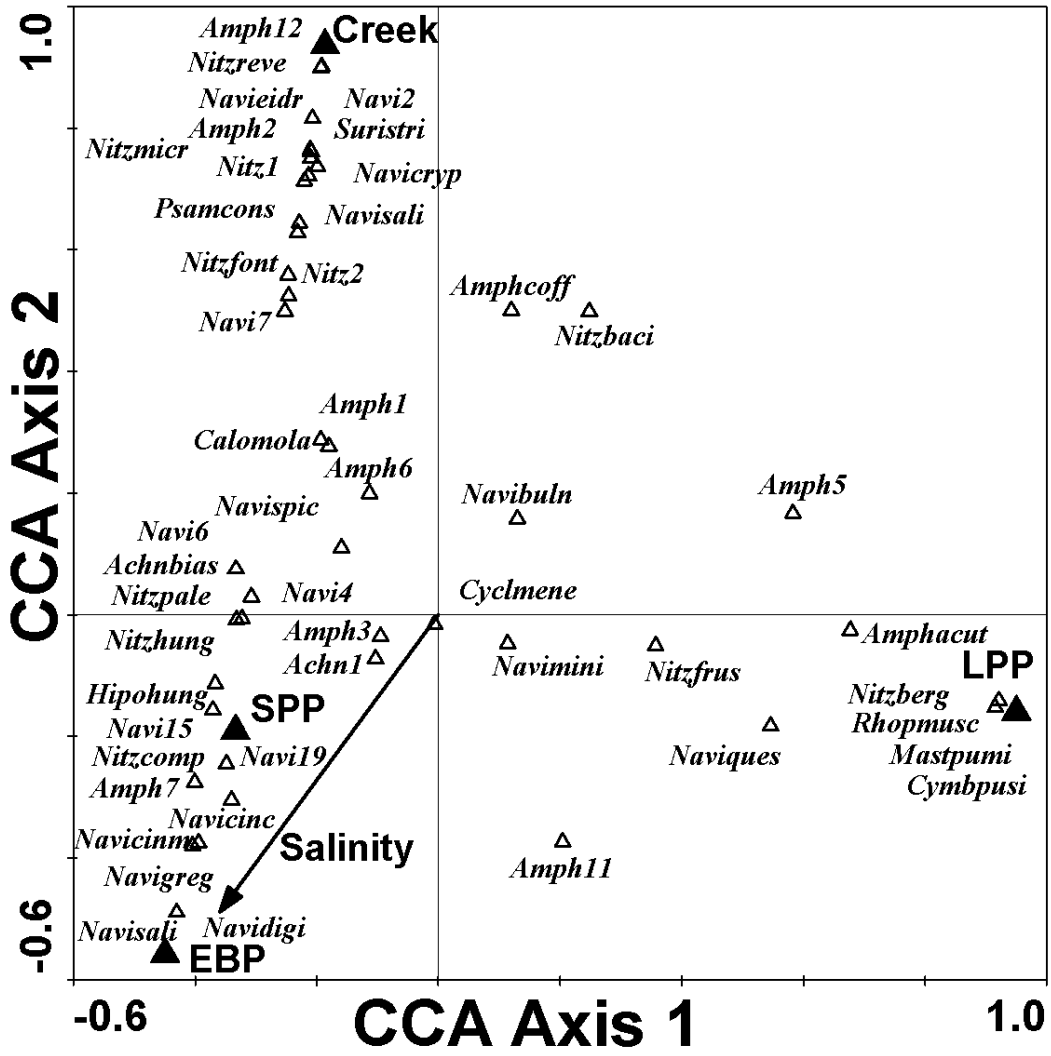


Figure 13. CCA biplot showing diatom species, habitat types and salinity (ppt)



CHAPTER 3

THE DIATOM FLORA OF THE SALT PLAINS NATIONAL WILDLIFE REFUGE

ABSTRACT

The Salt Plains National Wildlife Refuge (SPNWR) is a dynamic athalassic hypersaline habitat located in northwestern Oklahoma in Alfalfa County. Diatoms have been found to occupy sites ranging from freshwater up to saturated brine. Aquatic habitats at the SPNWR can be characterized into four main categories small permanent pools (SPP), large permanent pools (LPP), ephemeral brine pools (EBP), and flowing perennial streams (FPS). Though many species are widespread, each of these habitat types has a unique assemblage. I present here light micrographs of taxa found from sites at the SPNWR, with some notes about their ecological preferences.

INTRODUCTION

Diatoms are important primary producers in most aquatic habitats. They impact cycles such as the carbon and silica cycles, and can respond quickly to environmental change. These qualities have led to diatoms being used as model organisms to assess environmental degradation in modern ecosystems, as well as reconstructing past environments. Currents estimates of global diatom species diversity range from 2×10^4 to 2×10^5. The difference in the two numbers is mainly due to the level of taxonomic refinement.

Diatomists, especially recently, have began to notice the importance of subtle differences in diatom valve morphology that previously had been overlooked. While diatom taxonomy has almost entirely been based upon the morphology of the frustule, it seems that at least in some cases this morphological species concept has been too broadly defined. Mann and Droop (1996) found six phenodemes within the species *Sellaphora pupula*, which they recommend to be designated as separate species. This use of fine-grained taxonomy makes an already difficult task even harder, by forcing the investigator to document the subtle but consistent morphological characteristics that may denote a separate species. The increased taxonomic resolution gained by such fine-grained taxonomy will begin to reveal morphologically cryptic taxa, as well as give us a better understanding of diatom biogeography (Mann 1999).

In this study I investigate the diatom flora of the Salt Plains National Wildlife Refuge in western Oklahoma, Alfalfa County. This site is the result of Permian salt deposits percolating up through the sandy soil and eventually into the surface waters. Diatoms have been found at sites ranging in salinity from freshwater up to saturated

brine. I identified a total of 107 species and varieties of diatoms. I present here light micrographs of all taxa with notes on their taxonomy and ecology.

METHODS

STUDY SITE

The SPNWR covers an area of about 65 km^2. The samples used in this study were taken in an area that is a flat expanse of salt encrusted sand. Salt accumulates on the soil surface to form a crust up to 3 cm thick, or dissolves in pools and streams. Several streams dissect the salt flats, flowing to the east into the Great Salt Plains Reservoir. These streams are the only source of low salinity water on the salt flat. Other aquatic habitats include pools that form immediately after rain events and periodic flooding of the streams. In terms of salinity these pools are the most dynamic habitats at the SPNWR. After floods recede these pools are filled with freshwater. However, depending on the total evaporation rate, these pools can reach saturated conditions in under two weeks.

Four habitat types can be distinguished at the SPNWR based on magnitude and variation in salinity, large permanent pools (LPP), small permanent pools (SPP), ephemeral brine pools (EBP) and flowing perennial streams (FPS). I found only one LPP at the SPNWR. The LPP is characterized by having a moderate and stable salinity. SPP sites are located near creeks, in areas that have been eroded during high flow forming a shallow depression. SPP sites have high but relatively stable salinities. EBP sites are located in the flood plain of the creek systems in ephemeral channel systems. These sites are sometimes located at the level of the water table and therefore persist through long dry periods. EBP sites have high and variable salinities.

SAMPLING AND ANALYSIS

I collected surface sediment samples from a diversity of aquatic habitats at the SPNWR throughout the summer of 2004, using a turkey baster. Samples consisted of a 50 ml mixture of sediment and water. Salinities were measured directly from each sample using a handheld refractometer. I used 3% formalin to preserve samples.

Samples were processed using methods to remove modified from Battarbee et al. (2001). A sub-sample of water and sediment was taken from each tube and mixed with 25 ml of 30% H_2O_2 and heated until frothing of the mixture subsided. Water was added as needed. The final step of oxidation was to add 15 ml of HCl. This step removed any carbonates present, as well as any residual organic matter. This mixture was then cooled and poured into 50 ml centrifuge tubes. Water was added to each tube to bring it up to 50 ml if necessary. Tubes were centrifuged at 200 RPM for 15 minutes, then the top 30 ml of supernatant was removed using an aspirator. This procedure was repeated at least 6 times, or until the resulting supernatant was at neutral pH. This cleaned diatom material was used for making mounted slides.

In order to make microscope slides for viewing diatoms, the cleaned diatom material was resuspended and diluted in deionized water until almost clear. The amount of water added is dependant upon the density of small particles in the cleaned material. The diluted suspension was then pipeted onto coverslips and allowed to dry overnight. The coverslips were then mounted in Naphrax.

Slides were observed at 1000x magnification on a Nikon E600 light microscope with phase contrast objectives. Diatoms were identified according to Krammer et al. (1999a and b; 2004 a and b), Patrick and Reimer (1966 and 1975), Round et al. (1990),

and Cumming et al. (1995). Photographs were taken of each taxon using a Nikon coolpix 5000 camera. A total of 20 samples with 5 from each of the four habitat types were used in this investigation, with 300 individuals counted on each slide. Relative abundances for taxa were calculated pooling the 5 samples for each habitat type.

RESULTS

In this investigation I identified a total of 107 species and varieties. Appendix A lists all taxa found in this investigation. Of these diatoms 12 were found at more than 90% of sites. 20 species accounted for 80% of all diatoms encountered. 36 species were found to occur at only one site. The most speciose genera were *Navicula*, *Amphora*, and *Nitzschia*. Most diatom species at the SPNWR are found in low abundance, and are also rare. The sites with the highest species richness were the FPS, with a total of 80 species. The site with the lowest species richness was the LPP, with a total of 26. Appendix B shows light micrographs of all taxa encountered in this study.

Distinct diatom assemblages were found to occur at each of the four site types in this study. The SPP, EBP and FPS sites were similar in species composition with SPP and EBP having a subset of species from FPS. LPP differed markedly from the other sites in species composition, having several dominant taxa that were not found at the other sites.

The diatom assemblages of the FPS share many taxa with the SPP and EBP sites. Of the 80 tax found at the FPS 21 were not found at the SPP and EBP sites. The most abundant taxa (relative abundance > 5%) at the FPS were *Navicula salinarium*, *Nitzschia*

sp. 2, *Navicula* sp. 2, *Psamodictyon constrictum*, *Amphora* sp.6, and *Nitzschia reversa*. Of these species all but *Amphora* sp.6 reach their highest relative abundances at the FPS.

The SPP sites are dominated by three taxa *Navicula cincta* and *Navicula digitoradiata*, and *Amphora* sp.6, with relative abundances of 32, 8 and 7% respectively. Both *Navicula cincta* and *Amphora* sp.6 reach their highest relative abundances at SPP sites. The EBP sites are dominated by *Navicula digitoradiata* and *Navicual cincta* with relative abundances of 30 and 28%, respectively.

Some diatom taxa such as *Mastogloia pumila* and *Cymbella pusilla* occur only at the LPP where they can be dominant in the assemblage (40 and 4% relative abundance, respectively). *Rhopalodia musculus* was found as a single valve at the SPP, while it reaches a relative abundance of 2.4% at the LPP.

DISCUSSION

Diatoms found at the SPNWR are a mixture of freshwater, marine, brackish and potentially new taxa. Patterns of abundance show that several species of *Navicula* are well adapted for life in the saltiest sites, but are able to survive at a range of sites. These species include *Navicula cincta* and *Navicula digitoradiata*. Euryhalinity of these *Navicula* species allows them to take advantage of rapidly changing salinities that are common at the SPNWR.

Some species such as *Mastogloia pumilla* are restricted in their distribution to sites with specific characteristics. Because it has such a limited range of suitable environmental conditions, *M. pumilla* does not occur at other sites, but is able to dominate when conditions are optimal. In general, the most successful diatoms at the

SPNWR are able to tolerate a broad range in salinities. The most widespread diatoms are those that can tolerate a wide range of conditions such as *Amphora* sp.6 and *Navicula cincta*.

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CHAPTER 4

DIATOM SIZE DISTRIBUTIONS IN FOUR BENTHIC SAMPLES FROM THE SOUTHWESTERN UNITED STATES

ABSTRACT

Traditional allometry has shown that many anatomical, physiological, and ecological traits scale as a function of organism size. Some research suggests that the scaling exponent of power functions used to describe allometric relationships supports the possibility of a universal biological scaling law. However, the value of this exponent is a matter of debate. In order to better understand the level of applicability for general allometric models, here I investigate the relationship between diatom abundance and biovolume in four benthic samples from the southwestern United States, and compare the results with those found for other organisms. Results from this study suggest that scaling exponents at small spatial scales vary such that neither the -3/4 nor the -3/2 predictions can be rejected, but at larger spatial scales -3/4 can be rejected.

INTRODUCTION

Allometric equations have been used to describe many characteristics of organisms including physiological, anatomical and ecological traits. Allometric relationships are based on a power function of the form $Y=Y_oM^b$, where Y is the dependent variable, M is body mass, b is a power exponent and Y_o is a normalization constant. The use of power law models to describe ecological scaling parameters has been viewed with some criticism (LaBarbera 1989), but more recent work suggests that such scaling relationships are universal to all organisms (West, Brown et al. 1997). Specific examples dealing with vascular plants (Enquist, Brown et al. 1998), mammals (Damuth 1981), and phytoplankton (Belgrano, Allen et al. 2002) suggest that population density scales as $M^{-3/4}$, a relationship which reflects metabolic constraints. Other workers suggest a more geometric model where density scales as $M^{-3/2}$ (Agusti, Duarte et al. 1987). The debate on universality of allometric relationships is not confined only to the nature of the relationship but also to their existence. Schmid et al (2000) report on the population density and body size in a stream community, stating that "Variation in the regression slope among different taxonomic groups indicates that these communities are not governed universally by a single ecological or energetic rule.". Clearly there is no consensus concerning a general scaling law. Due to these recent findings, interest in allometric relationships has increased and the results may eventually lead to an explanation of the mechanisms behind scaling in biology.

To date little work has focused on the allometric relationships of diatom assemblages (Baillie 1987). Belgrano et al. (Belgrano, Allen et al. 2002) suggest a $M^{-3/4}$ relationship for the density of phytoplankton and terrestrial plants. Here, my objective is

to report on the relationships I found between diatom abundance and biovolume in four benthic samples from the southwestern United States, and to compare these results to those presented in the literature.

METHODS

SAMPLES

The four samples used in this investigation were collected throughout the southwestern United States in 2004 and 2005. The first sample was taken from Eagle's Nest Lake State Park in the northeastern New Mexico. Eagles Nest Lake was constructed in 1918 and covers an area of 890 hectares. The sample consisted of near shore sediment and small clumps of macro algae. The second sample was collected from Salt Wash near Turnbow Cabin in Arches National Park in Utah. Salt Wash is one of the few permanent streams in Arches National Park, and as the name implies it accumulates gypsum and other salts from Salt Valley, which it drains. This sample was composed of sand sized sediment and periphyton material. The third sample was collected from a rock seep on the north rim of Grand Canyon National Park in Arizona. The seep was formed in a sandstone layer in the Supai Group. The sample consisted of scrapings from the seep including some carbonate precipitate. The fourth sample was collected from Boot Spring in Big Bend National Park in Texas. The sample was taken in an area of large potholes, where the streambed is formed of bedrock. The sample consisted of scrapings from the bedrock, macrophyte algae, and fine sediments. A summary of sample information is given in Table 4.

CELL COUNTS AND MEASUREMENT

Diatom samples were prepared and mounted according to Batterbee et al. (Battarbee et al. 2001). Upon cleaning, dilutions were made of the cleaned sample to provide an optimum number of valves for counting and making measurements. Cell counts were carried out along transects on each slide until 500 individual valves were counted. Each valve was identified to the highest taxonomic unit possible, usually species.

Cell biovolumes were calculated according to Hillebrand et al. (1999). Most valves were visible in valve view only allowing for the x and y axis to be easily measured. If girdle view was not available for a taxon, then the Vernier scale on the fine focus knob was used to measure the distance from the valve face to the edge of the mantle. Average biovolume for the sufficiently abundant taxa was calculated by using the modal linear dimensions (Hillebrand et al 1999) based on 5 individuals. In rare taxa it was sometimes necessary to use fewer measurements due to scarcity of valves.

DATA ANALYSIS

Cell counts and volumes for each species at each site were used for data analysis. Since the focus of the study was on the patterns of diatom size in relation to abundance, species abundances were grouped into 200 μm^3 size classes. Data analyses were performed for individual sites as well as combining abundances of all size classes for all sites. For both analyses $\log_{10}$- transformed size classes and biovolumes were used in least squares regressions to determine the scaling exponent. Only size classes with values greater than zero could be transformed.

RESULTS

Information for the site of each sample is given in Table 4. The Eagles Nest Lake sample contained the highest total biovolume, mean cell biovolume, species richness and number of size classes of the four samples. The lowest values of total biovolume and mean biovolume were found at Grand Canyon National Park. Raw values of cell biovolume range from 15.5 to 11,869μm^3. There was a half an order of magnitude difference in mean cell volume between Grand Canyon and Eagles Nest Lake. Summary statistics for each sample and across all samples are given in Table 5.

The regression models for each site are given in Figures 14-17. Figure 18 gives a model of all samples combined. The 95% confidence intervals and slopes for each regression are given in Table 2. The slopes were highest for Eagles Nest Lake and Grand Canyon National Park and lowest at Arches and Big Bend National Parks. None of the individual site slopes were significantly different than -3/4 (Table 2). The regression model for all samples combined shows a slope of -1.6, significantly steeper than -3/4 and indistinguishable from -3/2 (Table 2).

DISCUSSION

There seems to be a consistent inverse relationship between density and body size in most communities of organisms. The data presented in this study support this hypothesis. The smallest diatoms were generally the most abundant and the largest tend to be the least abundant. The individual regression models for each site vary in slope from -1.42 to -0.63. Based on the 95% confidence intervals of these regressions, neither the -3/4 nor the -3/2 models proposed to explain the relationship between density and

biomass can be rejected. However, the model which combines all samples supports the -3/2 prediction and excludes the value of -3/4.

Variations in slopes between sites could have several explanations. Finkel et al (Finkel, Irwin et al. 2004) show that resource limitation alters the expected 3/4 size scaling of metabolic rates in phytoplankton. Therefore if metabolism is a determining factor in the body size-abundance relationship of diatoms then individuals that can better acquire resources and acclimate to resource availability would be more abundant. Animal grazing also may influence size distributions in diatom assemblages. Wimpenny (Wimpenny 1973) shows that populations of *Skelotonema costatum* and *Ditylum brightIllii* increase in cell size under the influence of grazing. Habitat complexity is also likely to affect diatom size distributions. Bergey (1999) found that under abrasive disturbances, substrates with small crevice size tend to support a higher proportion of small diatoms, whereas substrates with larger crevices supported a larger rage of sizes. Any one or a combination of the above cases could alter diatom size distributions from predicted values, and even lead to a bimodal size distributions as suggested by Baillie (1986).

Studies investigating the allometric relationship between organism size and abundance tend to be either local or global in scope. Local studies generally use individuals as the basic unit, resulting in individuals of different species being grouped into size classes. Global studies use species as the basic units, with each having a mean value for size. Because I was interested in the abundance of certain sized cells I incorporated aspects of both types of studies, using average biovolume of a species, then

grouping species into size classes. Since this investigation has components of both types of studies, it is difficult to directly compare results with the literature.

As is the case with many organisms, diatom assemblages show an inverse relationship between abundance and "body" size. The limited data collected from the four sites in this study cannot rule out either the proposed $M^{-3/4}$ or the $M^{-2/3}$ relationships. Therefore for diatoms it seems that there may be considerable site to site variation in the allometric exponent. However, small sample sizes may be an issue in my individual site analysis; the pooled data set did statistically favor the -3/2 model. Variations are possibly due to spatial and temporal variations in the biotic and abiotic conditions at each site. Due to the limited number of samples included in this study, it is not possible to conclude that universal allometric principles exist. Despite the limitations in this study, diatoms may be excellent organisms to study allometric relationships in natural populations as well as laboratory cell culture studies. More work is needed to clarify any general patterns that may exist.

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Tables

Table 4. Sample information

	W8	W20	W29	W35
Location	Eagles Nest Lake, New Mexico New Mexico	Arches National Park, Utah Park, Utah	Grand Canyon National Park National Park	Big Bend National Park National Park
Date	8/10/04	8/14/04	8/18/04	1/1/05
Latitude	36 58.523	38 44.191	-	-
Longitude	103 23.802	109 31.138	-	-
Type	Sediment, Macrophyte	Epilithic	Epilithic	Epilithic, Epipellic

Table 5. Summary statistics for the four samples and all samples combined

	Sample				
Location	NM	UT	AZ	TX	all
Total vol µ3	512320.3	209930.5	139924.1	220557.6	1082732.5
Mean vol µ3	1024.6	419.9	279.8	441.1	541.4
Shannon	2.7	1.4	1.8	0.8	4.3
Richness	31.0	13.0	9.0	9.0	62.0
Number size classes	14.0	9.0	7.0	5.0	17.0
Slope	-1.1	-0.8	-1.4	-0.7	-1.6
Max Volume µ3	11429.6	3553.3	11869.2	3368.0	11869.2
Min Volume µ3	15.8	18.9	34.9	15.5	15.5
95% CI	-1.6 to -0.6	-2.8 to 1.3	-2.5 to -0.4	-3.4 to 2.1	-2 to 1.1

Figure Legends

Figure 14. The scaling relationship between log_{10}- transformed abundance and biovolume (μm^3) for Eagles Nest Lake State Park, New Mexico (slope and 95% confidence intervals are given in Table 5)

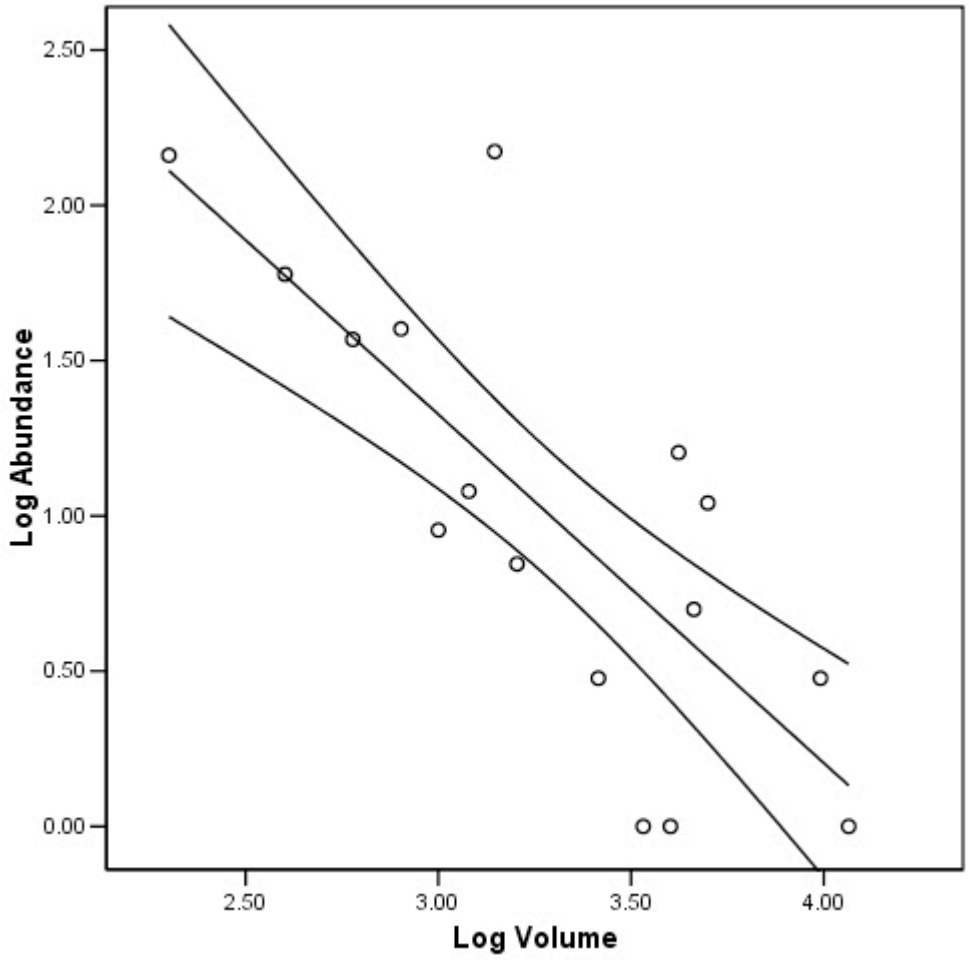


Figure 15. The scaling relationship between log_{10}- transformed abundance and biovolume (μm^3) for Arches National Park, Utah (slope and 95% confidence intervals are given in Table 5)

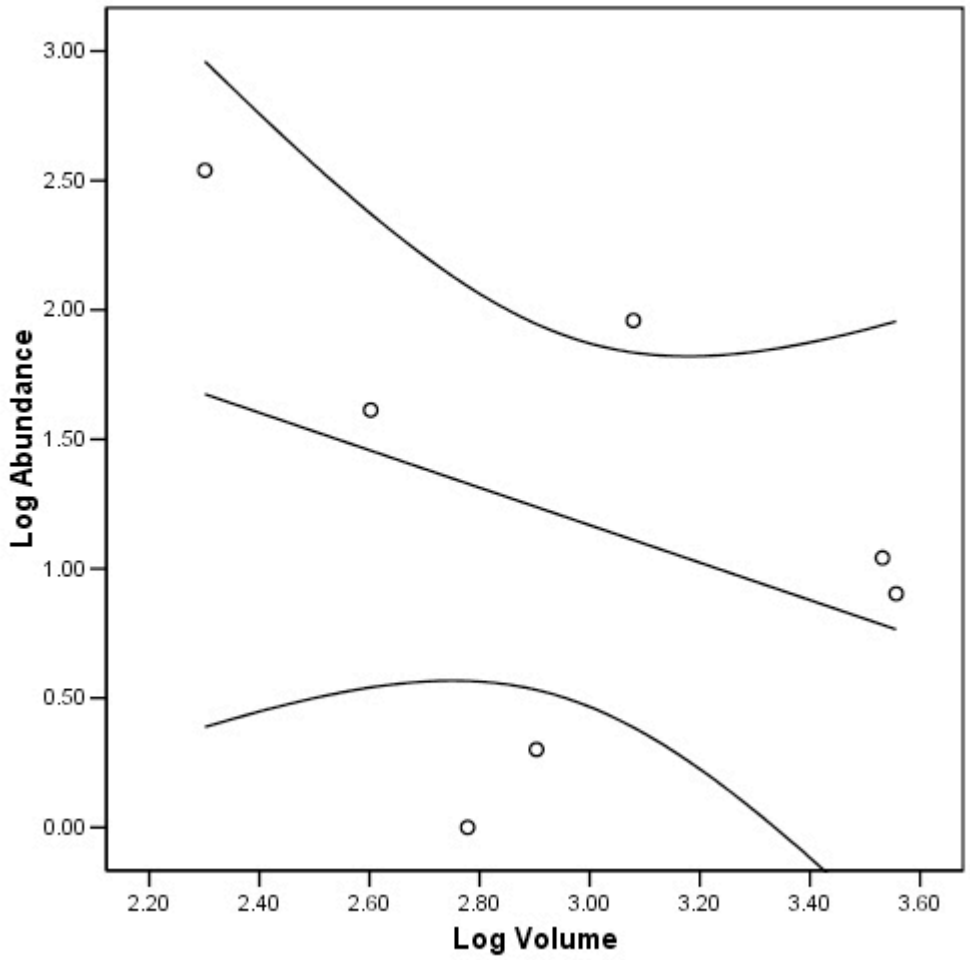


Figure 16. The scaling relationship between log_{10}- transformed abundance and biovolume (μm^3) for Grand Canyon National Park, Arizona (slope and 95% confidence intervals are given in Table 5)

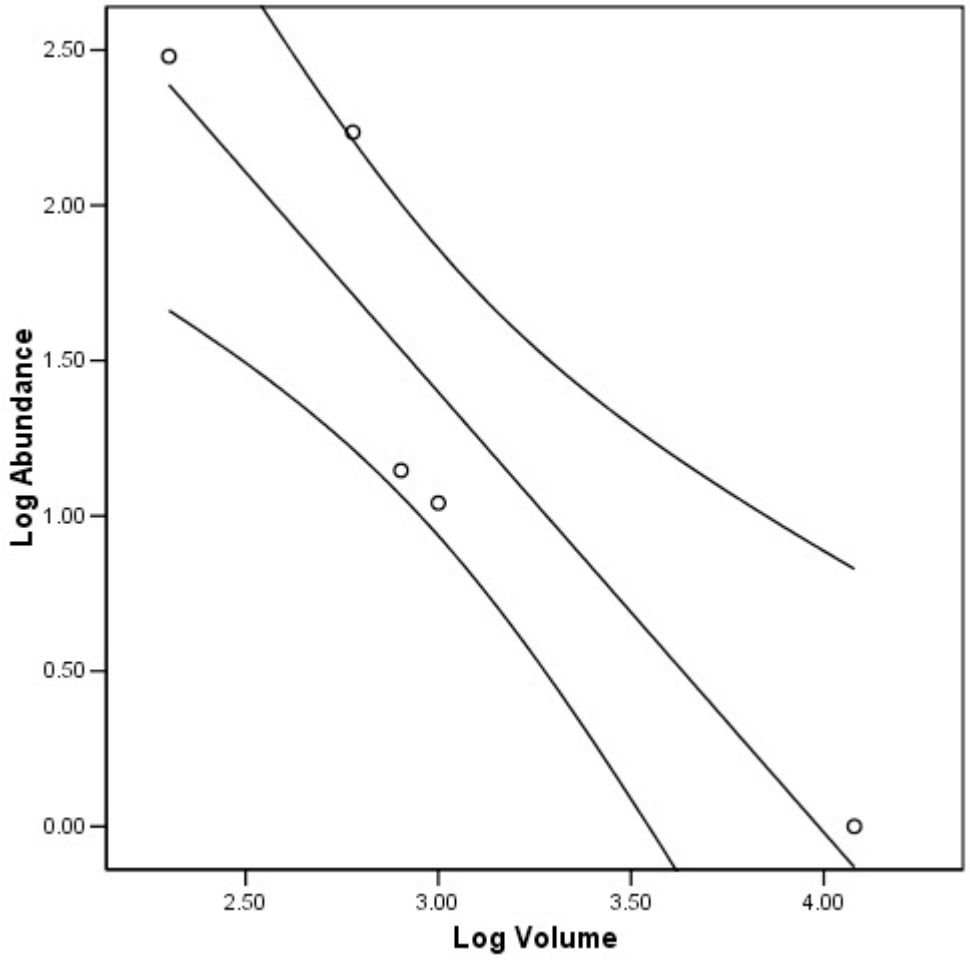


Figure 17. The scaling relationship between log_{10}- transformed abundance and biovolume (μm^3) for Big Bend National Park, Texas (slope and 95% confidence intervals are given in Table 5)

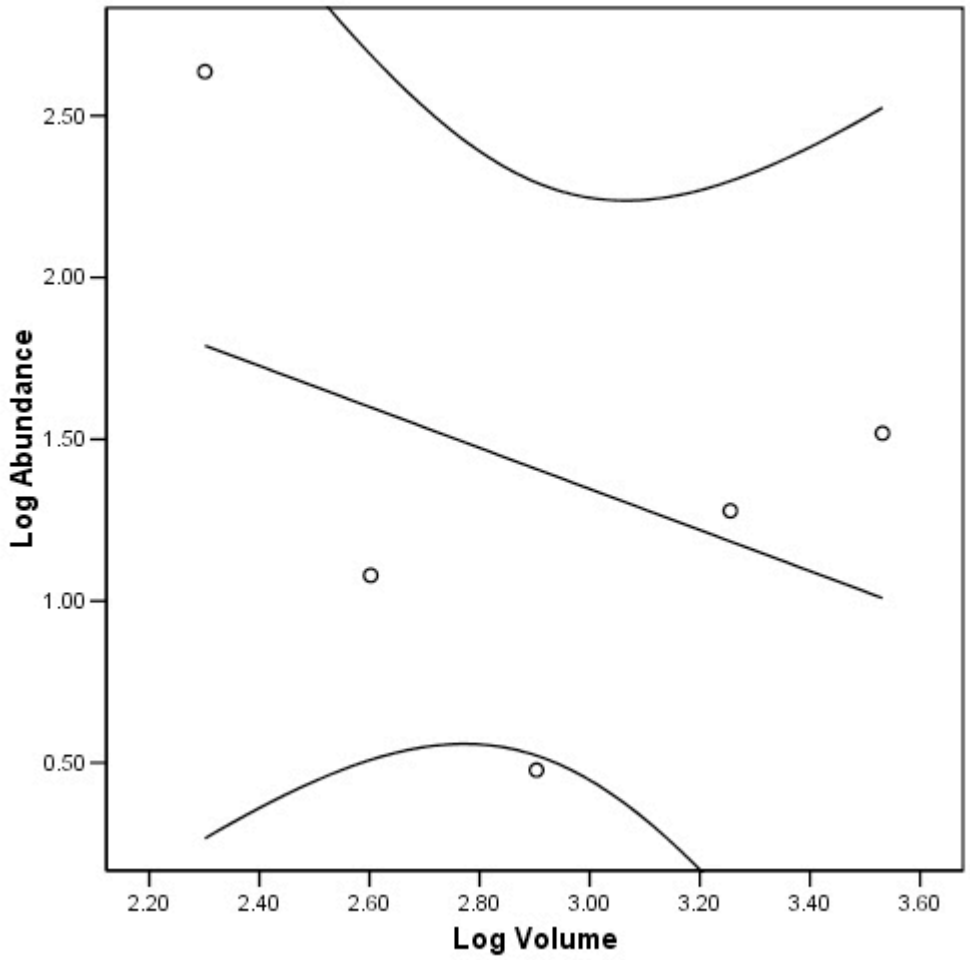
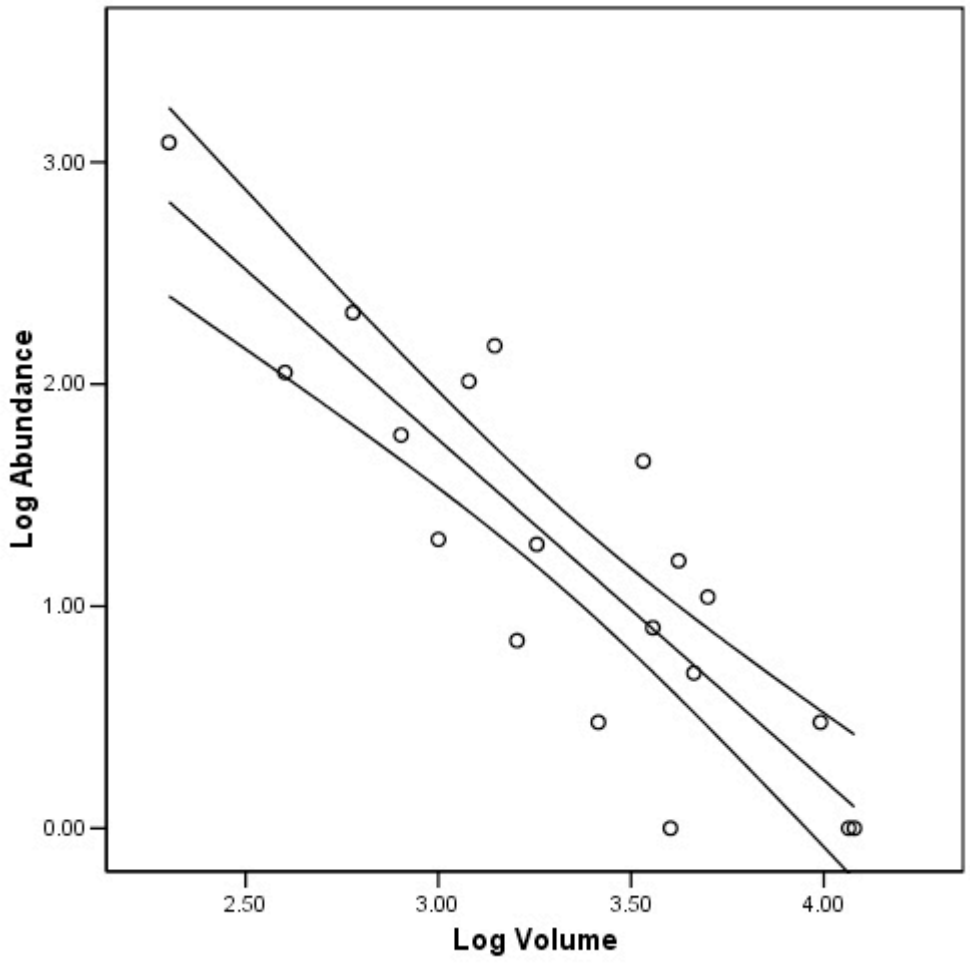


Figure 18. The scaling relationship for log_{10}- transformed abundance and biovolume (μm^3) combining all samples (see Table 5 for slope and 95% confidence interval)



Appendix A. List of diatom species found at the SPNWR. Species names are followed in parentheses by the plate number and photo letter referenced in Appendix B

Centric Diatoms
Coscinodiscophyceae
Thalassiosirophycidae
Thalassiosirales

Stephanodiscaceae
Cyclotella sp. *1* (4,f)
Cyclotella meneghiniana Kützint 1844 (5,a)
Centric sp. *1* (4,b)
Chaetocerotophycidae
Chaetocerotales
Chaetoceraceae
Chaetoceros sp. spore (4,c)

Araphid Diatoms
Fragilariophyceae
Fragilariophycidae
Fragilariales
Fragilariaceae
Diatoma vulgaris Bory 1824 (5,d)
Opephora martyi Héribaud 1902 (14,a)

Monoraphid Diatoms
Bacillariophyceae
Bacillariophycideae
Achnanthales
Achnanthaceae
Achnanthes sp. *1* (1,a)
Achnanthes biasolettiana Grunow in Cleve & Grunow 1880 (1,c)
Achnanthes levanderi Hustedt 1933 (1,f)
Achnanthes lemmermannii Hustedt 1933 (1,d)
Achnanthes linearis (W. Smith) Grunow sensu auct. Nonnull. (1,e)
Achnanthes sp. *2* (1,b)
Cocconeis disculus (Schumann) Cleve in Cleve & Jentzsch 1882 (4,d)
Cocconeis placentula Ehrenberg 1838 (4,e)

Biraphid Diaotms
Symmetric Naviculoid
Naviculales
Naviculaceae
Mastogloia pumila (Cleve & Möller 1879) Cleve 1895 (6,h)

Gyrosigma nodiferum (Grunow) Reimer 1966 (6,d)
Caloneis molaris (Grunow) Krammer 1985 (4,a)
Caloneis amphisbaena (Bory) Cleve 1894 (3,e)
Diploneis puella (Schumann) Cleve 1894 (5,c)
Plagiotropis arizonica Czarnecki 1984 (14,b)
Fallacia pygmaea (Kützing) A.J. Stickle & D.G. Mann 1990 (6,b)
Luticola cohnii (Hilse) D.G. Mann 1990 (6,f)
Luticola undulata (Hilse in Rabenhorst) D.G. Mann 1990 (6,g)
Navicula salinarum Grunow in Cleve &Grunow 1880 (10,g)
Navicula sp. *2* (7,a)
Navicula cincta (Ehrenberg) Ralfs in Pritchard 1861 (9,e)
Navicula bulnheimii Grunow in Van Heurck 1880 (9,c)
Navicula sp. *7* (8,a)
Navicula eidrigiana Carter 1979 (10,a)
Navicula sp. *4* (7,c)
Navicula sp. *8* (8,b)
Navicula spicula (Hickie) Cleve 1894 (10,i)
Navicula minima Grunow in Van Heurck 1880 (10,d)
Navicula sp. *6* (7,e)
Navicula sp. *5* (7,d)
Navicula sp. *3* (7,b)
Navicula sp. *18* (9,a)
Navicula sp. *9* (8,c)
Navicula sp. *17* (8,g)
Navicula circumtexta F. Meister ex Hustedt in AWF Schmidt 1934 (9,g)
Navicula digitoradiata (Gregory) Ralfs in Pritchard 1861 (9,i)
Navicula radiosa Kützing 1844 (10,f)
Navicula salinicola Hustedt 1939 (10,h)
Navicula sp. *15* (8,f)
Navicula sp. *19* (9,b)
Navicula cf. *9* (9,d)
Navicula cincta minuta Grunow in Van Heurck 1880 (9,f)
Navicula gregaria Donkin 1861 (10,c)
Navicula sp. 20 (10,e)
Navicula cryptocephala Lange-Bertalot 1985 (9,h)
Navicula sp. *10* (8,d)
Navicula explanata Hustedt 1948 (10,b)
Navicula sp. *11* (8,e)
Hippodonta hungarica Grunow 1860 (6,e)

Eunotioid-Asymmetrical Naviculoid Diatoms

Naviculales

Catenulaceae

Amphora sp. *6* (2,a)
Amphora coffeaeformis (Agardh) Kützing 1844 (3,a)

Amphora acutiuscula Kützing 1844 (2,g)
Amphora sp. *12* (2,f)
Amphora sp. *5* (1,j)
Amphora sp. *3* (1,i)
Amphora sp. *7* (2,b)
Amphora pediculus (Kützing) Grunow 1880 (3,b)
Amphora perpusilla Grunow (1884-87) (3,c)
Amphora sp. *10* (2,d)
Amphora sp. *11* (2,e)
Amphora sp. *2* (1,h)
Amphora sp. *9* (2,c)

Cymbellaceae

Cymbella pusilla Grunow in A. Schmidt et al. 1875 (5,b)

Gomphonemataceae

Gomphonema parvulum (Kützing) Kützing 1849 (6,c)

Keeled Diatoms

Bacillariales

Bacillariaceae

Bacillaria paradoxa Gmelin 1791 (3,d)
Nitzschia sp. *2* (11,b)
Nitzschia reversa W. Smith 1853 (13,g)
Nitzschia sp. *1* (11,a)
Nitzschia fonticola Grunow in Cleve & Möller 1879 (12,d)
Nitzschia palea (Kützing) W. Smith 1856 (13,d)
Nitzschia microcephala Grunow in Cleve & Möller 1878 (13,b)
Nitzschia pura Hustedt 1954 (13,e)
Nitzschia bacilliformis Hustedt 1922 (11,g)
Nitzschia thermaloides Hustedt 1955 (13,i)
Nitzschia sp. *3* (11,c)
Nitzschia frustulum (Kützing) Grunow in Cleve & Grunow 1880 (12,f)
Nitzschia sp. *7* (11,e)
Nitzschia hungarica Grunow1862 (12,g)
Nitzschia sp. *8* (11,f)
Nitzschia laevis Hustedt 1939 (12,h)
Nitzschia scalpelliformis (Grunow) Grunow in Cleve &Grunow 1880 (13,h)
Nitzschia compressa (Bailey) Boywr 1916 (12,a)
Nitzschia filiformis (W. Smith) Van Heurck 1896 (12,c)
Nitzschia sp. fragment (12,e)
Nitzschia lanceola minutula Grunow in Cleve & Grunow 1880 (13,a)
Nitzschia modesta Hustedt in Brendemühl 1949 (13,c)
Nitzschia sp. *6* (11,d)

Nitzschia bergii Cleve-Euler 1953 (11,h)
Nitzschia commutata Grunow in Cleve & Grunow 1880 (12,b)
Nitzschia clausii Hantzsch 1860 (11,i)
Nitzschia pusilla Grunow 1862 (13,f)
Psamodictyon constrictum (Gregory) D.G. Mann 1990 (14,c)

Surirellales

Entomoneidaceae

Entomoneis paludosa subsalina (W. Smith) Reimer 1975 (6,a)
Entomoneis sp. 1 (5,e)

Surirellaceae

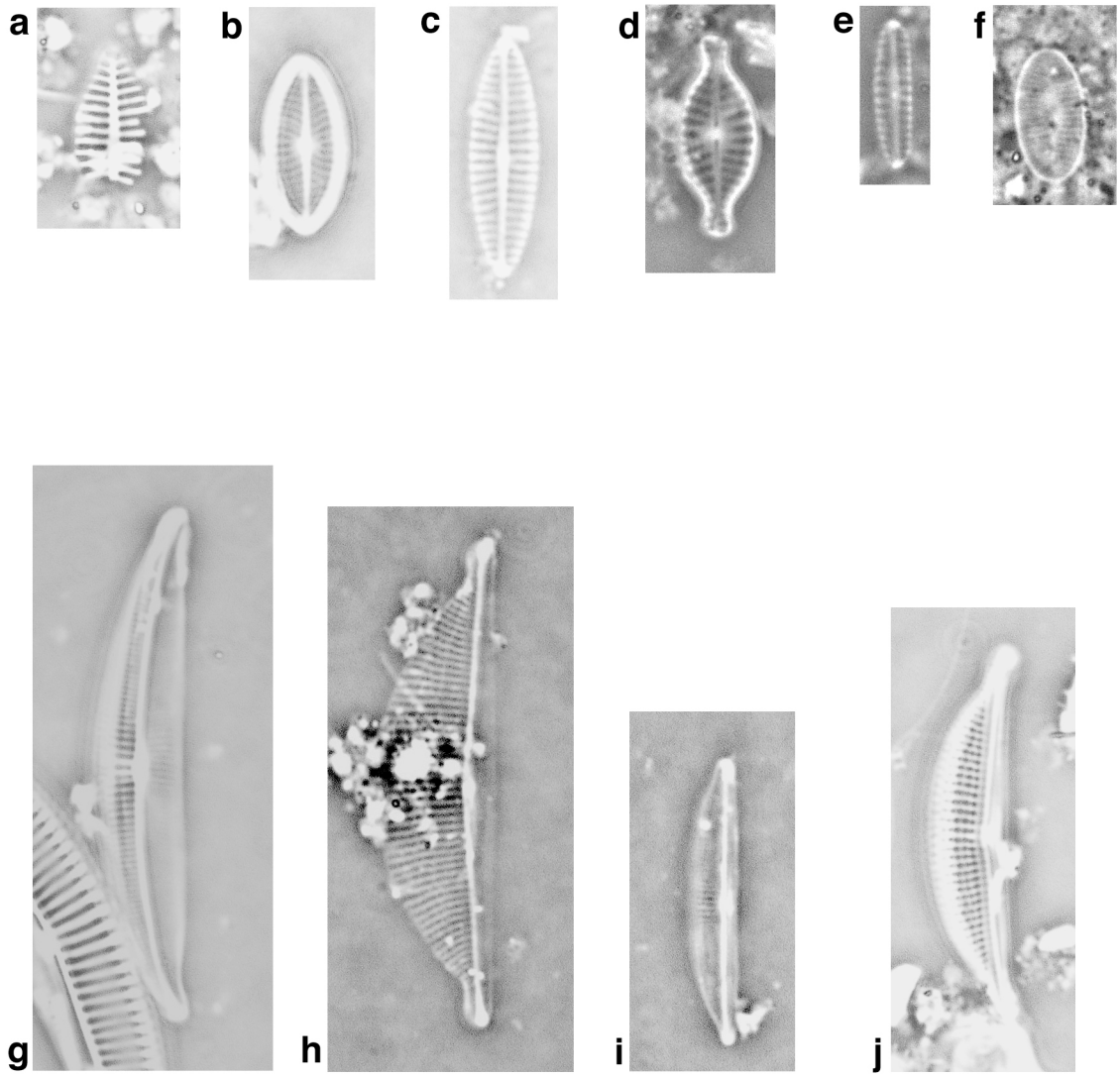
Surirella striatula Turpin 1828 (16,a)
Surirella sp. 2 (15,b)
Surirella sp. 1 (15,a)
Surirella sp. 3 (15,c)
Surirella angusta Kützing 1844 (15,d)
Surirella brebissonii Krammer & Lange-Bertalot 1987 (15,e)
Surirella ovalis Brébisson 1838 (15,f)

Rhopalodiales

Rhopalodiaceae

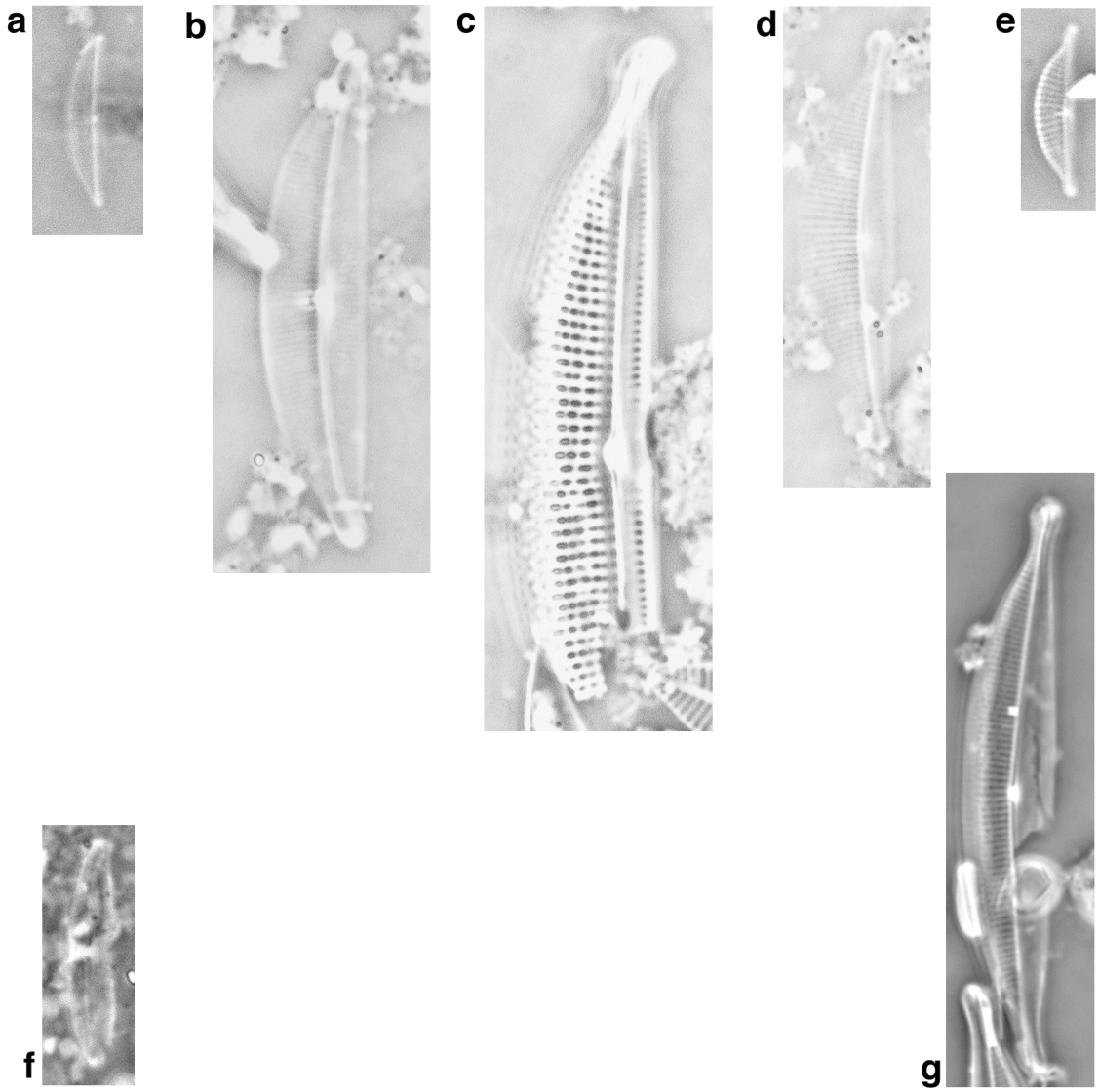
Rhopalodia musculus (Kützing) O. Müller 1899 (14,d)

Appendix B. Photomicrographs of diatoms found at the SPNWR. Length and width are given in μ in parentheses
Plate 1



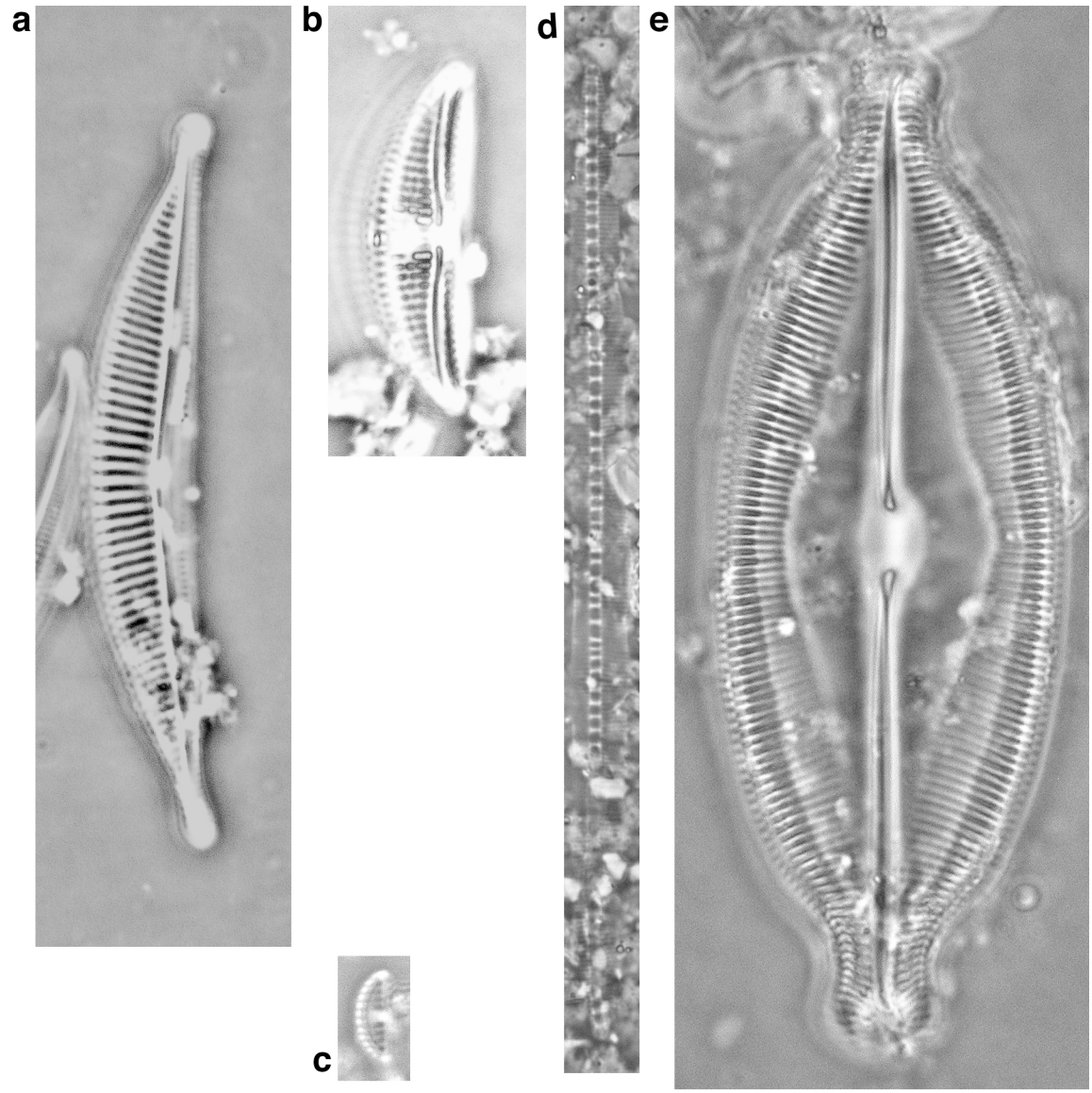
a. *Achnanthes* sp. 1 (l=8 , w=3.5)
b. *A.* sp. 2 (l=12 , w=5)
c. *A. biasoleattiana* (l=17 , w=4)
d. *A. lemmermannii* (l=13 , w=5.5)
e. *A. linearis* (l=10 , w=3)
f. *A. levanderi* (l=8 , w=5)
g. *Amphora* sp. 1 (l=34 , w=6)
h. *A* sp. 2 (l=32 , w=8)
i. *A.* sp. 3 (l=19 , w=3)
j. *A.* sp. 5 (l=24 , w=5)

Plate 2



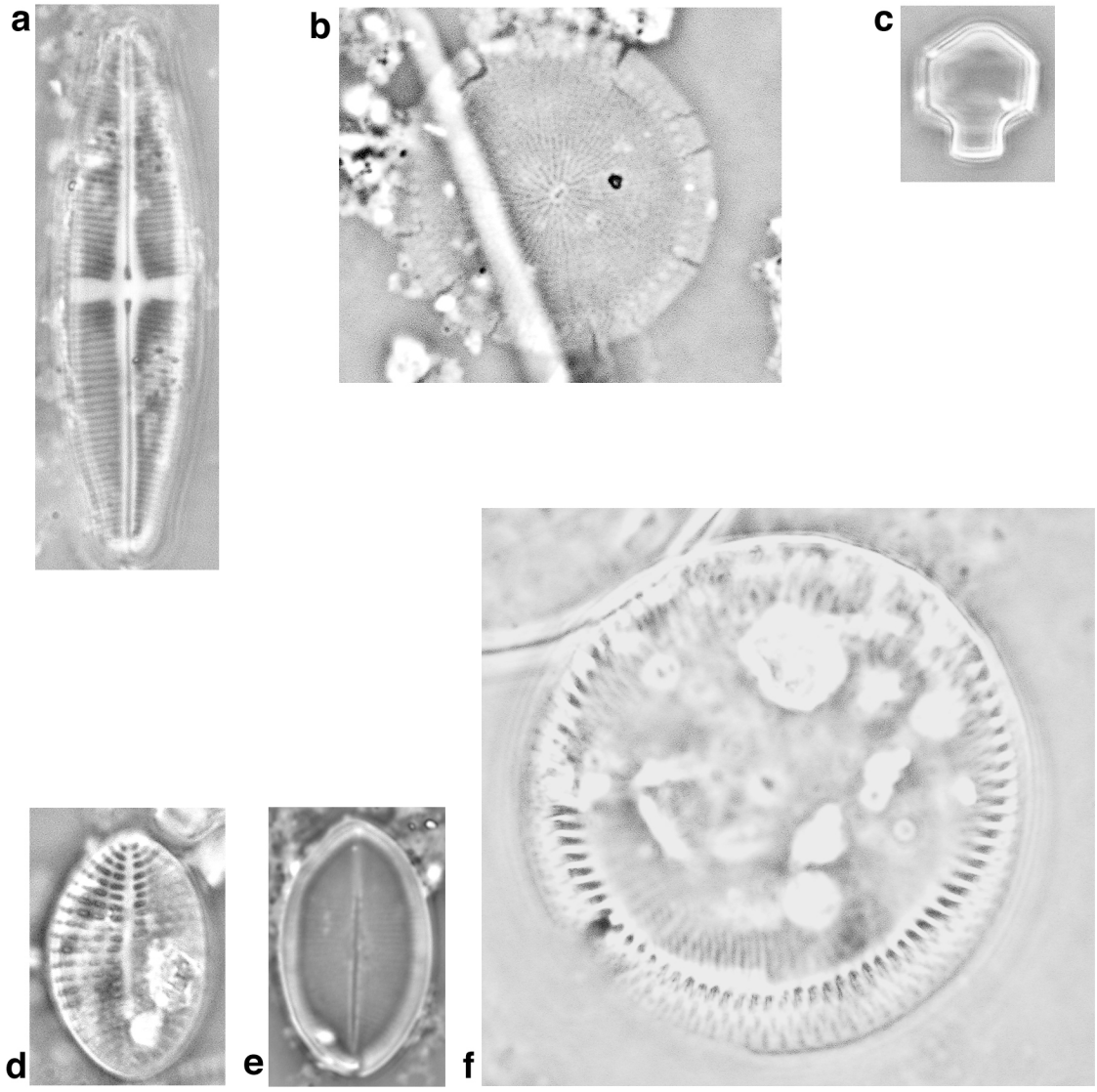
a. *Amphora* sp. 6 (l=12, w=2.5)
b. *A.* sp. 7 (l=25, w=6)
c. *A.* sp. 9 (l=54, w=9)
d. *A.* sp. 10 (l=28, w=7)
e. *A.* sp. 11 (l=11.5, w=2.5)
f. *A.* sp. 12 (l=16, w=4.5)
g. *A. acutiuscula* (l=39, w=7)

Plate 3



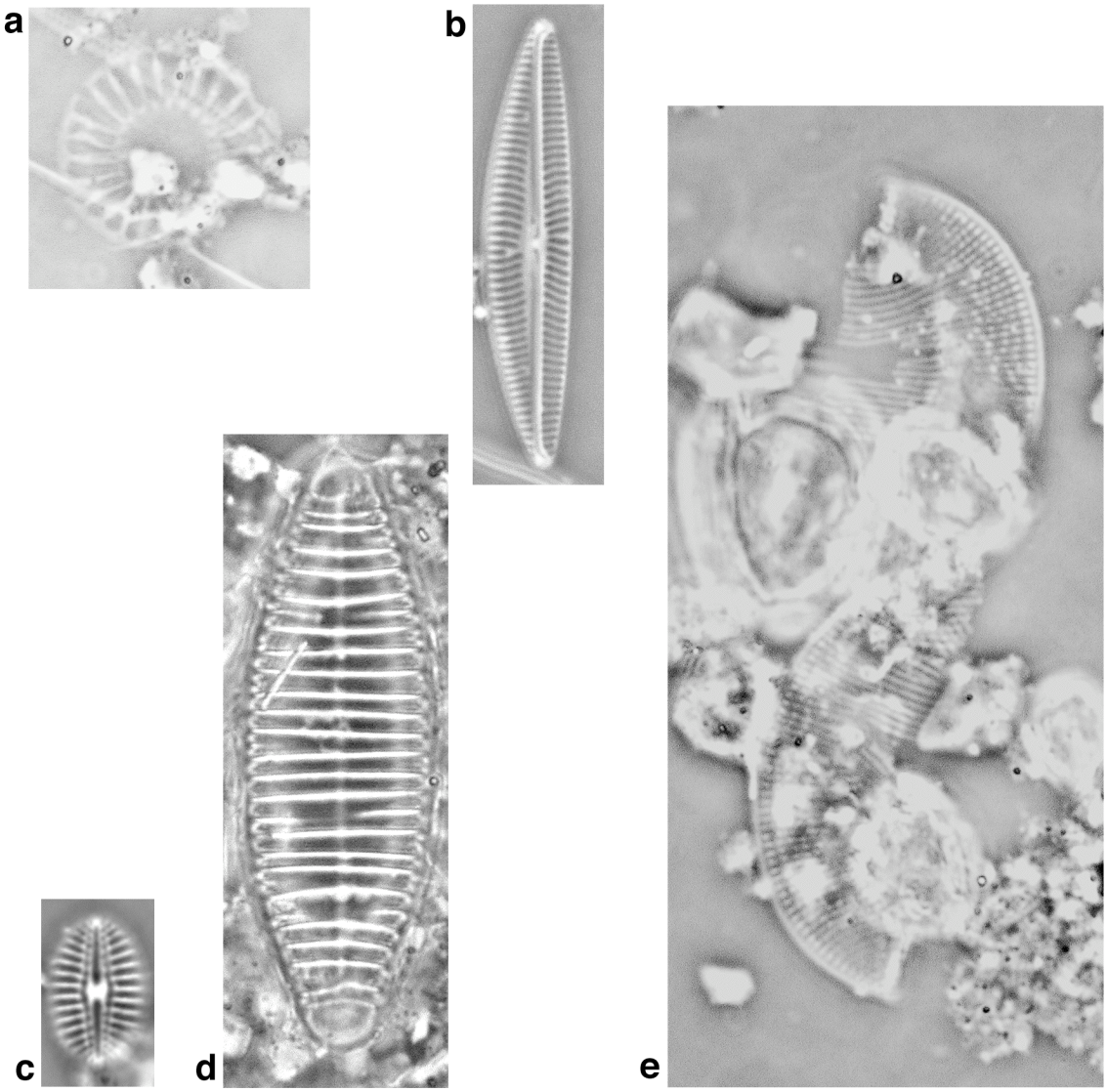
a. *Amphora coffeaeformis* (l=50, w=7)
b. *A. pediculus* (l=23, w=6)
c. *A. perpusilla*(l=6, w=3)
d. *Bacillaria paradoxa* (l=95, w=7)
e. *Caloneis amphisbaena* (l=70, w=25)

Plate 4



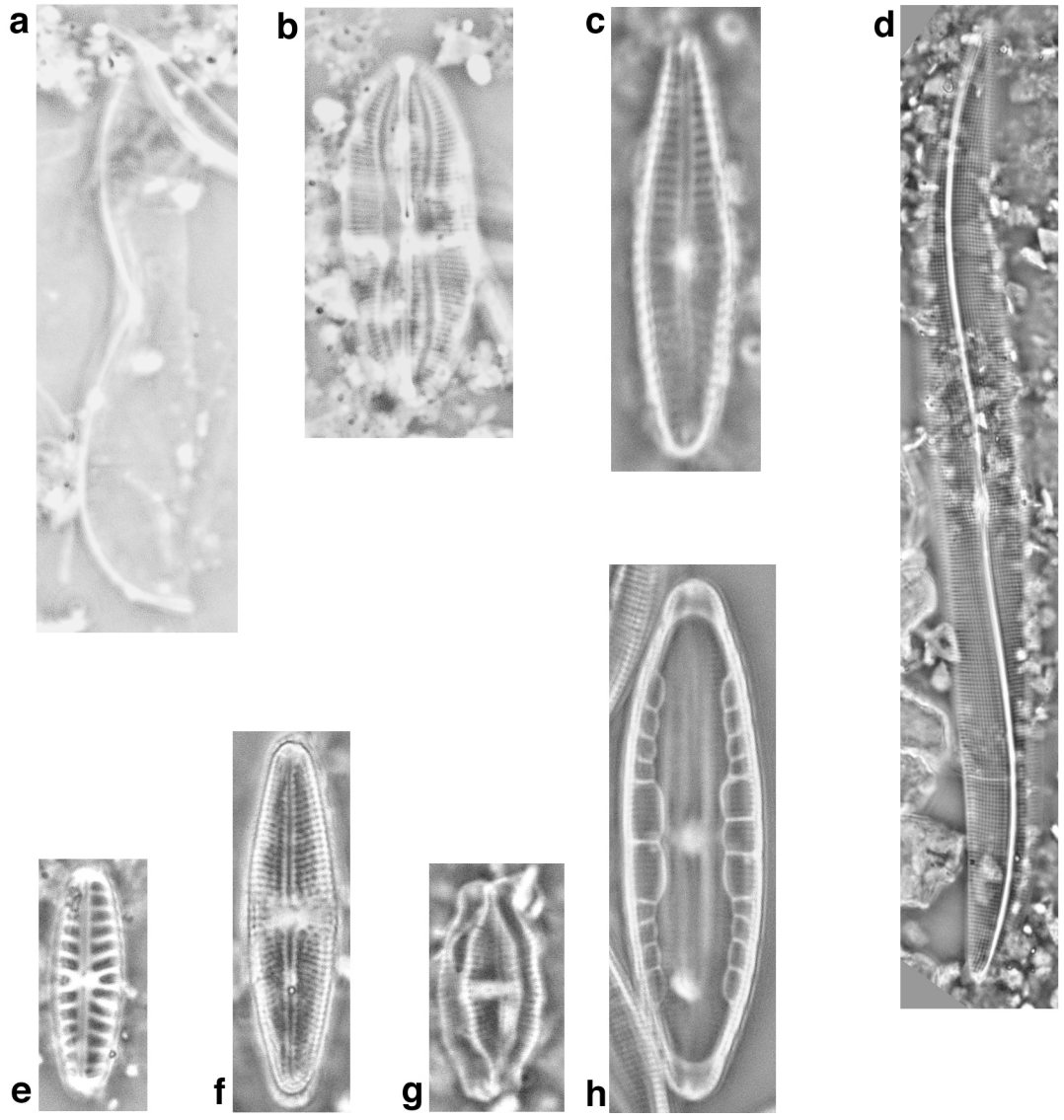
a. *Caloneis molaris* (l=38, w=10)
b. *Centric* sp. 1 (d=21)
c. *Chaetoceros* sp. spore (l=7, w=5.5)
d. *Cocconeis disculus* (l=17, w=12)
e. *C. placentula* (l=18, w=10)
f. *Cyclotella* sp. 1 (d=64)

Plate 5



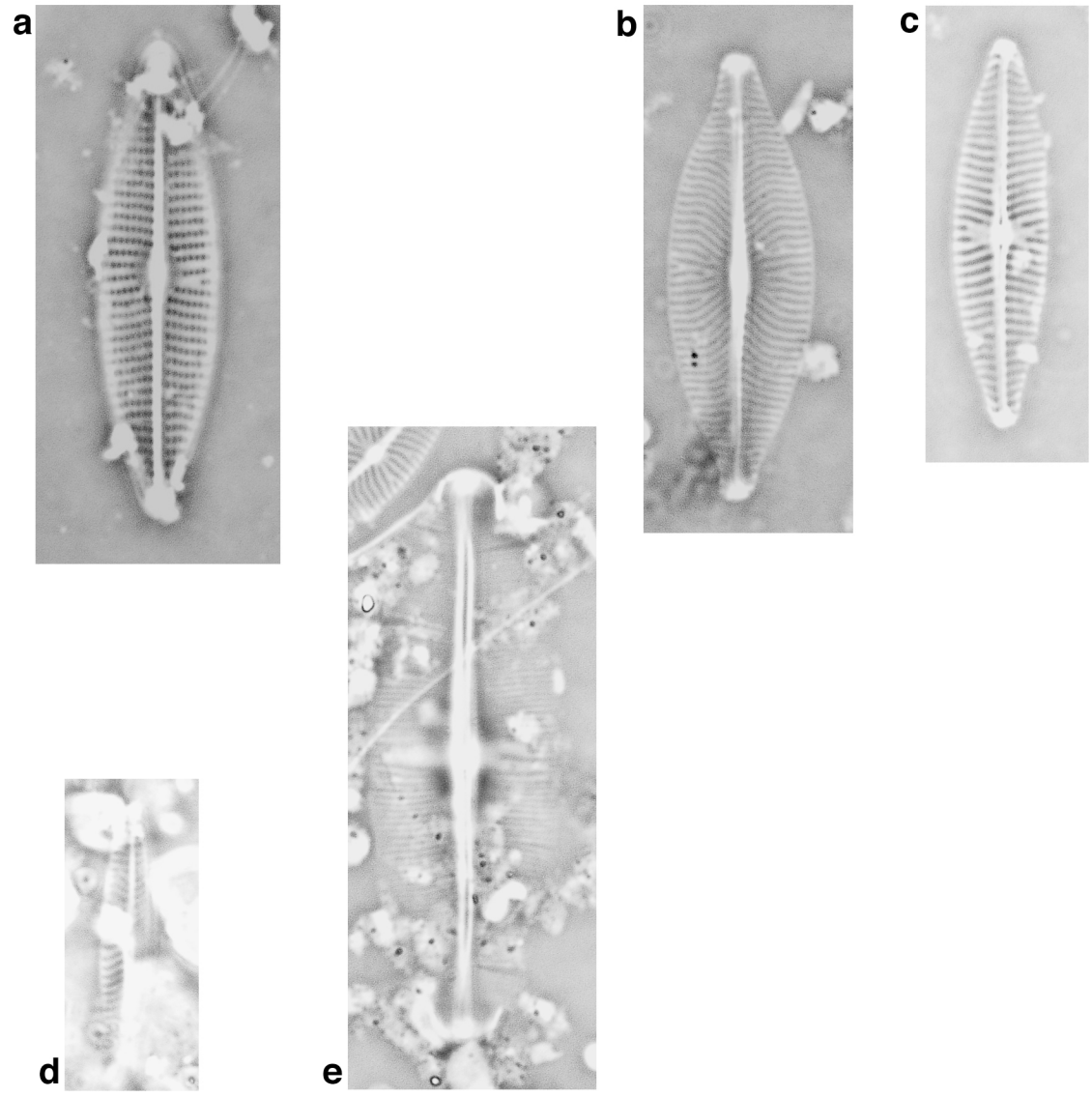
a. *Cyclotella meneghiniana* (d=16)
b. *Cymbella pusilla* (l=26, w=6)
c. *Diploneis puella* (l=10, w=7)
d. *Diatoma vulgaris* (l=40, w=14)
e. *Entomoneis* sp. 1 (l=54, w=15)

Plate 6



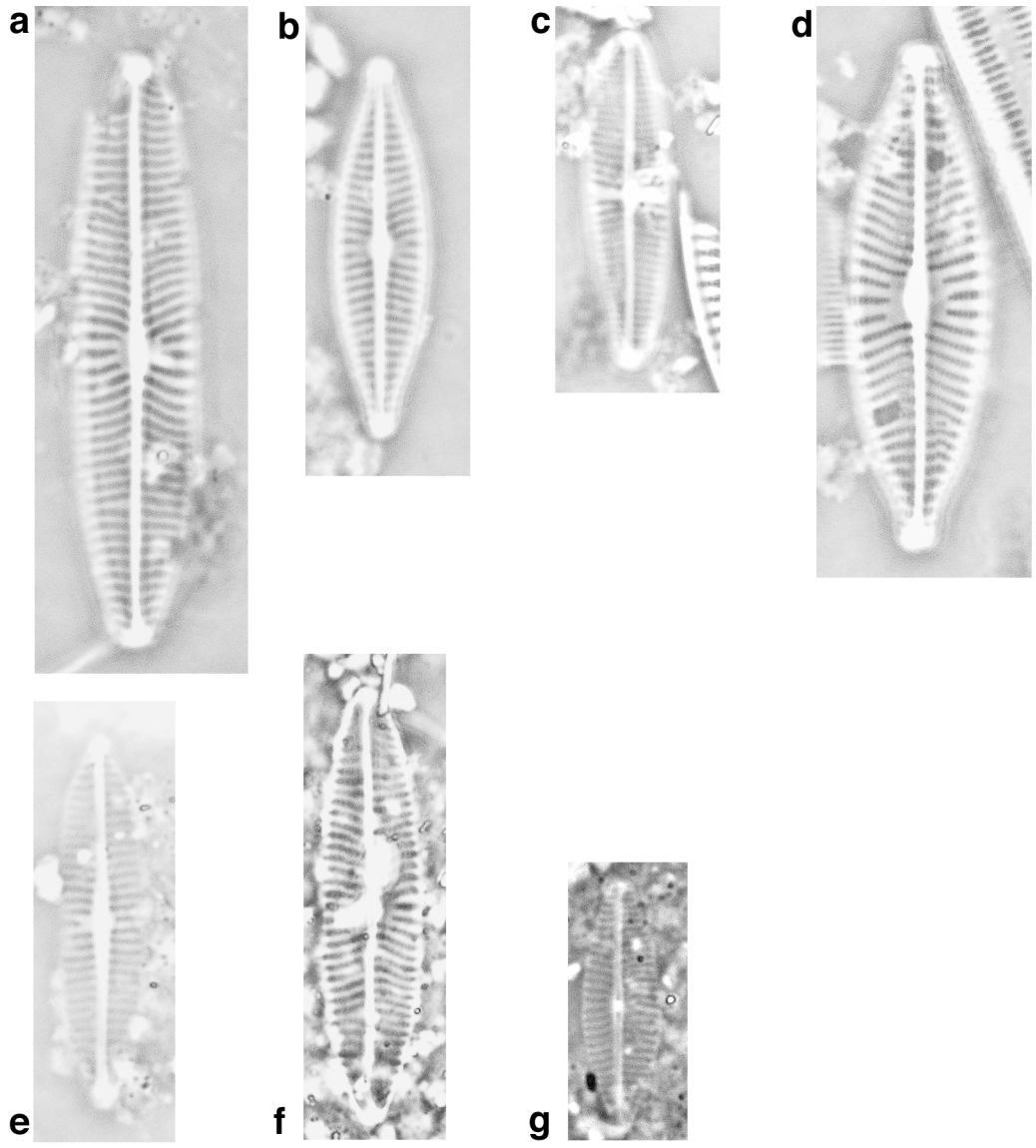
a. *Entomoneis paludosa subsalina* (l=37, w=4)
b. *Fallacia pygmaea* (l=23, w=9)
c. *Gomphonema parvulum* (l=27, w=5)
d. *Gyrosigma nodiferum* (l=113, w=12)
e. *Hippodonta hungarica* (l=15, w=5)
f. *Luticola cohnii* (l=24, w=7)
g. *Luticola undulata* (l=17, w=5)
h. *Mastogloia pumila* (l=37, w=10)

Plate 7



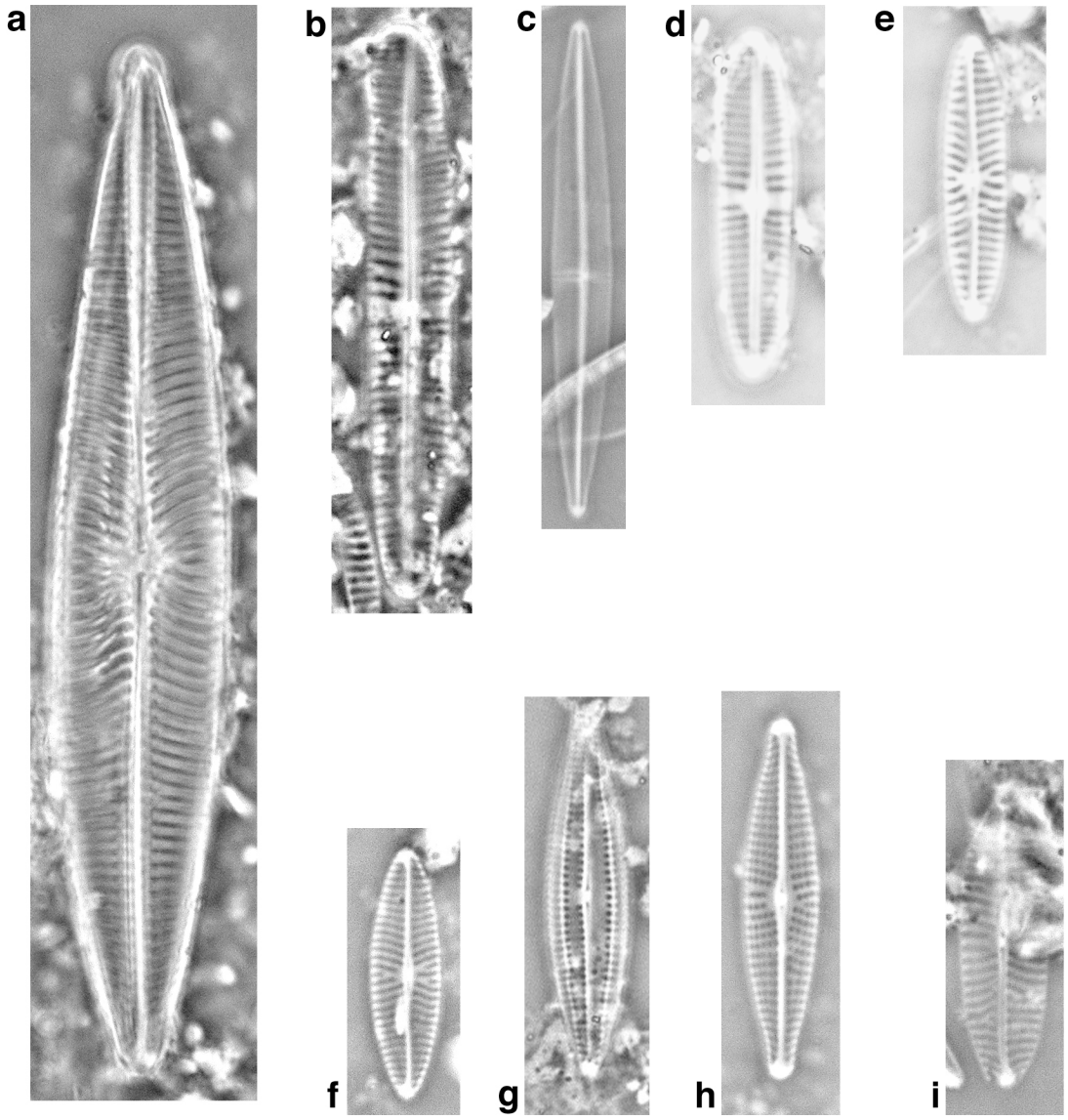
a. *Navicula* sp. 2 (l=32, w=8)
b. *N.* sp. 3 (l=29, w=10)
c. *N.* sp. 4 (l=27, w=6.5)
d. *N.* sp. 5 (l=20, w=4)
e. *N.* sp. 6 (l=38, w=13)

Plate 8



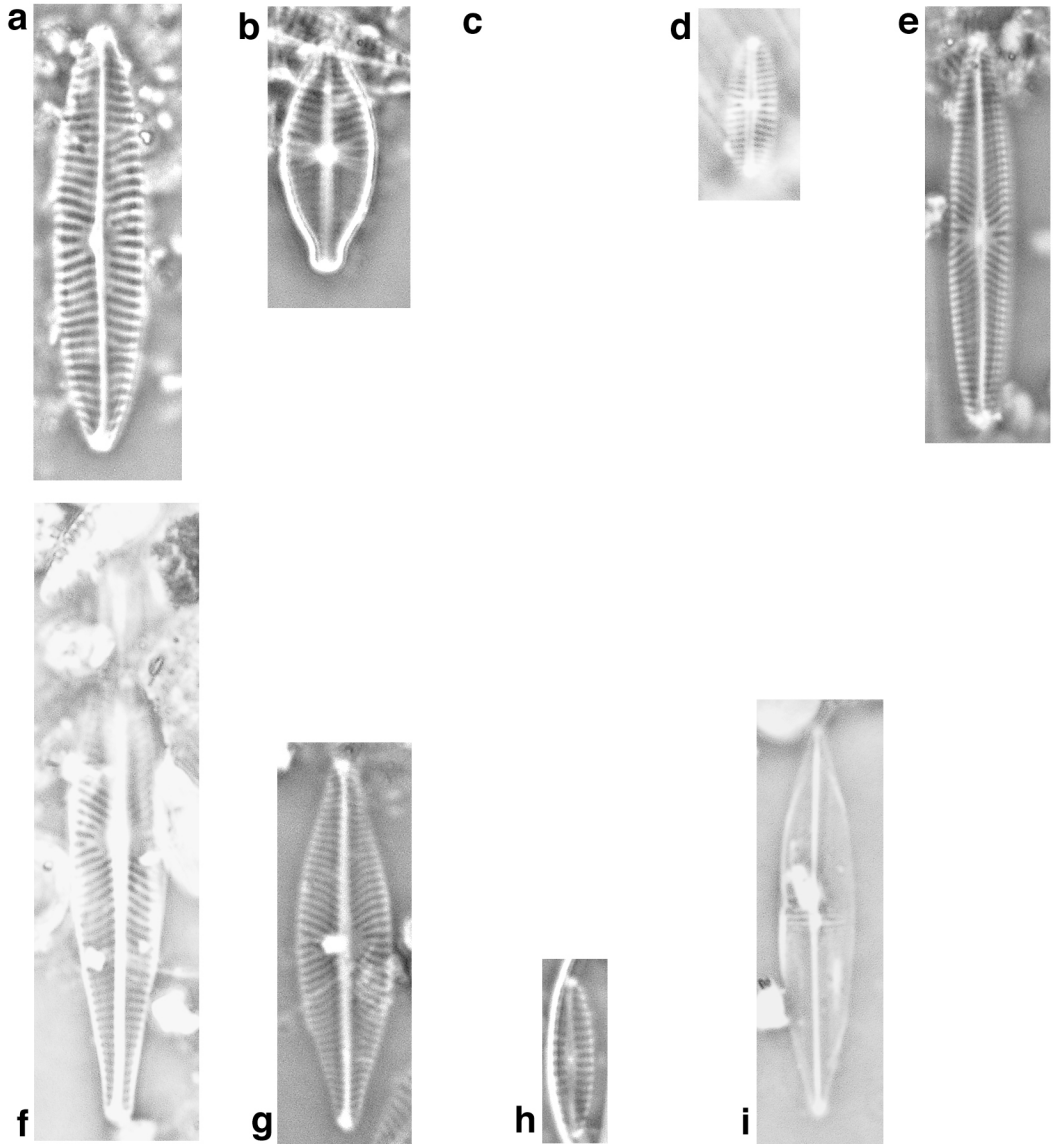
a. *Navicula* sp. 7 (l=48, w=9)
b. *N.* sp. 8 (l=25, w=7)
c. *N.* sp. 9 (l=21, w=6)
d. *N.* sp. 10 (l=33, w=9.5)
e. *N.* sp. 11 (l=24, w=6)
f. *N.* sp. 15 (l=28, w=7.5)
g. *N.* sp.17 (l=17, w=6)

Plate 9



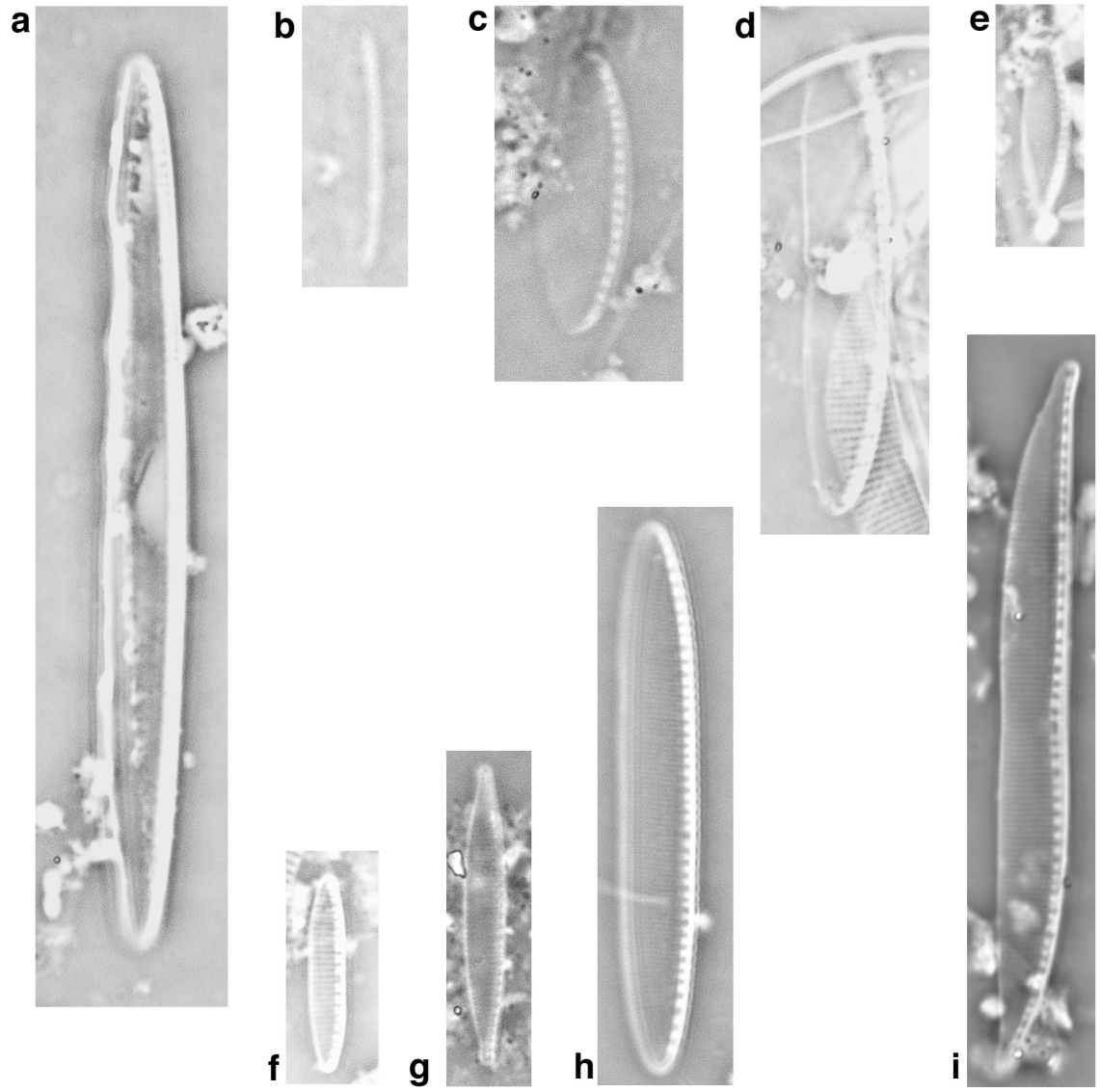
a. *Navicula* sp. 18 (l=70, w=12)
b. *N.* sp. 19 (l=38.5, w=6)
c. *N. bulnheimii* (l=33, w=4)
d. *N.* cf sp. 9 (l=22, w=6)
e. *N. cincta* (l=19, w=4.5)
f. *N. cincta minuta* (l=16, w=5)
g. *N. circumtexta* (l=29, w=7)
h. *N. cryptocephala* (l=24, w=5.5)
i. *N. digitoradiata* (l=20, w=6)

Plate 10



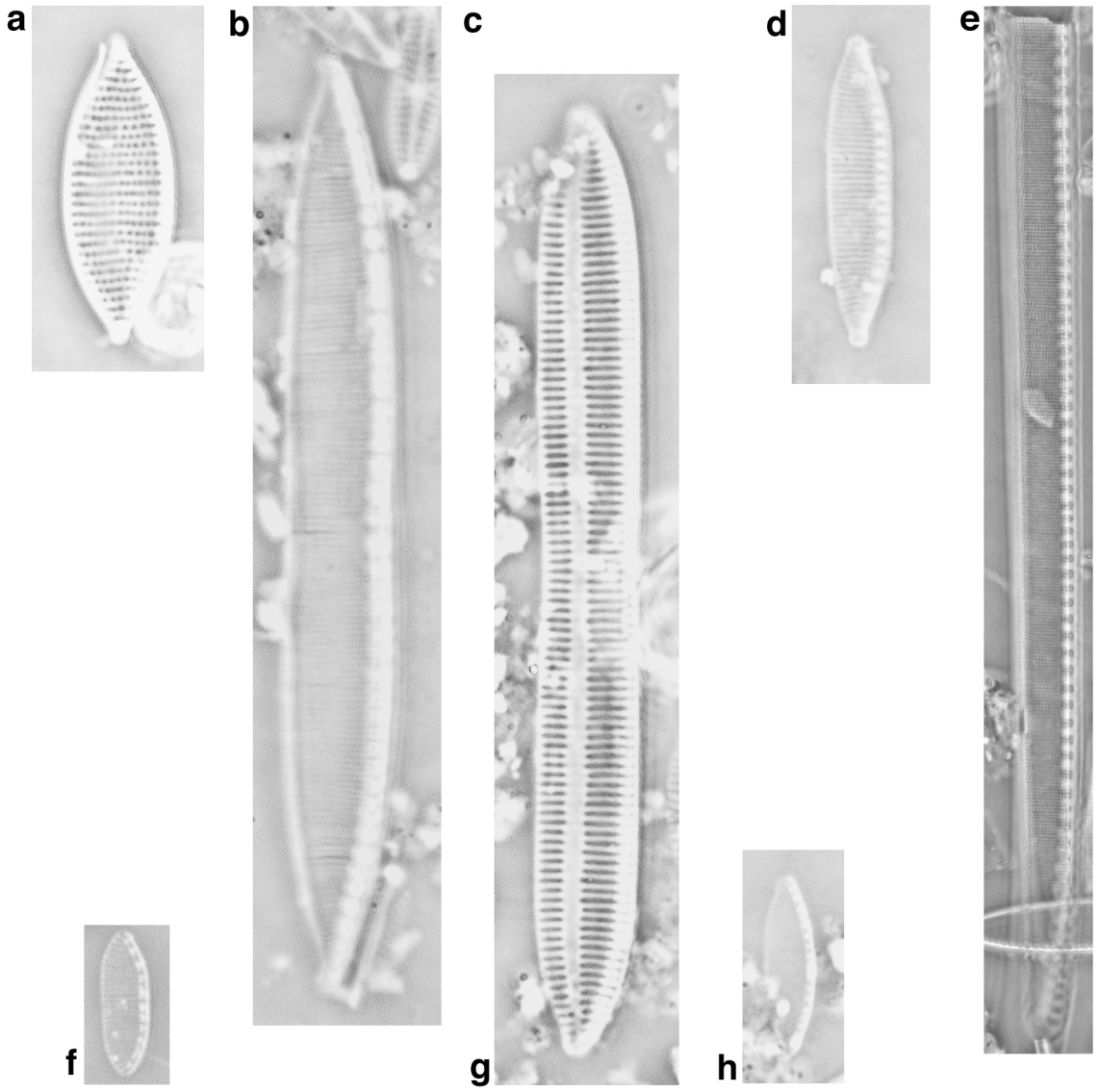
a. *Navicula eidrigiana* (l=23, w=6)
b. *N. explanata* (l=16.5, w=6.5)
c. *N. gregaria* (missing)
d. *N. minima* (l=9, w=4)
e. *N.* sp. 20 (l=15, w=3.5)
f. *N. radiosa* (l=37, w=6.5)
g. *N salinarium* (l=24, w=6.5)
h. *N. salinicola* (l=11, w=3)
i. N. spicula (l=25, w=5.5)

Plate 11



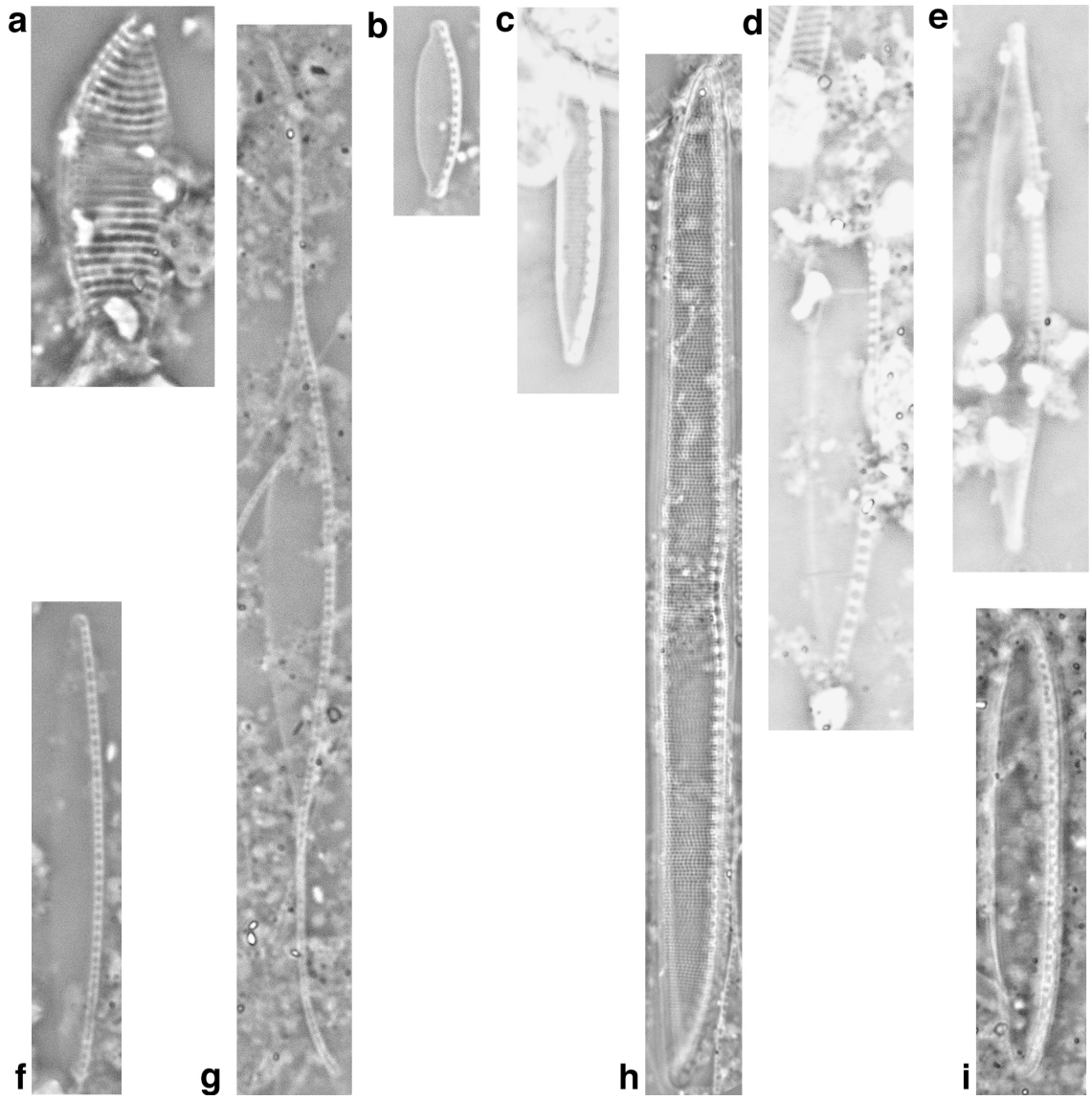
a. *Nitzschia* sp. 1 (l=58, w=5.5)
b. *N.* sp. 2 (l=16, w=3)
c. *N.* sp 3 (l=19, w=6)
d. *N.* sp. 6 (l=34, w=6)
e. *N.* sp. 7 (l=12, w=3)
f. *N.* sp. 8 (l=13, w=3)
g. *N.* bacilliformis (l=21, w=3)
h. *N. bergii* (l=38, w=6.5)
i. *N. clausii* (l= 45, w=5)

Plate 12



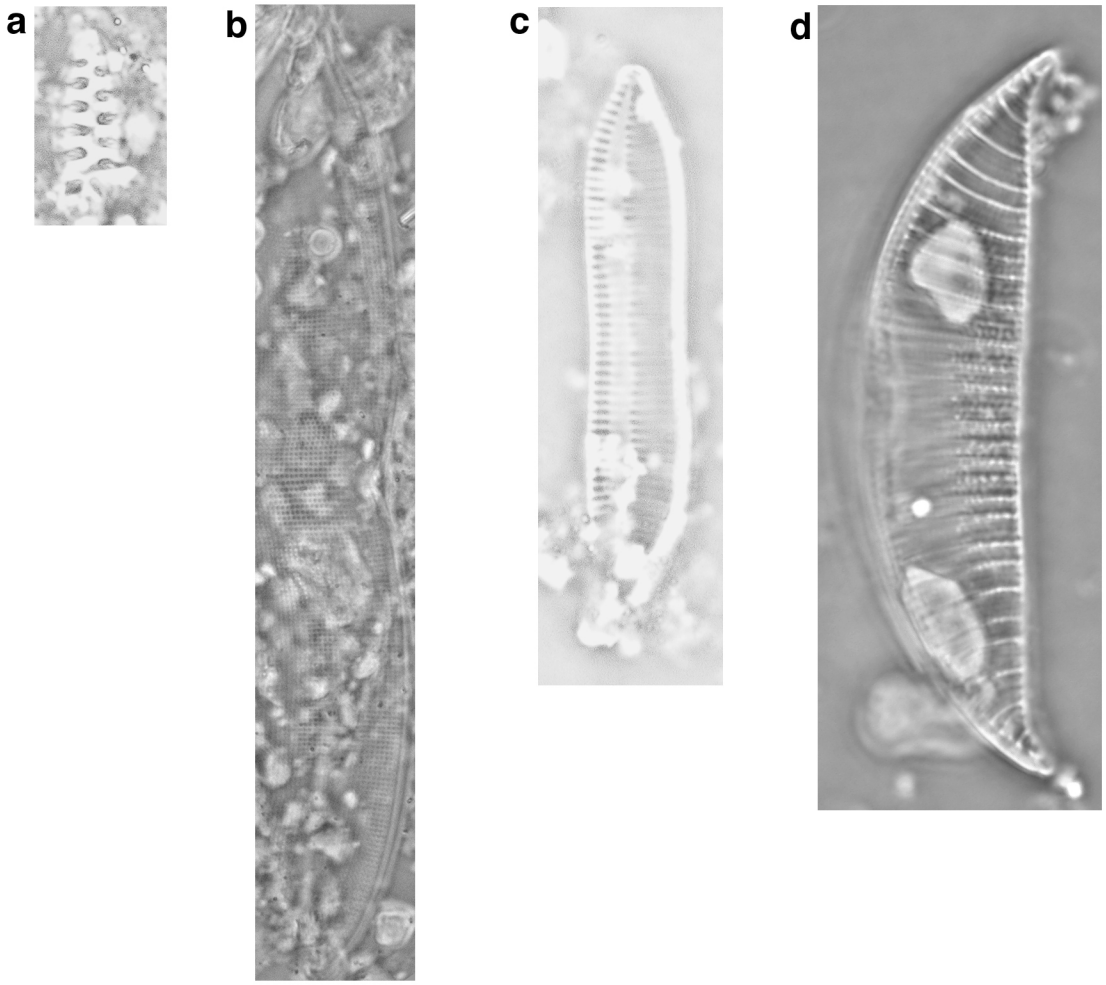
a. *Nitzschia compressa* (l=21, w=7)
b. *N. commutata* (l=62, w=6)
c. *N. filiformis* (missing)
d. *N. fonticola* (l=21, w=4.5)
e. *N.* sp. fragment (l=110, w=7.5)
f. *N. frustulum* (l=10, w=3.5)
g. *N hungarica* (l=63, w=6)
h. *N. laevis* (l=12, w=4)

Plate 13



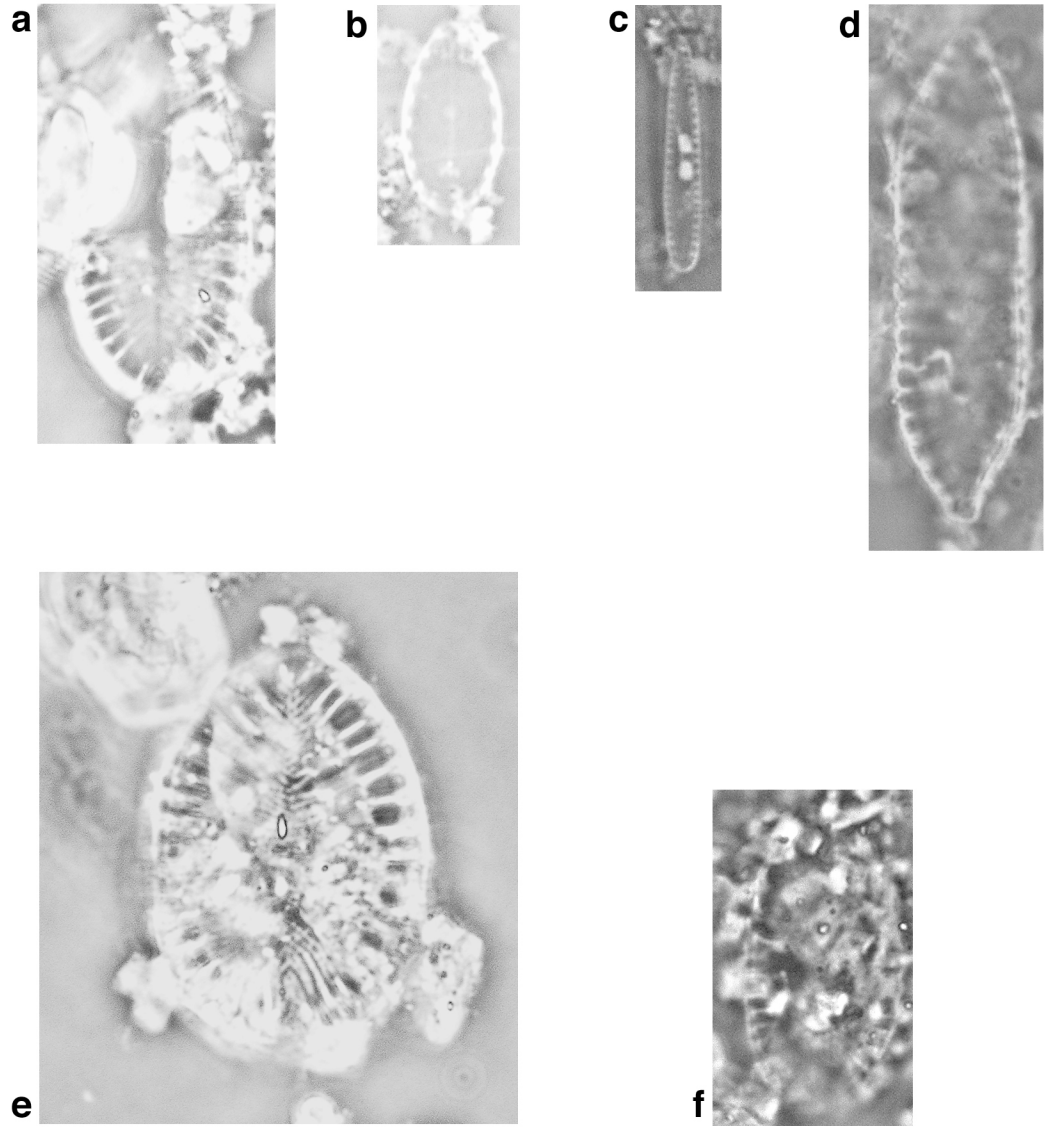
a. *Nitzschia lanceola minutula* (l=17, w=4.5)
b. *N. microcephala* (l=12.5, w=3.5)
c. *N. modesta* (l=21, w=3)
d. *N. palea* (l=44, w=5)
e. *N. pura* (l=35, w=4)
f. *N. pusilla* (l=34, w=3.5)
g. *N. reversa* (l=107, w=5)
h. *N. scalpeliformis* (l=112, w=9)
i. *N. thermaloides* (l=38, w=6)

Plate 14



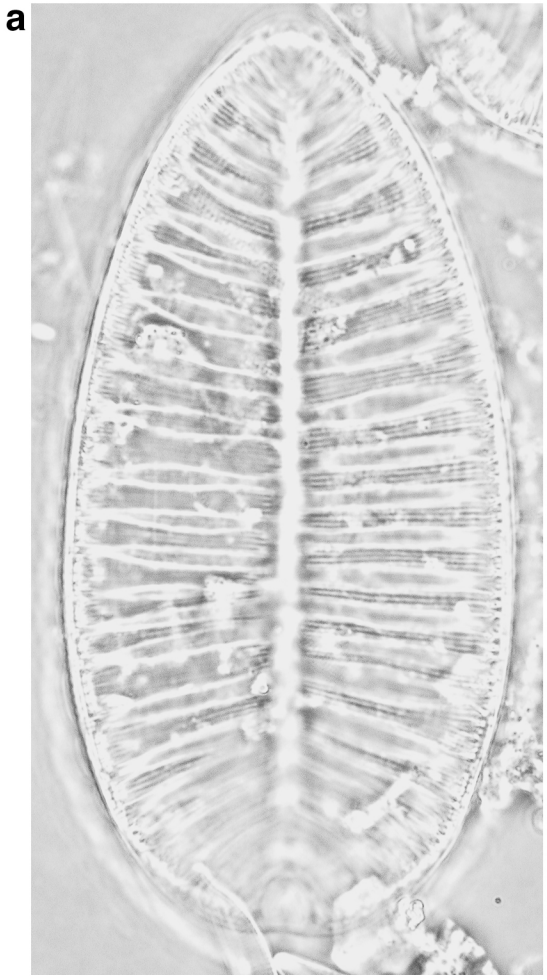
a. *Opephora martyi* (l=13, w=5)
b. *Plagiotropis arizonica* (l=115, w=20)
c. *Psamodictyon constrictum* (l=36, w=6.5)
d. *Rhopalodia musculus* (l=29, w=9)

Plate 15



a. *Surirella* sp. 1 (l=23, w=11)
b. *S.* sp. 2 (l=13.5, w=6.5)
c. *S.* sp. 3 (l=16, w=2.5)
d. *S. angusta* (l=32.5, w=9)
e. *S. brebissonii* (l=37, w=19)
f. *S. ovalis* (l=20, w=11)

Plate 16



a. *Surirella striatula* (l=69, w=35)

VITA

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Thesis: THE DIATOM ASSEMBLAGES OF THE SALT PLAINS NATIONAL WILDLIFE REFUGE AND DIATOM ALLOMETRY IN THE SOUTHWESTERN UNITED STATES

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