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Abstract

Although freshwater turtles and their epibiotic hosts are a good model for studying epibiotic interactions (including basking, the effects of turtle species, and geographic variation), information on diatom-turtle relationships are sparse, primarily documenting diatoms on two turtle species. The objective of this study was to characterize diatoms on freshwater turtles by comparing assemblages across: 1) four species: the common snapping turtle (*Chelydra serpentina*), the false map turtle (*Graptemys pseudogeographica*), the eastern mud turtle (*Kinosternon subrubrum*) and the common musk turtle (*Sternotherus odoratus*) and 2) the spatial range of the common snapping turtle (from Oklahoma, Arkansas, Illinois, Wisconsin, and New York). Turtle specimens came from museum collections at the Sam Noble Oklahoma Museum of Natural History and The Field Museum in Illinois. Six standardized areas on the turtle carapace were sampled for diatoms. Diatom assemblages were significantly different across all turtle species. *Luticola* cf. *goeppertiana* occurred on 97% of Oklahoma turtles and abundance differed with the following pattern: false map turtles > common snapping turtles > common musk turtles > eastern mud turtles. Diatom assemblages on common snapping turtles were different across states (OK ≠ IL, WI, NY, with AR intermediate). *Luticola* cf. *goeppertiana* occurred on 84% of sampled common snapping turtles and Oklahoma turtles had a higher mean abundance than the other four states. Observations of *Luticola* taxa, including *Luticola* cf. *goeppertiana* on turtles in both the northern and southern hemisphere indicates that this genus occurs on a variety of turtle species, and the species of *Luticola* found on turtles differs spatially. This research

shows a new use of museum specimens that allows efficient data collection and prevents unnecessary collection of live turtles.

Introduction

Hard-surfaced, benthic substrates can be a limiting resource in aquatic habitats because of a high abundance of organisms that settle and establish on these surfaces (Jackson 1977). This living biofilm is observed readily on rocks, submerged logs, and other coarse organic matter in both freshwater and marine ecosystems (Golladay and Sinsabaugh 1991, Gorbushina 2007). Living organisms can also host organisms on their surfaces, referred to as epibionts. Unlike non-living substrates which may not chemically influence the community assemblage on the substrate (e.g. Bergey 2005), the skin of living organisms is chemically active such as absorption and secretion of nutrients. The substrate of the host can influence the ecology of the epibionts (Wahl et al. 2012). Epibionts are often characterized by a smaller body size and shorter life span than their hosts (Wahl et al. 1997) and range from sessile organisms that attach to the body of the host to loosely associated, free-living organisms (Railkin 2003). In contrast, organisms that host epibionts tend to have a larger body size and longer life span (Wahl and Mark 1999). Some hosts have a rough surface texture, which may facilitate the recruitment of epibionts (e.g. Petraitis 1990).

Interaction between epibionts and their hosts can take a variety of forms, including mutualism, commensalism, and parasitism, with gradation among these types (Leung and Poulin 2008). Epibionts can provide camouflage for the host, such as the epibiotic algae, bryozoans, and sponges that live on the jewel box clam and help conceal their clam host from sea star predators. These epibionts rapidly colonize the rough surface of the clams, which have a greater epibiotic density than artificial, smooth shells (Vance 1978). Rough substrates provide a refuge from physical disturbance, which promotes successful establishment by small organisms (Bergey 1999), including marine larvae. Similarly, living freshwater mussels have higher algal and invertebrate densities than empty shells and differences among mussel species correspond to mussel activity and shell structure (Spooner and Vaughn 2006). Epibionts may harm their host decreasing creasing buoyancy (diatoms on *Daphnia* spp.; Allen et al. 1993), competing for food (filter feeding zebra mussels and their filter-feeding unionid mussel hosts; Strayer and Smith 1996), increasing rates of predation (crab predation is higher on the marine mussel *Carcinus* with barnacle epibionts; Wahl et al. 1997), or increasing physiological stress (increasing filtering rates or reducing fecundity in *Daphnia*; Allen et al. 1993, Stirnadel and Ebert 1997). The association of epibionts and hosts may change with epibiont density. For example, crayfish worms (Branchiobdellida) can be commensals at low densities, become mutualists by cleaning the exoskeleton of crayfish at higher densities (Lee et al. 2009), and become parasitic at high densities (Longshaw 2011). Populations of these epibionts can be regulated by the host, as crayfish remove some branchiobdellids during cleaning (Farrell et al. 2014) and *Daphnia* lose their epibionts during molting (Duneau and Ebert 2012). At the community level, epibiosis can be beneficial. For example, epizoic macroalga on snail shells contribute up to one third of the primary productivity in a stream (e.g. Stock et al. 1987) and snail shells can provide hard substrates for algal colonization in soft-bottomed ponds (Abbott and Bergey 2007).

Epibionts generally do not have a preference for a particular host and the epibiotic relationship tends to be facultative (Wahl and Mark 1999). This is particularly true of algae, which are a diverse group of organisms in freshwater environments (Stevenson et al. 1996). Algae are common in benthic habitats, occurring on non-living hard substrates (e.g. submerged rocks and wood; Potapova and Charles 2005) and on living substrates (Round 1971). Diverse assemblages of freshwater algae have been found on plant and animal substrates such as macrophytes, copepods, cladocerans, mussels, and snails (Millie and Lowe 1983, Møhlenberg and Kaas 1990, Gaiser and Bachmann 1994, Francoeur et al. 2002, Abbott and Bergey 2007). In contrast to these diverse assemblages, host-specificity occurs in a few algal-host associations. The epiphytic diatom *Lemnicola hungarica* is specific to duckweeds (especially *Lemna* spp.; Buczko 2007) and the epizoic diatom *Synedra cyclopum* is associated with zooplankton, including *Daphnia* and *Cyclops* (Gaiser and Bachmann 1994). The curved diatom *Cocconeis pediculus* is usually associated with the filamentous alga *Cladophora glomerata*, where its density may exclude other epiphytes (Bergey et al. 1995, Malkin et al. 2009). Recently, two new diatom species, *Tursiocola podocnemicola* and *Luticola deniseae* were described on the red-headed river turtle (*Podocnemis erythrocephala*, Spix 1924) in the Amazon Basin. These two taxa were not found on other substrates from the same habitat (Wetzel et al. 2010, Wetzel et al. 2012).

Freshwater macroalgae can also be host-specialists (Ziglar and Anderson 2005, Garbary et al. 2007). The filamentous green alga *Arnoldiella chelonum*, formerly known as *Basicladia chelonum* (Boedeker et al. 2012), was found on 85% of western pond turtles sampled in Oregon (Bury et al. 2015) and 94% of sampled common snapping turtles from the Mississippi River in Illinois (Ziglar and Anderson 2005). *A. chelonum* also commonly occurs on other hard-shelled turtle species in the United States, including the eastern mud turtle, map turtle, musk turtle, painted turtle, red-bellied turtle, and the red-eared slider (Edgreen et al. 1953, Belusz and Reed 1969, Ernst and

Norris 1978). Algal species within *Arnoldiella* have been found on turtles distributed elsewhere in the world. *A. chelonum* was reported on Blanding's turtles in Canada and Geoffroy's Side-necked turtle in Brazil (Garbary et al. 2007, Zanelli et al. 2009). A similar species, *Arnoldiella crassa* was reported on the Japanese pond turtle (Yoneda 1952). *Arnoldiella* has rarely been reported on substrates other than turtles (Edgreen et al. 1953) and can still persist on the carapace despite the variable conditions imposed by turtle basking and burrowing behaviors (Proctor 1958).

Characteristics of turtles, including their shell morphology, ecology, and behavior, may influence their epizoic algal communities. *Arnoldiella chelonum* occurrence and density tends to be lower on red-eared sliders and higher on common snapping turtles and eastern mud turtles, due to the morphology of the turtle shell and degree of basking (Edgreen et al. 1953, Proctor 1958). However, it is unknown how turtle characteristics influence epizoic diatom diversity, composition, and abundance. To date, two floristic studies have described diatoms on freshwater turtles, both on the European pond turtle (*Emys orbicularis*, Linnaeus 1758) in Turkey (Soylu et al. 2006, Ersanli and Gonulol 2015). These two studies highlight the paucity of information on diatoms on freshwater turtles. Furthermore, there are few studies comparing epizoic diatom composition on hosts in relation to environmental conditions and characteristics of the hosts' ecology (Totti et al. 2010).

Turtles and their epizoic diatoms are a good model system to study aquatic host-epibiont relationships because turtle shells provide a large and sturdy substrate for diatom attachment. Diatoms are speciose and species composition can be used to indicate environmental conditions. Diatoms are small enough to show differential colonization and loss in relation to different turtle shell morphologies and behavior (e.g. basking and hibernation), which likely affects the composition of epibiotic diatoms on the shell. In addition, turtles are well represented in musuem collections and use of preserved tutles to study epibionts allows efficient study of species across their ranges.

The overall objective of this study was to understand how the ecology and distribution of turtle hosts influences the epizoic diatom assemblages on their shells, using specimens from museum collections. The specific objectives were: 1) determine if there is a specific host association between any diatom species and turtles; 2) investigate diatom assemblages across four turtle species that vary in basking behavior; and 3) assess how diatom assemblages vary across the range of a single species, the common snapping turtle.

Materials and Methods

Turtle sampling

The following species were used to compare diatom assemblages across turtle species: the common snapping turtle (*Chelydra serpentina*), the false map turtle (*Graptemys pseudogeographica)*, the eastern mud turtle (*Kinosternon subrubrum)*, and the common musk turtle (*Sternotherus odoratus)*. These foci species were chosen based on 1) their occurrence in Oklahoma and 2) diverse shell morphology and ecology such as basking behavior. Adults were used because juvenile turtles tend to have fewer algae on the carapace (Edgreen et al. 1953). Nine replicate turtles for each of the four species were sampled from the herpetology collection at the Sam Noble Museum of Natural History, Oklahoma (Table 1). If possible, specimens that originated from the same location were chosen to reduce the effect of environmental variation influencing the diatom assemblages. Turtles were sampled from neighboring counties when it was not possible to obtain turtle specimens from the same locality (Fig 1a).

To assess diatom assemblages across states, the common snapping turtle was chosen because this turtle species is widely distributed in the United States (Ernst and Lovich, 1994). Regions chosen for this study were Oklahoma (n = 9 turtles), Arkansas (n = 4), Illinois (n = 5), Wisconsin (n = 4), and New York (n = 3). These states were chosen to provide replication of at least three turtle specimens per state, based on available specimens (Table 2). Oklahoma turtles were sampled at the Sam Noble Oklahoma Museum of Natural History and turtles from all other states were sampled at the Field Museum of Natural History in Chicago, Illinois (Fig 1b).

Three vertebral scutes and a total of three costal and marginal scutes were sampled to obtain a representative sample of the diatom community on the turtle carapace (Fig 2). The surface area sampled on the carapace was standardized by placing a plastic tube with a 1" internal diameter on top of the six, sampled scutes. A test tube brush (diameter: 1.3 cm) was placed inside the plastic tube, and brushed in a clockwise motion ten times. After sampling each scute, the sample on the brush was washed into a 20 mL scintillation vial (Sigma-Aldrich, St. Louis, MO) with 70% ethanol. The sampling protocol was approved by the Institutional Animal Care and Use Committee (IACUC), tracking number R14-008.

Diatom Processing and Analysis

For diatom species identification, samples were processed to eliminate the organic material. Samples were dried on 20 mm x 20 mm coverslips. The coverslips were placed on a Pryex® glass petri dish (55 mm diameter). The petri dish was placed in a muffle furnace set at 450˚C for 1.5 hours. Coverslips were mounted on microscope slides with Naphrax mounting medium (PhycoTech, Inc., St. Joseph, MI). Diatoms were viewed under 1000X magnification using an Olympus CX41 microscope and were identified using Krammer and Lange-Bertalot (1986) and Diatoms of the United States website (www.westerndiatoms.colorado.edu). Diatoms were counted to 200 valves by scanning transects across the coverslip. For samples with less than 200 valves, all the diatom valves in the sample were counted.

Statistical Analysis

Raw counts of diatom valves were pre-treated with a square root transformation to allow the intermediate species to contribute to the dissimilarity between diatom assemblages on 1) the four turtle species and 2) the common snapping turtle across five states (intermediate species are species that are not common or rare). Non-metric Multidimensional Scaling (NMDS) was performed with Bray Curtis similarities. Two separate, One-way Permutation Analysis of Variance (PERMANOVA) analyses with 999 permutations were performed to compare the diatom assemblages across 1) four turtle species and 2) common snapping turtles across five states. Associated pair-wise tests were used to identify which turtle species and states differed in their diatom assemblages. Similarity Percentage Analysis (SIMPER) was used to identify which diatom taxa contributed to the pair-wise comparisons that were significantly different. The data were analyzed with PRIMER version 6 (Primer-E Ltd, Plymouth Marine Laboratory, Plymouth, U.K.)

Results

Diatoms on turtle species of Oklahoma

A total of eighty-seven diatom species were documented across the four turtle species. Sixty-six percent of the diatom taxa on the turtles were potentially motile species, and thirty-four percent consisted of attached forms including, adnate, pad, erect, and stalked forms. The mean Shannon Diversity ranged from 1.18-2.00. The mean number of diatom taxa per turtle species were: 7.4 $\pm$0.7 SE on common snapping turtles; 9.1 $\pm$0.5 SE on eastern mud turtles; 14.1 $\pm$2.4 SE on false map turtles; and 18.0 $\pm$2.7 SE on common musk turtles. The combined mean diatom taxa per individual turtle was 12.2 $\pm$1.14 SE (range: 4-29).

The mean number of diatom valves per turtle species were: 16.2 $\pm$1.6 SE on eastern mud turtles; 68.3 $\pm$26.3 SE on common snapping turtles; 157.8 $\pm$21.2 SE on the false map turtles; and 200 $\pm$0.0 SE on eastern mud turtles. The regression between the number of valves counted and the mean species richness was significant (Fig 3; p = 0.01, R^2 = 0.80), indicating that turtles with more diatoms had more diatom species.

Nine diatom taxa were found on all four turtle species (Fig 4), with *Luticola* cf. *goeppertiana* occurring on most turtles (35 of 36 turtles). The most abundant diatoms (>2% mean abundance) on each turtle species were: *Luticola* cf. *goeppertiana* (6%) on common snapping turtles; *Luticola* cf. *goeppertiana* (9.3%) and *Achnanthidium minutissimum* (2.9%) on false map turtles; *Luticola* cf. *goeppertiana* (4.6%), *Nitzschia amphibia* (4.0%), *Achnanthidium* sp. 2 (3.2%), *Gomphonema olivaceum* (3.2%) and *Eunotia bilunaris* (2.1%) on common musk turtles. Eastern mud turtles did not have diatoms greater than >2% abundance, although *Luticola* cf. *goeppertiana* was the most abundant taxon (1.7%).

The NMDS ordination showed separation among the turtle species (Fig 5). The One-way PERMANOVA revealed that the diatom assemblages were significantly different across each turtle species (pseudo-F = 4.51, $p<0.01$) and pair-wise comparisons showed that all of the four species were different from each other. *Gomphonema olivaceum* contributed to the most dissimilarity (Table 3) between common musk turtles (mean abundance: 3.2%) compared to eastern mud turtles (<1%) and common snapping turtles (0%). *Luticola* cf. *goeppertiana* contributed to the most dissimilarity to the remaining four of the six pair-wise comparisons. False map turtles had the highest abundance of *Luticola* cf. *goeppertiana* (9.3%), followed by common snapping turtles (6%), common musk turtles (4.6%) and eastern mud turtles (1.7%). The presence and absence of taxa (often in <1% abundance) also contributed to differences between pair-wise comparisons of turtles.

A few diatom taxa were only found on a single turtle species. Two diatom taxa were only found on false map turtles and not on any other turtles (*Cymbella affinis* and *Tryblionella apiculata*). Likewise, eight diatom taxa were only found on common musk turtles (*Achnanthidium* sp. 2, *Diadesmis confervacea*, *Eunotia incisa*, *Eunotia minor*, *Eunotia naegeli*, *Fragilaria capucina*, *Frustulia rhomboides*, and *Lemnicola hungarica*). There were no diatom taxa that strictly occurred on common snapping turtles and the eastern mud turtles.

Diatoms on the common snapping turtle across regions

A total of 106 diatom species were found on common snapping turtles across the five sampled states. The mean Shannon Diversity ranged from 1.13-2.19. Six diatom taxa were found on all common snapping turtles (Fig 6) with *Luticola* cf. *goeppertiana* occurring on the most turtles (21 of 25 turtles). The mean number of diatom taxa from the following states were: 7.0 ±3.7 SE on Arkansas turtles; 7.3 ±0.8 SE on Oklahoma turtles; 15.6 ±4.2 SE on Illinois turtles; 18 ±7.4 SE on New York turtles; and 21.3 ±7.0 SE on Wisconsin turtles. The combined mean diatom taxa per common snapping turtle was 12.4 ±1.9 SE (range: 2-37).

The mean number of diatom valves per turtle species were: 20.8 ±8.2 SE on Arkansas turtles; 68.0 ±26.0 SE on Oklahoma turtles; 82.5 ±26.5 SE on Wisconsin turtles; 88.8 ±40.5 SE on Illinois turtles; and 141 ±59.0 SE on New York turtles. The regression between the mean number of diatoms counted and species richness among states was positive, although there was no difference in richness (Fig 7; $p>0.05$, $R^2 = 0.47$). Intermediate diatom counts had a highly variable number of species, such as the diatom counts on Oklahoma, Wisconsin, and Illinois turtles.

The most abundant diatoms (>2% mean abundance) on common snapping turtles from each state were: *Frustulia rhomboides* (2.9%) on Wisconsin turtles; *Luticola* cf. *mutica* (6.1%) and *Planothidium lanceolatum* (2.0%) on New York turtles; and *Luticola* cf. *goeppertiana* on Arkansas turtles (2.2%), Wisconsin turtles (2.2%), New York turtles (3.2%), Illinois turtles (3.3%), and Oklahoma turtles (6%).

Diatom assemblages on the common snapping turtle were significantly different across states (pseudo-F = 2.20, $p<0.01$; see Fig 8). Specifically, diatom assemblages on Oklahoma turtles were different from Illinois, Wisconsin, and New York turtles, whereas Arkansas diatom assemblages did not differ from Oklahoma or the Illinois-Wisconsin-New York turtles. Oklahoma turtles had a higher mean abundance of *Luticola* cf. *goeppertiana* (6%) compared to Illinois turtles (3.3%), New York turtles

(3.2%) and Wisconsin turtles (2.2%). Other taxa that contributed to differences between states (Table 4) include a greater abundance of *Luticola* cf. *mutica* (6.1%) on New York turtles compared to Oklahoma turtles (<1%) and the presence of *Frustulia rhomboides* (2.9%) on Wisconsin turtles and this taxon's absence on Oklahoma turtles.

Common snapping turtles from each state hosted diatom taxa that were not found on turtles from other states. Twenty-two diatom taxa were only found on Wisconsin turtles (*Achnanthidium minutissimum*, *Achnanthes* sp. 2, *Cavinula cocconeiformis*, *Cymatopleura solea*, *Eunotia circumborealis*, *Eunotia flexuosa*, *Eunotia paludosa*, *Eunotia serra* var. *diadema*, *Eunotia* sp. 1, *Eunotia* sp. 2, *Fragilaria* sp. 1, *Gomphonema gracile*, *Gyrosigma exilis*, *Navicula cinta*, *Pinnularia subcapitata*, *Pinnularia viridis*, *Sellaphora* sp. 1, *Stauroneis anceps*, *Stauroneis constricta*, *Staurosirella pinnata*, *Stephanodiscus* sp. 1, and *Tabellaria fenestrata*). Thirteen diatom taxa were only found on New York turtles (*Caloneis silicula*, *Caloneis* sp. 1, *Cyclotella bodanica*, *Diatoma tenuis*, *Diploneis subovalis*, *Discostella stelligera*, *Frustulia vulgaris*, *Gomphonema acuminatum*, *Gomphonema angustatum*, *Navicula leptostriata*, *Navicula trivialis*, *Pinnularia appendiculata*, and *Rhopalodia brebissonii*). Eleven diatom taxa were only found on Oklahoma turtles (*Achnanthidium* sp.1, *Bacillaria paradoxa*, *Cavinula scutelloides*, *Cymbella neocistula*, *Cymbella* sp. 1, *Diploneis parma*, *Gomphonema clevei*, *Navicula radiosa*, *Navicula salinarum*, *Navicula veneta*, and *Nitzschia pellucida*). Similarly, eleven diatom taxa were only found on Illinois turtles (*Amphora libyca*, *Caloneis schumanniana* var. *peisonis*, *Cyclotella ocellata*, *Gomphonema olivaceum*, *Neidium bisulcatum*, *Neidium* sp. 1, *Pinnularia gibba* var. *mesogongyla*, *Pinnularia streptoraphe*, *Sellaphora pupula*, *Tabularia fasiculata*, and unknown sp. 1). Three diatom taxa were only found on Arkansas turtles (*Navicula cari*, *Navicula* sp. 1, and *Rhopalodia musculus*). All of these diatom taxa that were exclusive on common snapping turtles from their states were present in <5% mean abundance.

Discussion

This study is the first comparison of freshwater epizoic diatom assemblages among turtle species and the first study of the spatial distribution of turtle-dwelling diatoms. Previous studies have described single, new diatom species (Wetzel et al. 2010, Wetzel et al. 2012) or listed diatoms on a single turtle species from a limited locale (Soylu et al. 2006, Ersanli and Gonulol 2015). Research on diatoms associated with marine turtles is similarly sparse. Majewska et al. (2015) studied diatom assemblages on 38 individual olive ridley turtles, *Lepidochelys olivacea* (Eschscholtz), and although samples were collected from the same locality, the species has a wide circum-tropical distribution with individuals traveling over long distances, making the study analogous to my across-states study of the common snapping turtle.

Two-thirds of the diatom species on turtles of Oklahoma were motile forms, which are capable of motility. This differs from Majewska et al. (2015), who found that most diatoms on marine olive ridley turtles’ forms were erect forms. A high proportion of motile diatoms are likely due to physical disturbance from the turtle hosts’ behavior, including burrowing and brushing against logs, vegetation, and other substrates, in contrast to the open ocean habitat of olive ridley turtles, where such physical substrates are less common. Physical disturbance prevents algal communities from developing complex architecture (including erect forms), whereas protection from disturbance allows 3-D architecture to develop (Luttenton and Rada 1986).

Comparison across turtle species

Diatom assemblages differed across each turtle species sampled within Oklahoma. Possible reasons for the observed differences among turtles are: 1) the degree of basking; 2) abrasion; 3) turtle habitat type; 4) shedding carapace lamina; and 5) water quality differences among collection sites. The degree of basking varies across turtle species, which influences the variation in epizoic diatom abundance. The common musk turtles basks below the surface of the water (Mahmoud 1969) and this species had the greatest abundance of diatoms (200 valves) among the four turtle species, presumably because the diatoms were not exposed to desiccation from aerial exposure. Similarly, 86% of common musk turtles sampled in Pennsylvania had macroalgae on the carapace (Ernst 1986). The two species with intermediate diatom abundances, false map turtles and common snapping turtles, bask on shorelines and emergent rocks and logs (Boyer 1965). A report found that 40% of common snapping turtles and 5% of *Graptemys* species (similar to the false map turtle) sampled hosted macroalgae on the carapace (Edgreen et al. 1953). Eastern mud turtles had the lowest diatom abundance and typically remain submerged on the bottom of fine-substrate habitats (Mahmoud 1969), where algae may be light limited.

Epibionts can also be subjected to abrasion, which may impact the epizoic diatoms. Turtles such as the common snapping turtle burrow in the mud for long periods in the winter (Meeks and Ultsch 1990), which restricts diatoms' access to light. Turtle activities such as mating and contact with other turtles can also cause abrasion and remove epibionts (Frick and Pfaller 2013). Experimentally, it has been shown that abrasion reduces diatom density on algal-enriched caddisfly cases, which changes the distribution of algae (Bergey and Resh 1994). A similar process may also occur on turtle carapaces.

Habitat differences among turtles likely influence the composition of the epizoic diatom assemblage. Different species of turtles in Oklahoma were associated with particular habitats that varied in river structure, water flow, and depth (Riedle 2009). Common snapping turtles and common musk turtles in Oklahoma were associated with streams and backwaters. In contrast, false map turtles were found in deep, slow-moving water with clay substrates (Riedle 2009). Eastern mud turtles were associated in habitats with a shallow depth and abundant, emergent vegetation (Mahmoud 1969, Riedle et al. 2015). Museum specimens lacked specific habitat descriptions and the two turtle species with similar habitat preferences (common snapping and common musk turtles) had different diatom assemblages. Consequently, no definitive conclusions could be made on habitat effects.

Turtles shed carapace lamina from the scutes, especially during growth and epibionts associated with shed lamina would be lost (Caine 1986). Juvenile turtles have few macroalgae, which was partially attributed to their faster rate of shedding relative to older turtles (Neil and Allen 1954). Although we sampled adult turtles, it is possible that previous shedding of lamina affected diatom abundance on some specimens. This differs from hosts that frequently shed, such as *Daphnia*, which can molt as often as every 2-4 days during the summer, losing their epibiotic diatoms (Bottrell et al. 1976).

Diatoms are sensitive to water quality (Smol and Stoermer 2010) and different collection sites may have different water quality. The use of museum specimens precluded getting water quality measurements. The four turtle species were collected from three sampling areas in the state, with two species collected in Marshall County (eastern mud turtles and false map turtles). Although these two species were collected near the OU Biological Station and water quality should be similar, the species' hosted different diatom assemblages. This indicates that the ecology and behavior of turtles influence the diatom assemblage composition beyond water quality effects.

Comparison across states

Diatom assemblages on the common snapping turtle were significantly different across states. One trend was that contiguous states, specifically Oklahoma and Arkansas, or Wisconsin and Illinois did not significantly differ in their diatom assemblages. Contiguous states likely share similar environmental characteristics. This pattern did not always hold true for greater, geographic distance. Whereas Oklahoma and Illinois-Wisconsin-New York turtles had different assemblages, Arkansas assemblages did not differ from either of these two groups. The similarity of diatom assemblages in Arkansas to Illinois-Wisconsin-New York assemblages may be related to these four states being classified as Eastern Temperate Forests (Omernik's Ecoregion level I), whereas Oklahoma is in the Great Plains Ecoregion.

The difference between the Oklahoma and Illinois-Wisconsin-New York diatom assemblages was primarily Oklahoma turtles having the higher abundance of the diatom *Luticola* cf. *goeppertiana*. *Luticola* is an aerophilic genus (Johansen 2010), and a greater abundance on Oklahoma turtles indicates that these turtles spent more time basking (and exposure to the air). The annual activity of common snapping turtles appears to be longer in lower latitudes and shorter in higher latitudes (e.g. Lovich 1988) and basking behavior probably follows the same pattern, with more basking in

Oklahoma and Arkansas. Common snapping turtles in Illinois were active from February to December whereas common snapping turtles from Ontario, Canada are active from June to October (Obbard and Brooks, 1981).

The differences that we observed among diatom assemblages on turtles from different states could potentially be due to a combination of spatial and environmental factors. Two large-scale patterns that influence the distribution of benthic diatoms in US Rivers are latitude and pH. Latitude is discussed in the effects of geographical separation. The pH gradient from eastern to western US transitions from acidic waters to alkaline waters (Potapova and Charles 2002). This pH gradient likely explains the presence of slightly acidic taxa, including *Tabellaria flocculosa*, *Pinnularia* species, and *Eunotia* species, that were only present on the more eastern Illinois, Wisconsin, and New York turtles. In addition, fifty-seven percent of the 106 diatom taxa on common snapping turtles were found in only one state. This could potentially indicate that local environmental variables influenced the diatom assemblages (e.g. Pan et al. 1996). Future work is needed to analyze which variables are important for influencing epizoic diatom communities on turtles.

The genus *Luticola* was characteristic of turtles, regardless of species and site. *Luticola* cf. *goeppertiana* occurred on 97% of the Oklahoma turtles and 84% of the common snapping turtles in this study. One possibility for the prevalence of *Luticola* on turtles is the ability to tolerate desiccation while the turtles bask. Subaerial diatom taxa including *Luticola* have reduced external openings, which could be an adaptation for decreasing water loss (Lowe et al. 2007). The reduced openings may be an adaptation for *Luticola* to persist on the turtle carapace, despite the variable conditions imposed by basking behavior. Depending on the turtle species and season, basking occurs in air temperatures ranging from 10-44ºC (Boyer 1965, Mahmoud 1969). These basking ranges may differentially desiccate aquatic taxa in comparison to subaerial and terrestrial taxa. Souffreau et al. (2010) experimentally tested the tolerance of benthic diatoms to desiccation, comparing the response of aquatic taxa to terrestrial taxa. Diatoms were heated in an incubator to +40ºC. The results showed that more terrestrial taxa survived than did aquatic taxa (Souffreau et al. 2010).

More than one species of *Luticola* may be associated with turtles. In addition to *Luticola* cf. *goeppertiana* found in this study, a second *Luticola* species (*L*. cf. *uruguayensis*) was found on turtles in the Little River, Oklahoma (Wu, unpublished data). Similarly, Wetzel et al. (2010) found *Luticola deniseae* on the red-headed Amazon River turtle. This diatom was a new species present on the turtle and not on other substrates in the same habitat (Wetzel et al. 2010). Observations of three *Luticola* taxa on turtles in both the northern and southern hemisphere indicate that this genus is adapted to living on turtles. *Luticola* occurs on a variety of turtle species and the species of *Luticola* found on turtles differs spatially.

Use of museum specimens

Museum-based research provided the opportunity to characterize diatom diversity in relation to the natural history of turtles and diatom biogeography on the common snapping turtle, which would have been more difficult to accomplish with live turtles. Benefits of using museum collections include a combination of saving time, reducing research costs, avoiding unnecessary duplication of specimens (Suarez and Tsutsui 2004), and eliminating stress to live turtles. Limitations associated with using museum turtle specimens for studying epizoic diatoms are: 1) obtaining turtles from the same or known locality (including a lack of associated environmental data) and 2) possible effects of turtle processing. In the comparison of diatom assemblages across turtles, I attempted to reduce the environmental variation by sampling turtles from the same locality. This was not always possible because multiple specimens from the same site were not always present and many specimens lacked specific locality data.

Another challenge with using museum specimens is the effects of turtle processing. For example, museum personnel might remove filamentous algae from the shells. Although past history of curation at the Sam Noble Museum of History is not known, algal scrapping is not a current practice and has not been documented in their database (Jessa Watters, personal communication). Algae are not routinely removed from turtles at the Field Museum (Alan Resetar, personal communication). Even if filamentous algae were removed, sampling six areas on the carapace may reduce the impacts on the sampled diatom assemblage.

Beyond the scope of this study, museum collections can be used to evaluate diatom assemblages to infer environmental change. Shirey et al. (2008) assessed the ecological changes in the Rio Grande by comparing diatom assemblages in the guts of the silvery minnow, using museum specimens from 1874 to 1978 (pre and post damming). The differences in the diatom assemblages across time were likely due to river regulation (Shirey et al. 2008). A similar study assessed diatoms in the guts of several fish species comparing “paleo” assemblages (1925-1948) to “modern” assemblages (2003 and 2007), finding only 3 of 22 sites improved in biological integrity (Lavoie and Campeau 2010). Likewise, a time series of epizoic diatoms could be used to infer temporal water quality changes through time. Habitat degradation is a serious threat to reptile populations including turtles (Gibbons et al. 2000). The application of museum specimens to infer water quality conditions of turtles' habitats could be used for freshwater turtle conservation and habitat restoration.

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Table 1: Turtle specimens sampled from the Sam Noble Museum of Natural History Museum, Oklahoma.

OMNH Catalog Number	Turtle Species	County, State
27453	*Chelydra serpentina*	Murray, OK
7991	*Chelydra serpentina*	Pawnee, OK
19093	*Chelydra serpentina*	Cleveland, OK
10160	*Chelydra serpentina*	Seminole, OK
5577	*Chelydra serpentina*	Cleveland, OK
5571	*Chelydra serpentina*	N/A
10921	*Chelydra serpentina*	Seminole, OK
12877	*Chelydra serpentina*	Cleveland, OK
5573	*Chelydra serpentina*	Cleveland, OK
27586	*Graptemys pseudogeographica*	Marshall, OK
27584	*Graptemys pseudogeographica*	Marshall, OK
27588	*Graptemys pseudogeographica*	Marshall, OK
27587	*Graptemys pseudogeographica*	Marshall, OK
27575	*Graptemys pseudogeographica*	Marshall, OK
27175	*Graptemys pseudogeographica*	Marshall, OK
27591	*Graptemys pseudogeographica*	Marshall, OK
27338	*Graptemys pseudogeographica*	Marshall, OK
26912	*Graptemys pseudogeographica*	Marshall, OK
27320	*Kinosternon subrubrum*	Marshall, OK
27332	*Kinosternon subrubrum*	Marshall, OK
27337	*Kinosternon subrubrum*	Marshall, OK
27334	*Kinosternon subrubrum*	Marshall, OK
27317	*Kinosternon subrubrum*	Marshall, OK
27336	*Kinosternon subrubrum*	Marshall, OK
27335	*Kinosternon subrubrum*	Marshall, OK
27318	*Kinosternon subrubrum*	Marshall, OK
27550	*Kinosternon subrubrum*	Marshall, OK
35402	*Sternotherus odoratus*	McCurtain, OK
35407	*Sternotherus odoratus*	McCurtain, OK
35400	*Sternotherus odoratus*	McCurtain, OK
37864	*Sternotherus odoratus*	McCurtain, OK
35408	*Sternotherus odoratus*	McCurtain, OK
35399	*Sternotherus odoratus*	McCurtain, OK
35398	*Sternotherus odoratus*	McCurtain, OK
43532	*Sternotherus odoratus*	Le Flore, OK
35403	*Sternotherus odoratus*	McCurtain, OK

Table 2. Common snapping turtle specimens sampled from the Field Museum of Natural History, Illinois.

FMNH Catalog Number	Turtle Species	County, State
3291	*Chelydra serpentina*	N/A, IL
37198	*Chelydra serpentina*	Grundy, IL
164575	*Chelydra serpentina*	Cook, IL
22738	*Chelydra serpentina*	Du Page, IL
8108	*Chelydra serpentina*	N/A, IL
8941	*Chelydra serpentina*	N/A. AR
8812	*Chelydra serpentina*	N/A, AR
8939	*Chelydra serpentina*	N/A, AR
8942	*Chelydra serpentina*	N/A, AR
14717	*Chelydra serpentina*	N/A, WI
13057	*Chelydra serpentina*	N/A, WI
164577	*Chelydra serpentina*	Racine, WI
24224	*Chelydra serpentina*	Oneida, WI
92006	*Chelydra serpentina*	Wayne, NY
92007	*Chelydra serpentina*	Saratoga, NY
92010	*Chelydra serpentina*	Monroe, NY

Table 3. SIMPER results of the mean abundance of diatom taxa that contributed the most difference between pair-wise comparisons of turtle species.

Diatom Taxa	Snapping	Map	Mud	Musk
Achnanthidium minutissimum	0.54	2.85	0.33	0.00
Achnanthidium sp. *2*	0.00	0.00	0.00	3.31
Cyclotella meneghiniana	0.00	0.27	0.60	0.16
Diploneis parma	0.38	1.62	0.33	0.19
Gomphonema clavatum	0.66	1.61	0.36	1.37
Gomphonema olivaceum	0.00	0.19	0.11	3.21
Gomphonema parvulum	0.22	1.71	0.27	0.87
Luticola cf. *goeppertiana*	6.00	9.25	1.71	4.60
Nitzschia amphibia	0.67	0.78	0.41	3.96
Nitzschia frustulum	0.27	0.36	0.00	2.66
Pinnularia microstauron	0.00	0.00	0.93	0.52

Table 4. SIMPER results of the mean abundance of diatom taxa that contributed the most difference between pair-wise comparisons of common snapping turtles across states.

Diatom Taxa	Oklahoma	Arkansas	Illinois	Wisconsin	New York
Aulacoseira granulata	0.11	0.00	1.70	0.25	1.14
Cocconeis placentula	0.00	0.25	0.00	0.35	1.79
Eunotia incisa	0.16	0.00	0.00	1.11	0.00
Fragilaria capucina	0.00	0.35	1.89	1.06	0.91
Frustulia rhomboides	0.00	0.00	0.00	2.89	0.47
Luticola cf. *goeppertiana*	6.00	2.23	3.30	2.21	3.19
Luticola cf. *mutica*	0.84	1.25	0.20	0.93	6.12
Nitzschia amphibia	0.67	0.25	0.63	0.85	1.37
Nitzschia frustulum	0.27	0.97	1.18	0.00	1.37
Nitzschia inconspicua	0.11	0.25	1.73	1.72	1.76
Pinnularia microstauron	0.00	0.00	0.00	1.78	0.00
Planothidium lanceolatum	0.16	0.00	0.63	0.56	2.00

Fig 1. Origin of museum turtle specimens. The numbers in each symbol represents the sample size of turtles from their origin of location. Dots shown in the middle of the county (Fig 1a) and state (Fig 1b) means the origin of the sample is unknown beyond the county and state, respectively.

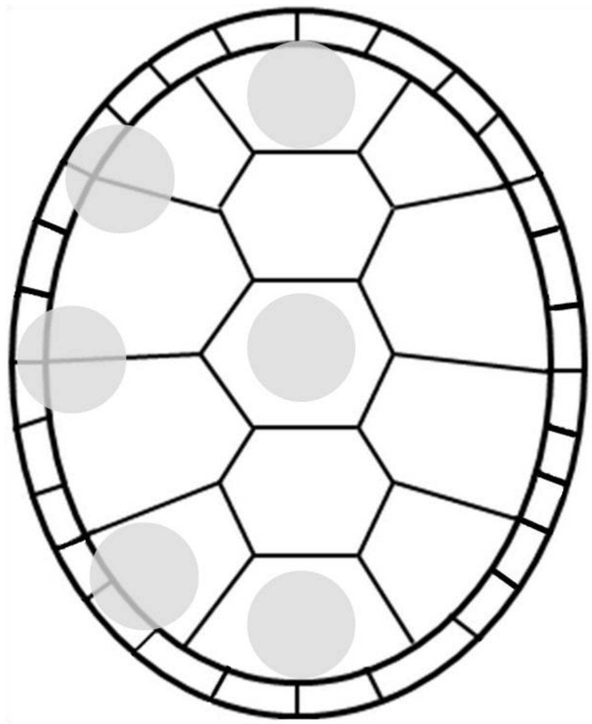

Fig 2. Areas sampled on the turtle shell. The shaded circles represent the standardized areas sampled for diatoms.

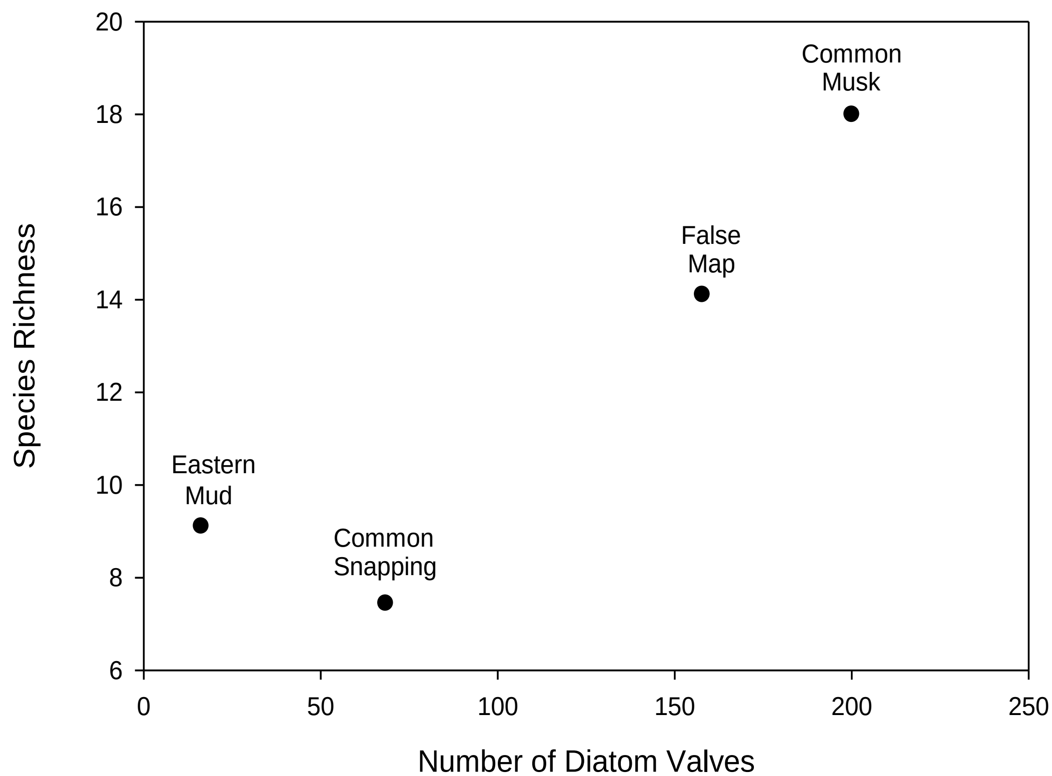

Fig 3. The mean diatom species richness in relation to the mean number of diatom valves counted on each turtle species.

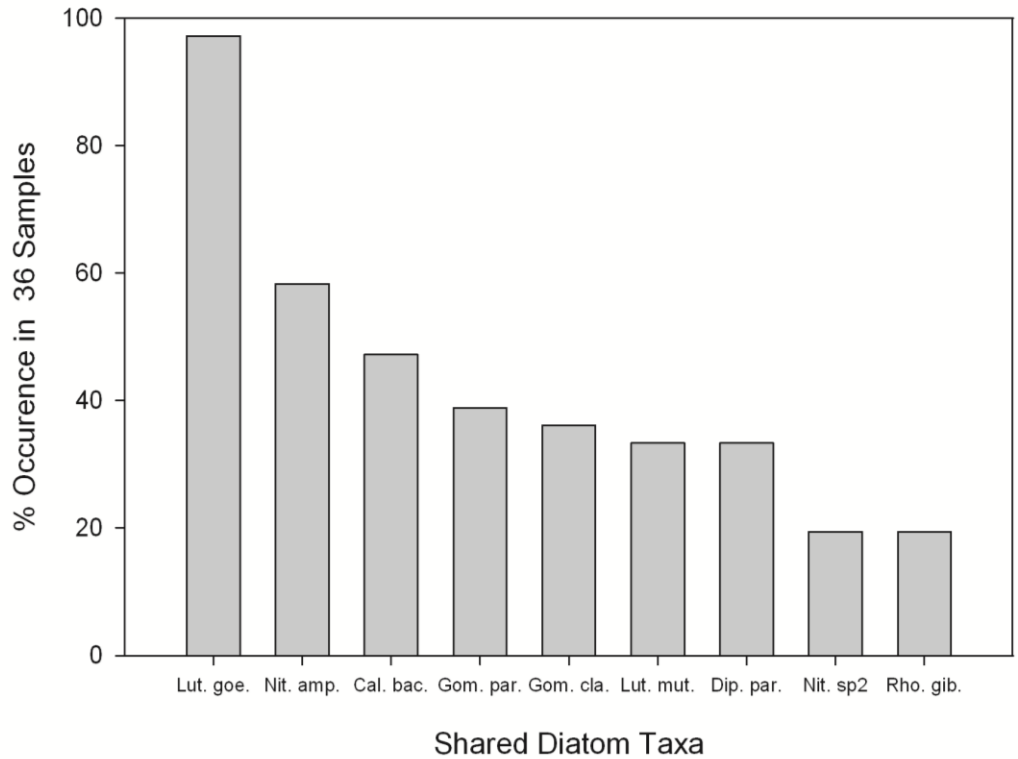

Fig 4. Diatom taxa present on all turtle species. The full diatom species names are: *Luticola* cf. *goeppertiana, Nitzschia amphibia, Caloneis bacillum, Gomphonema parvulum, Gomphonema clavatum, Luticola* cf. *mutica, Diploneis parma, Nitzschia* sp. 2, and *Rhopalodia gibba*.

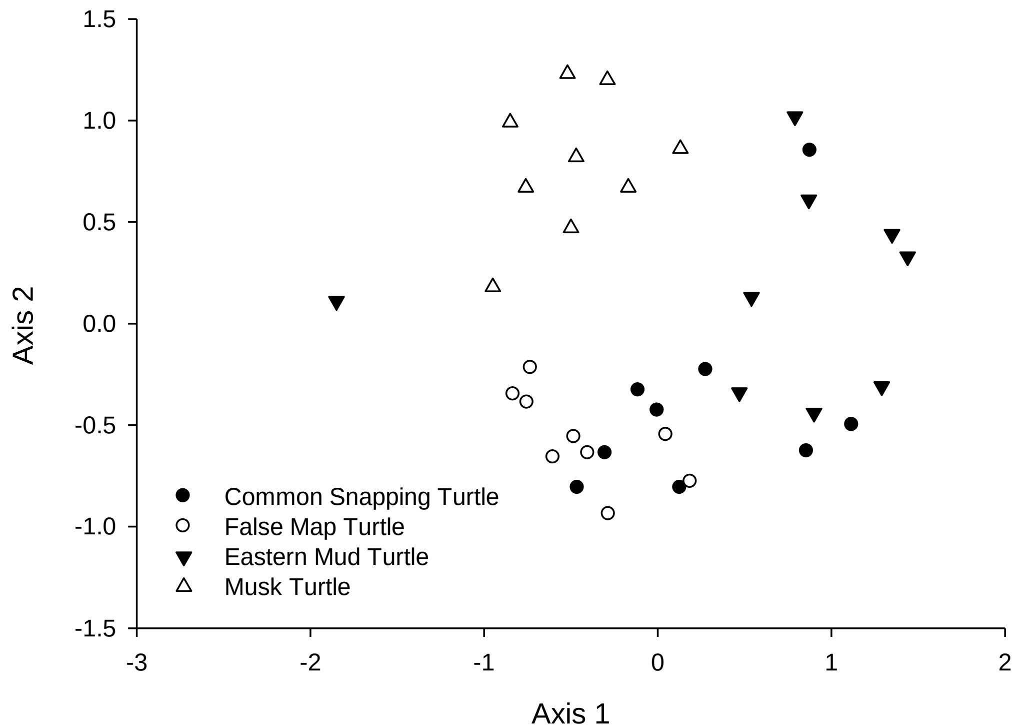

Fig 5. NMDS plot of diatom assemblages across turtle species. 3D Stress = 0.14.

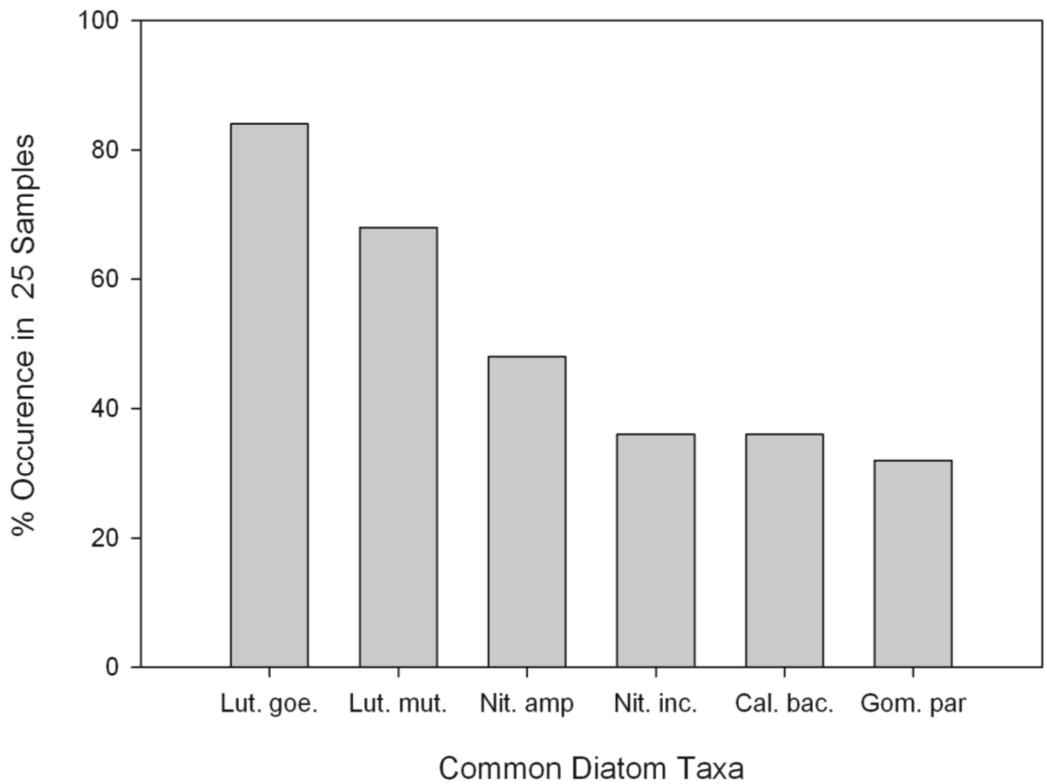

Fig 6. Diatom taxa present on the common snapping turtle across region. The full diatom species names are: *Luticola* cf. *goeppertiana*, *Luticola* cf. *mutica*, *Nitzschia amphibia*; *Nitzschia inconspicua*, *Caloneis bacillum* and *Gomphonema parvulum*.

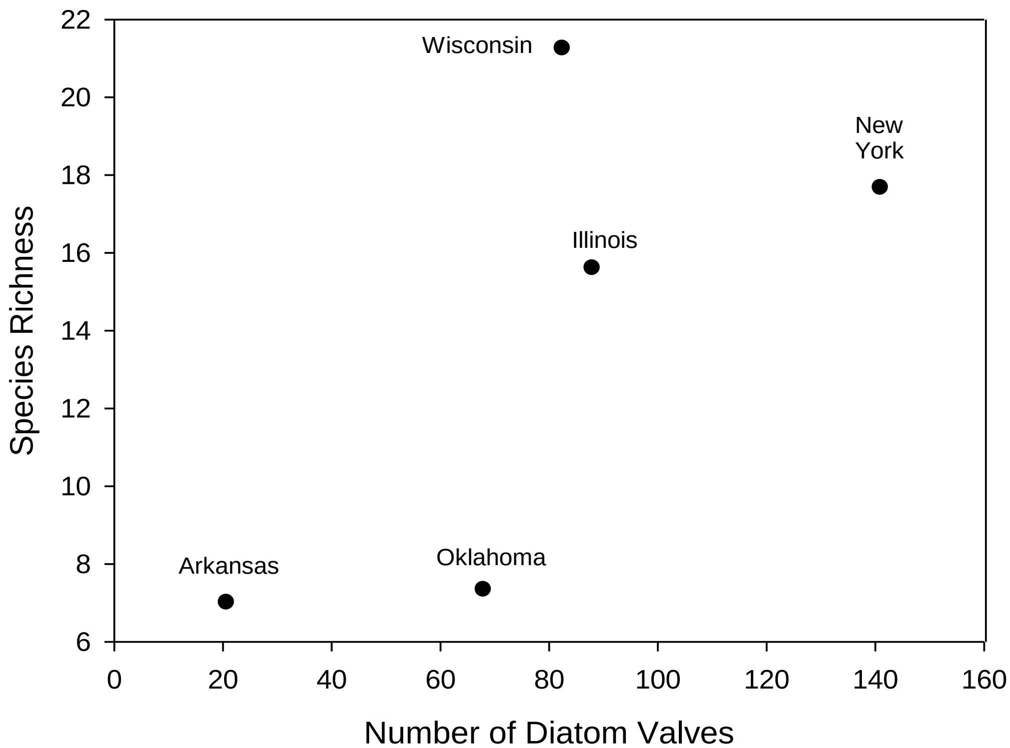

Fig 7. The mean diatom species richness in relation to the mean number of diatom valves counted on each turtle species.

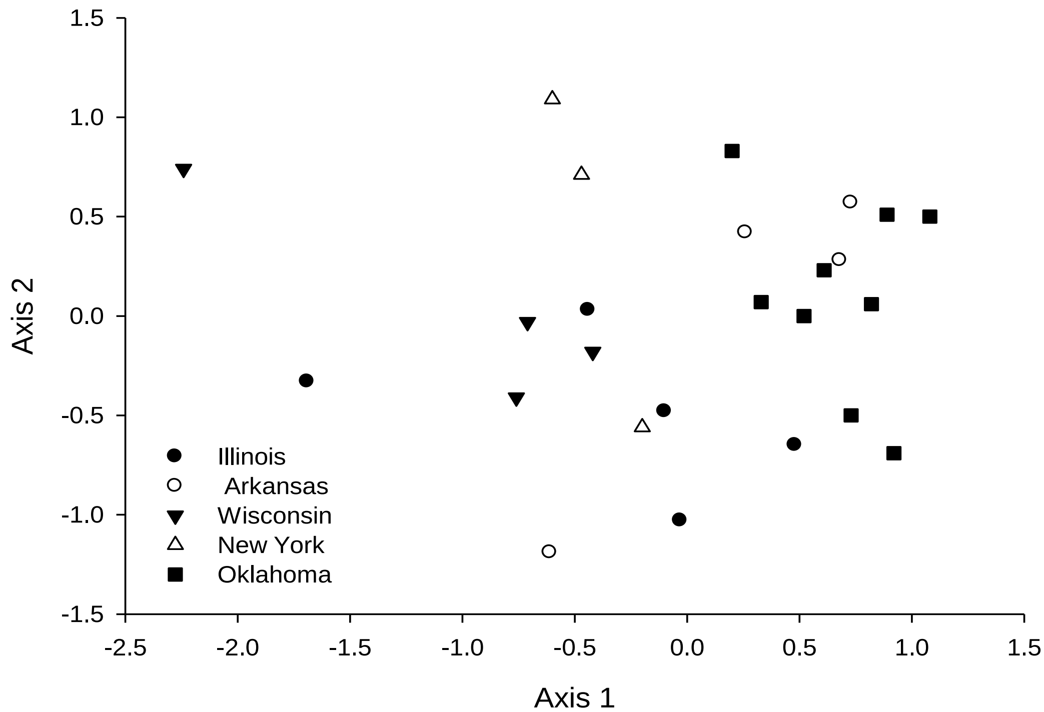

Fig 8. NMDS plot of diatom assemblages on the common snapping turtle across region. 3D Stress = 0.12.

Appendix A. The mean relative abundance of diatom taxa on each turtle species. The number in parenthesis represents the number of turtles that hosted that diatom taxon.

Diatom Taxa	Common Snapping	False Map	Eastern Mud	Common Musk
Achnanthes conspicua	0.00 (0)	0.00 (0)	1.85 (2)	0.00 (0)
Achnanthes delicatula	0.00 (0)	0.07 (1)	0.00 (0)	0.00 (0)
Achnanthes sp. 1	0.00 (0)	0.06 (1)	0.00 (0)	0.00 (0)
Achnanthidium minutissimum	2.27 (4)	7.89 (5)	1.99 (3)	0.00 (0)
Achnanthidium sp. 1	3.85 (3)	0.07 (1)	0.00 (0)	5.72 (2)
Achnanthidium sp. 2	0.00 (0)	0.00 (0)	0.00 (0)	9.06 (7)
Actinocyclus sp. 1	0.32 (1)	1.63 (1)	0.00 (0)	0.00 (0)
Amphora libyca	0.00 (0)	0.00 (0)	0.65 (1)	0.00 (0)
Amphora ovalis	0.00 (0)	0.00 (0)	0.00 (0)	0.06 (1)
Amphipleura pellucida	0.00 (0)	0.00 (0)	0.00 (0)	0.11 (2)
Aulacoseira granulata	0.00 (0)	0.17 (1)	0.00 (0)	1.89 (2)
Bacillaria paradoxa	0.00 (0)	0.06 (1)	0.00 (0)	0.00 (0)
Caloneis bacillum	0.63 (3)	1.02 (7)	1.45 (2)	0.50 (5)
Caloneis schumanniana	1.23 (1)	0.00 (0)	0.00 (0)	0.00 (0)
Caloneis silicula	0.00 (0)	0.11 (1)	0.93 (1)	0.00 (0)
Cocconeis pediculus	0.00 (0)	0.07 (1)	0.00 (0)	0.11 (1)
Cocconeis placentula	0.00 (0)	0.17 (1)	0.00 (0)	2.50 (5)
Cyclotella meneghiniana	0.00 (0)	0.28 (2)	5.07 (5)	0.11 (1)
Cyclotella sp.1	0.00 (0)	0.06 (1)	0.00 (0)	0.00 (0)
Cymbella affinis	0.00 (0)	0.79 (4)	0.00 (0)	0.00 (0)
Cymbella amplificata	0.24 (1)	0.29 (2)	0.00 (0)	0.00 (0)
Cymbella cistula	0.00 (0)	1.84 (4)	0.93 (1)	0.00 (0)
Cymbella neocistula	1.21 (1)	0.34 (1)	0.00 (0)	0.00 (0)
Cymbella tumida	0.00 (0)	0.00 (0)	0.53 (1)	0.00 (0)
Diadesmis confervacea	0.00 (0)	0.00 (0)	0.00 (0)	3.11 (4)
Discostella stelligera	0.00 (0)	0.00 (0)	0.44 (1)	0.00 (0)
Diploneis oblongella	0.00 (0)	0.12 (2)	0.65 (1)	0.00 (0)

Diatom Taxa	Common Snapping	False Map	Eastern Mud	Common Musk
Diploneis parma	3.51 (3)	2.76 (5)	2.31 (3)	0.17 (1)
Diploneis sp. 1	0.00 (0)	0.07 (1)	1.51 (2)	0.00 (0)
Encyonema elginense	0.00 (0)	0.00 (0)	0.00 (0)	0.22 (2)
Encyonema silesiacum	0.00 (0)	0.61 (4)	5.52 (4)	1.39 (7)
Encyonema sp. 1	0.00 (0)	0.11 (1)	0.00 (0)	0.00 (0)
Encyonema triangulum	0.00 (0)	1.10 (4)	0.62 (1)	0.00 (0)
Encyonopsis microcephala	1.01 (1)	0.71 (4)	0.00 (0)	0.00 (0)
Epithemia adnata	0.00 (0)	0.00 (0)	1.47 (2)	0.61 (3)
Eunotia bilunaris	0.24 (1)	0.00 (0)	0.00 (0)	3.50 (7)
Eunotia formica	0.00 (0)	0.00 (0)	0.00 (0)	0.28 (1)
Eunotia incisa	0.00 (0)	0.00 (0)	0.00 (0)	0.83 (2)
Eunotia minor	0.00 (0)	0.00 (0)	0.00 (0)	1.00 (2)
Eunotia naegeli	0.00 (0)	0.00 (0)	0.00 (0)	1.33 (2)
Eunotia pectinalis var. *undulata*	0.00 (0)	0.00 (0)	0.00 (0)	0.61 (2)
Fragilaria capucina	0.00 (0)	0.00 (0)	0.00 (0)	0.94 (4)
Fragilaria tenera	0.00 (0)	0.88 (5)	0.53 (1)	0.00 (0)
Frustulia rhomboides	0.00 (0)	0.00 (0)	0.00 (0)	0.67 (2)
Gomphonema affine	0.06 (1)	0.06 (1)	0.00 (0)	0.00 (0)
Gomphonema clavatum	0.89 (3)	3.31 (5)	4.01 (2)	3.00 (3)
Gomphonema gracile	0.63 (1)	0.13 (1)	0.00 (0)	0.61 (3)
Gomphonema minutum	0.00 (0)	0.00 (0)	0.00 (0)	0.89 (5)
Gomphonema olivaceum	0.00 (0)	0.20 (1)	0.85 (1)	13.4 (5)
Gomphonema parvulum	0.58 (2)	3.91 (5)	2.09 (2)	0.83 (5)
Hantzschia amphioxys	1.44 (2)	0.00 (0)	0.00 (0)	0.11 (2)
Hippodonta capitata	0.00 (0)	0.28 (4)	2.26 (3)	0.00 (0)
Hippodonta capitata var. *hungarica*	0.00 (0)	0.07 (1)	2.78 (2)	0.00 (0)
Lemnicola hungarica	0.00 (0)	0.00 (0)	0.00 (0)	1.56 (5)
Luticola cf. *goeppertiana*	60.5 (9)	62.2 (9)	23.1 (8)	12.6 (9)
Luticola cf. *mutica*	5.00 (4)	0.28 (2)	1.81 (2)	2.72 (4)
Navicula cari	0.00 (0)	0.00 (0)	2.16 (2)	0.11 (1)
Navicula clementis	0.00 (0)	0.00 (0)	0.00 (0)	0.17 (2)

Diatom Taxa	Common Snapping	False Map	Eastern Mud	Common Musk
Navicula cryptonella	0.00 (0)	0.00 (0)	3.03 (4)	1.50 (7)
Navicula phyllepta	0.00 (0)	0.00 (0)	0.62 (1)	0.00 (0)
Navicula radiosa	1.31 (3)	0.22 (2)	2.61 (1)	0.00 (0)
Navicula salinarum	0.33 (1)	0.00 (0)	0.11 (1)	0.00 (0)
Navicula veneta	1.72 (2)	0.00 (0)	0.00 (0)	0.00 (0)
Nitzschia amphibia	3.12 (6)	0.84 (4)	3.37 (3)	11.5 (8)
Nitzschia frustulum	0.56 (2)	1.16 (2)	0.00 (0)	8.89 (4)
Nitzschia inconspicua	0.00 (0)	0.20 (1)	0.44 (1)	0.39 (3)
Nitzschia pellucida	0.24 (1)	0.00 (0)	0.00 (0)	0.00 (0)
Nitzschia perminuta	0.00 (0)	0.00 (0)	0.44 (1)	0.33 (4)
Nitzschia sp. 1	1.03 (2)	0.46 (5)	0.00 (0)	0.00 (0)
Nitzschia sp. 2	1.23 (1)	0.87 (4)	1.23 (1)	0.06 (1)
Nitzschia sp. 3	0.00 (0)	0.00 (0)	0.62 (1)	0.00 (0)
Pinnularia microstauron	0.00 (0)	0.00 (0)	11.6 (4)	0.61 (2)
Pinnularia sp. 1	0.00 (0)	0.00 (0)	0.00 (0)	0.11 (1)
Pinnularia viridis	0.30 (2)	0.29 (4)	0.00 (0)	0.22 (2)
Planothidium lanceolatum	2.02 (1)	0.00 (0)	0.00 (0)	3.83 (6)
Rhopalodia gibba	1.87 (2)	0.17 (1)	0.93 (1)	0.61 (3)
Rossithidium sp. 1	2.02 (1)	0.00 (0)	1.68 (2)	0.50 (3)
Sellaphora pupula	0.00 (0)	0.17 (1)	3.92 (4)	0.22 (3)
Stauroneis constricta	0.00 (0)	0.00 (0)	0.00 (0)	0.06 (1)
Stauroneis phoenicenteron	0.00 (0)	0.00 (0)	0.00 (0)	0.28 (2)
Stephanodiscus niagarae	0.32 (1)	2.18 (4)	0.93 (1)	0.00 (0)
Synedra ulna	0.00 (0)	0.00 (0)	0.62 (1)	0.06 (1)
Tabularia fasciculata	0.32 (1)	0.83 (4)	0.00 (0)	0.06 (1)
Tabellaria flocculosa	0.00 (0)	0.00 (0)	0.00 (0)	0.06 (1)
Tryblionella apiculata	0.00 (0)	0.88 (5)	0.00 (0)	0.00 (0)
Unknown sp. 1	0.00 (0)	0.00 (0)	0.85 (1)	0.00 (0)
Unknown sp. 2	0.00 (0)	0.00 (0)	0.53 (1)	0.00 (0)

Appendix B. The mean relative abundance of diatom taxa on the common snapping turtle from each state. The number in parenthesis represents the number of turtles that hosted that diatom taxon

Diatom Taxa	Oklahoma	Arkansas	Illinois	Wisconsin	New York
Achnanthes sp. 1	0.00 (0)	0.00 (0)	0.54 (1)	7.44 (2)	0.17 (1)
Achnanthes sp. 2	0.00 (0)	0.00 (0)	0.00 (0)	0.19 (1)	0.00 (0)
Achnanthidium minutissimum	1.37 (2)	0.00 (0)	2.80 (2)	1.27(2)	2.62 (0)
Achnanthidium deflexum	0.00 (0)	0.00 (0)	0.00 (0)	0.47 (1)	0.00 (0)
Achnanthidium sp. 1	5.01 (3)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)
Achnanthidium sp. 2	0.00 (0)	0.00 (0)	1.62 (1)	0.00 (0)	0.00 (0)
Amphora libyca	0.00 (0)	0.57 (1)	0.00 (0)	0.19 (1)	0.00 (0)
Aulacoseira granulata	0.06 (1)	0.00 (0)	7.35 (2)	0.23 (1)	1.00 (2)
Bacillaria paradoxa	0.32 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)
Caloneis bacillum	0.63 (3)	0.57 (1)	2.45 (3)	0.58 (1)	0.17 (1)
Caloneis silicula	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.83(1)
Caloneis silicula var. *peisonis*	0.00 (0)	0.00 (0)	0.11 (1)	0.00 (0)	0.00 (0)
Caloneis schumanniana	0.00 (0)	0.57 (1)	0.32 (2)	0.00 (0)	0.17 (1)
Caloneis sp. 1	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.17 (1)
Cavinula cocconeiformis	0.00 (0)	0.00 (0)	0.00 (0)	0.47 (1)	0.00 (0)
Cavinula scutelloides	1.23 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)
Cocconeis pediculus	0.06 (1)	0.00 (0)	0.23 (1)	0.23 (1)	0.00 (0)
Cocconeis placentula	0.00 (0)	0.57 (1)	0.00 (0)	0.38 (1)	4.23 (3)
Cyclotella bodanica	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.17 (1)
Cyclotella meneghiniana	0.00 (0)	0.00 (0)	1.07 (2)	0.00 (0)	1.45 (1)
Cyclotella ocellata	0.00 (0)	0.00 (0)	1.67 (1)	0.00 (0)	0.00 (0)
Cymbella amplificata	0.24 (1)	0.00 (0)	0.50 (1)	0.00 (0)	0.67 (1)
Cymbella neocistula	0.24 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)
Cymatopleura solea	0.00 (0)	0.00 (0)	0.00 (0)	0.19 (1)	0.00 (0)
Cymbella sp. 1	0.32 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)
Diatoma tenuis	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	2.00 (1)
Diploneis oblongella	0.00 (0)	0.00 (0)	0.60 (1)	0.23 (1)	0.50 (1)

Diatom Taxa	Oklahoma	Arkansas	Illinois	Wisconsin	New York
Diploneis parma	3.59 (3)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)
Diploneis subovalis	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.33 (1)
Discostella stelligera	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.17 (1)
Encyonema minutum	0.00 (0)	0.00 (0)	0.11 (1)	2.75 (2)	0.00 (0)
Encyonema silesiacum	0.00 (0)	0.57 (1)	0.00 (0)	0.29 (3)	0.00 (0)
Encyonema triangulum	0.24 (2)	0.00 (0)	0.00 (0)	0.19 (1)	0.00 (0)
Encyonopsis microcephala	1.23 (1)	0.00 (0)	0.54 (1)	0.57 (1)	0.00 (0)
Epithemia adnata	0.00 (0)	0.00 (0)	4.62 (2)	0.19 (1)	0.00 (0)
Eunotia bilunaris	0.00 (0)	0.00 (0)	0.23 (1)	2.56 (3)	0.17 (1)
Eunotia circumborealis	0.00 (0)	0.00 (0)	0.00 (0)	0.23 (1)	0.00 (0)
Eunotia flexuosa	0.00 (0)	0.00 (0)	0.00 (0)	0.19 (1)	0.00 (0)
Eunotia incisa	0.48 (1)	0.00 (0)	0.00 (0)	19.2 (3)	0.00 (0)
Eunotia paludosa	0.00 (0)	0.00 (0)	0.00 (0)	0.19 (1)	0.00 (0)
Eunotia serra	0.00 (0)	0.00 (0)	0.00 (0)	0.23 (1)	0.00 (0)
Eunotia sp. 1	0.00 (0)	0.00 (0)	0.00 (0)	4.44 (1)	0.00 (0)
Eunotia sp. 2	0.00 (0)	0.00 (0)	0.00 (0)	0.29 (1)	0.00 (0)
Fragilaria capucina	0.00 (0)	1.14 (1)	7.22 (5)	1.90 (3)	0.67 (2)
Fragilaria sp. 1	0.00 (0)	0.00 (0)	0.00 (0)	0.19 (1)	0.00 (0)
Frustulia rhomboides	0.00 (0)	0.00 (0)	0.00 (0)	11.7 (3)	0.33 (1)
Frustulia vulgaris	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.17 (1)
Gomphonema acuminatum	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.17 (1)
Gomphonema affine	0.30 (2)	0.00 (0)	1.07 (2)	0.00 (0)	0.00 (0)
Gomphonema angustatum	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	1.78 (2)
Gomphonema clavatum	0.89 (3)	0.00 (0)	1.26 (1)	0.00 (0)	0.00 (0)
Gomphonema clevei	0.63 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)
Gomphonema gracile	0.00 (0)	0.00 (0)	0.00 (0)	0.88 (1)	0.00 (0)
Gomphonema minutum	0.00 (0)	0.57 (1)	0.23 (1)	0.00 (0)	0.50 (1)

Diatom Taxa	**Oklahoma**	**Arkansas**	**Illinois**	**Wisconsin**	**New York**
Gomphonema olivaceum	0.00 (0)	0.00 (0)	0.64 (2)	0.00 (0)	0.00 (0)
Gomphonema parvulum	0.62 (2)	1.25 (1)	1.54 (2)	3.13 (2)	0.17 (1)
Gyrosigma exilis	0.00 (0)	0.00 (0)	0.00 (0)	1.15 (1)	0.00 (0)
Hantzschia amphioxys	1.44 (2)	0.57 (1)	0.23 (1)	0.23 (1)	0.00 (0)
Lemnicola hungarica	0.00 (0)	0.00 (0)	3.81 (1)	0.00 (0)	0.17 (1)
Luticola cf. *geoppertiana*	61.2 (9)	54.3 (3)	17.6 (4)	7.16 (3)	9.83 (2)
Luticola cf. *mutica*	6.83 (6)	13.7 (4)	0.11 (1)	1.10 (3)	47.6 (3)
Meridion circulare	0.00 (0)	0.00 (0)	0.33 (2)	0.00 (0)	1.17 (1)
Navicula cari	0.00 (0)	0.57 (1)	0.00 (0)	0.00 (0)	0.00 (0)
Navicula cinta	0.00 (0)	0.00 (0)	0.00 (0)	0.29 (1)	0.00 (0)
Navicula cryptonella	0.00 (0)	2.08 (1)	3.91 (2)	3.70 (3)	0.83 (1)
Navicula leptostriata	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	1.33 (1)
Navicula radiosa	1.08 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)
Navicula salinarum	0.33 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)
Navicula veneta	1.48 (2)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)
Navicula sp. 1	0.00 (0)	1.70 (1)	0.00 (0)	0.00 (0)	0.00 (0)
Navicula trivialis	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.50 (1)
Neidium bisulcatum	0.00 (0)	0.00 (0)	1.11 (2)	0.00 (0)	0.00 (0)
Neidium sp. 1	0.00 (0)	0.00 (0)	1.11 (1)	0.00 (0)	0.00 (0)
Nitzschia amphibia	3.39 (6)	2.08 (1)	1.01 (1)	1.01 (3)	2.83 (1)
Nitzschia dissipata	0.00 (0)	1.70 (1)	1.67 (1)	0.53 (2)	0.17 (1)
Nitzschia frustulum	0.59 (2)	8.52 (1)	6.86 (3)	0.00 (0)	2.83 (1)
Nitzschia inconspicua	0.24 (1)	2.08 (1)	14.7 (3)	3.78 (3)	4.67 (1)
Nitzschia pellucida	0.48 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)
Nitzschia sp. 1	1.23 (1)	1.70 (1)	0.00 (0)	0.00 (0)	0.00 (0)
Pinnularia appendiculata	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.17 (1)
Pinnularia borealis	0.00 (0)	0.57 (1)	0.00 (0)	1.00 (2)	0.00 (0)
Pinnularia gibba	0.00 (0)	0.00 (0)	0.11 (1)	0.57 (1)	0.00 (0)
Pinnularia gibba var. mesogongyla	0.00 (0)	0.00 (0)	0.23 (1)	0.00 (0)	0.00 (0)
Pinnularia interrupta	0.00 (0)	0.00 (0)	0.00 (0)	2.11 (1)	0.17 (1)

Diatom Taxa	Oklahoma	Arkansas	Illinois	Wisconsin	New York
Pinnularia microstauron	0.00 (0)	0.00 (0)	0.00 (0)	4.38 (3)	0.00 (0)
Pinnularia streptoraphe	0.00 (0)	0.00 (0)	0.91 (1)	0.00 (0)	0.00 (0)
Pinnularia subcapitata	0.00 (0)	0.00 (0)	0.00 (0)	0.49 (2)	0.00 (0)
Pinnularia viridis	0.06 (1)	0.00 (0)	1.45 (2)	0.38 (1)	0.00 (0)
Placoneis clementis	0.00 (0)	0.57 (1)	0.00 (0)	0.00 (0)	0.17 (1)
Placoneis elginensis	0.00 (0)	0.00 (0)	0.11 (1)	0.58 (1)	0.00 (0)
Planothidium lanceolatum	2.47 (1)	0.00 (0)	1.42 (2)	0.96 (1)	6.40 (2)
Rhopalodia brebissonii	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.33 (1)
Rhopalodia gibba	1.39 (1)	0.00 (0)	1.27 (3)	0.00 (0)	0.33 (1)
Rhopalodia musculus	0.00 (0)	0.57 (1)	0.00 (0)	0.00 (0)	0.00 (0)
Rossithidium pusillum	0.00 (0)	3.41 (1)	0.00 (0)	0.00 (0)	0.33 (1)
Sellaphora pupula	0.00 (0)	0.00 (0)	1.34 (2)	0.00 (0)	0.00 (0)
Sellaphora sp. 1	0.00 (0)	0.00 (0)	0.00 (0)	0.19 (1)	0.00 (0)
Stauroneis anceps	0.00 (0)	0.00 (0)	0.00 (0)	3.51 (2)	0.00 (0)
Stauroneis constricta	0.00 (0)	0.00 (0)	0.00 (0)	0.19 (1)	0.00 (0)
Stauroneis phoenicenteron	0.00 (0)	0.00 (0)	0.11 (1)	0.00 (0)	0.17 (1)
Staurosirella pinnata	0.00 (0)	0.00 (0)	0.00 (0)	0.38 (1)	0.00 (0)
Stephanodiscus sp. 1	0.00 (0)	0.00 (0)	1.77 (2)	0.29 (1)	0.00 (0)
Tabularia fasciculata	0.00 (0)	0.00 (0)	0.95 (1)	0.00 (0)	0.00 (0)
Tabellaria fenestrata	0.00 (0)	0.00 (0)	0.00 (0)	0.93 (1)	0.00 (0)
Tabellaria flocculosa	0.00 (0)	0.00 (0)	1.77 (2)	3.42 (2)	1.45 (1)
Unknown sp. 1	0.00 (0)	0.00 (0)	0.34 (1)	0.00 (0)	0.00 (0)

Appendix C. One-way PERMANOVA results comparing diatom assemblages across turtle species. * Indicates a significant difference ($p<0.05$).

Source	d.f.	*SS*	*MS*	*Pseudo-F*	*P*
Turtle	3	31740	10580	4.5148	0.001*
Comparison of Turtles				*t*	*P*
Common Snapping, False Map				1.6045	0.012*
Common Snapping, Eastern Mud				1.7065	0.002*
Common Snapping, Common Musk				2.2714	0.001*
False Map, Eastern Mud				2.2747	0.001*
False Map, Common Musk				2.5509	0.001*
Eastern Mud, Musk				2.2448	0.001*

Appendix D. One-way PERMANOVA results comparing diatom assemblages on common snapping turtles across states. * Indicates a significant difference (p<0.05).

Source	d.f	*SS*	*MS*	*Pseudo-F*	*P*
Turtle	4	24456	6114	2.2012	0.001*

Comparison of States	*t*	*P*
Illinois, Arkansas	1.4133	0.088
Illinois, Wisconsin	1.1781	0.116
Illinois, New York	1.1243	0.182
Illinois, Oklahoma	1.7712	0.001
Arkansas, Wisconsin	1.5427	0.057
Arkansas, New York	1.3198	0.143
Arkansas, Oklahoma	1.0828	0.314
Wisconsin, New York	1.231	0.128
Wisconsin, Oklahoma	1.9044	0.002
New York, Oklahoma	1.6951	0.013

Appendix E: IACUC letter of approval for the turtle sampling protocol.

The University of Oklahoma

LABORATORY ANIMAL RESOURCES

4 April 2014
Shelly Wu
Biology Department/SNOMNH

Dear Ms. Wu:

The following AUS protocol was approved by the Institutional Animal Care and Use Committee.

Title of Application: **"Life on a shell: an integrative study of diatoms and turtles in natural history collections"**

Institution: University of Oklahoma

This protocol will cover a laboratory study on turtle specimens in the SNOMNH; aufuchs-type attachments to turtle shells will be examined; this graduate project will be supervised by Dr.. Carpenter. The Institutional Tracking number of **R14-008** is assigned to this AUS. Please reference the current number relative to communications about the activities. Approval is valid for a period of 3 years; renewal requires resubmission of new protocol for review. If significant changes are to be made during the approval period, please notify the committee using the appropriate form which is posted on the website (iacuc.ou.edu). A copy of this letter is required for the graduate college when the thesis reading copy is submitted.

The University of Oklahoma has an Animal Welfare Assurance on file with the Office of Laboratory Animal Welfare (A3240-01) which is in effect through June 2017 and the Institution is registered as a research facility with USDA (Certificate number 73-R-0100) through March 2016.

Sincerely,

William L. Shelton
IACUC Chair

Cc: IO

730 Van Vleet Oval, Richards Hall 314, Norman, Oklahoma 73019-6121 PHONE: (405) 325-2609