Responses of turtle assemblage to environmental gradients in the St. Croix River in Minnesota and Wisconsin, U.S.A.

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Abstract: We investigated how environmental gradients measured along the St. Croix River in Minnesota and Wisconsin, U.S.A., influenced the turtle assemblage. Among seven species, the five most common species were generalists and had wide distributions throughout the study area. However, patterns in assemblage structure were related to environmental gradients along the river. Sex ratios were male-dominated for the five most common species, and few or no juveniles were captured during the study. The first two canonical axes of a canonical correspondence analysis accounted for 92.7% of the variation in species–environment gradients. Most of the variation in distribution and abundance was attributed to gradients in channel morphology and physical characteristics along the river channel. Abundances of common snapping (*Chelydra serpentina*), false map (*Graptemys pseudogeographica*), and painted (*Chrysemys picta bellii*) turtles were associated with muck substrates and the number of basking sites (i.e., snags, rocks), which increased farther downstream. Abundance of spiny softshell turtles was closely related to increased water velocity and depth, which were related to hydraulic control points in the river. Abundance of common map turtles was associated with the presence of open sandy areas, uniform channel bottom, and gravel substrates. Geomorphic changes along the St. Croix River clearly influence the turtle assemblage and these specific relations should be considered in efforts to preserve and restore components of the assemblage.

Résumé : Nous avons examiné comment les gradients environnementaux mesurés le long de la rivière Ste-Croix au Minnesota et le Wisconsin, É-U, influencent les associations de tortues. Parmi sept espèces, les cinq plus communes étaient généralistes et leur répartition était bien étendue dans toute la zone de l'étude. Cependant, les associations étaient reliées à des gradients environnementaux spécifiques le long de la rivière. Les rapports mâles : femelles étaient supérieurs à 1 chez les cinq espèces les plus communes et peu de juvéniles (ou aucun) ont été capturés au cours de l'étude. Les deux premiers axes obtenus lors d'une analyse canonique des correspondances expliquaient 92,7% de la variation des gradients espèces-environnement. La part la plus importante de la variation dans la répartition et l'abondance était attribuable à des gradients morphologiques du canal principal de la rivière et à des gradients des caractéristiques physiques de ce canal. L'abondance des Chélydres serpentines (*Chelydra serpentina*), des Fausses Tortues géographiques (*Graptemys pseudogeographica*) et des Tortues peintes (*Chrysemys picta belli*) était associée aux substrats boueux et au nombre de sites de repos au soleil (i.e. enchevêtrements de végétation, pierres), plus abondants en aval. L'abondance des Tortues-molles à épines augmentait en fonction de la vitesse du courant et de la profondeur, elles-mêmes reliées à des points de régulation hydraulique dans le cours d'eau. L'abondance des Tortues géographiques était associée à la présence de zones ouvertes sablonneuses, de fonds uniformes et de substrats de gravier. Les changements géomorphologiques le long de la rivière Ste-Croix influencent clairement les associations de tortues et les efforts de conservation et de restauration des populations de tortues doivent tenir compte de ces relations spécifiques.

[Traduit par la Rédaction]

Introduction

The rapid decline in turtle populations, including many "common" species in North America, has increased the attention given to investigating the status of natural turtle populations (Lovich 1995). Turtles' life-history traits (e.g., low annual reproductive success, delayed sexual maturity), overexploitation, and habitat alteration and degradation (e.g., wetland drainage, fragmentation, pollution, sedimentation) are the major reasons suggested for declines (Dodd 1990; Congdon et al. 1993; LaClaire 1995; Lovich 1995). As riparian areas and aquatic systems continue to be drained, degraded, and isolated, riverine systems will play an increasingly important role in maintaining the ecological processes necessary to

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maintain regional populations in the future (Naiman et al. 1993).

Environmental gradients can have a significant influence on the community composition of turtle assemblages. Few studies have been conducted on species distributions and community composition of turtle assemblages in riverine systems. Abundances of different turtle species in rivers have been associated with local factors such as channel width (Shively and Jackson 1985), water depth (Plummer 1977; Bury 1979; Pluto and Bellis 1986), emergent vegetation (Buhlmann and Vaughan 1991; Giovanetto 1992), current velocity (Pluto and Bellis 1986; Buhlmann and Vaughan 1991), and number and availability of resting/basking sites (Williams and Christiansen 1981; Shively and Jackson 1985; Pluto and Bellis 1986; Buhlmann and Vaughan 1991; Fuselier and Edds 1994). However, in few of these studies were large sections of rivers covered or more than one species investigated. Understanding the underlying mechanisms affecting turtle assemblages and population processes in riverine systems will require a larger scale view that encompasses community dynamics, spatial distributions of communities, and the influence of abiotic and biotic factors on community patterns.

We investigated the spatial variation of turtle species along 100 km of the St. Croix River in Minnesota and Wisconsin, U.S.A., to examine what features of a river environment are important in structuring turtle assemblages. Additionally, we assessed longitudinal changes in community structure. Community structure and function in macroinvertebrate and fish communities have been found to shift in response to longitudinal gradients in stream characteristics such as temperature, water depth, current velocity, and substrate (Hynes 1970; Minshall et al. 1985). Longitudinal changes in turtle communities, however, have not been evaluated. We also present sex ratios and size–age structures, which are important demographic parameters for conservation work and may reflect additional pressures influencing the internal structure of the turtle community.

Materials and methods

Study area

In 1968, the St. Croix–Namekagon rivers and their riparian areas were established as a National Scenic Riverway (Wild and Scenic Rivers Act, Public Law 90-542) to preserve their outstanding scenic, recreational, cultural, and biotic values. Because few rivers in the United States have this level of protection, the St. Croix River provides an opportunity to study turtle assemblages and their habitat associations along a relatively undisturbed and high-quality river, particularly in the upper reaches. The St. Croix River, a sixth-order stream, flows 276 km from its headwaters at Solon Springs, Wisconsin, to its confluence with the Mississippi River at Prescott, Wisconsin (Fago and Hatch 1993; Fig. 1). It is essentially free-flowing except for a small dam near its headwaters and an 18 m high hydroelectric dam at Taylors Falls, Minnesota. This dam represents the division between the upper and lower basins, which also divides management strategies used by the U.S. Department of the Interior National Park Service. Management upstream of the dam is primarily oriented toward the river's natural scenic value, while below the dam, management is directed more toward recreational use. The dam at Taylors Falls is used in this paper to delineate the upper reaches from the lower reaches of the study area because of different levels of management and human use, as well as differences in channel characteristics.

Basin topography along the St. Croix River is primarily rolling glacial terrain ranging from flat outwash plains to knob and kettle end moraines. Our study area encompassed a 100-km segment of the St. Croix River from 2 km south of the Snake River to 3 km south of the Apple River tributary (Fig. 1). In the upper study reach, the river typically has one main channel that meanders through outwash plains on the Wisconsin side and glacial till on the Minnesota side. The channel has a low relief with an average gradient of 0.15 m/km (Fago and Hatch 1993). A few small islands exist, and are forested with sand banks or are sandy, open islands with scattered trees and herbaceous vegetation. In this area of the river, small (<15 ha) marsh areas occur but are disjunct from the main channel (Glenn-Lewin et al. 1992), and the riparian areas of stream banks are primarily wooded or grassy and essentially free of development.

Below the dam, the St. Croix River travels through a steep rock gorge, St. Croix Dalles, formed from retreating glacial waters traversing basaltic bedrock. Within this area, the river is deep and fast. Once through the Dalles, the river gradient drops, the channel widens, and the current slows (0.09 m/km; Fago and Hatch 1993). The river becomes braided with multiple channels and large forested islands. In this reach, the river has flowing, deep-river, marshy areas that grade into shallow areas that have exposed banks and mud flats; it also has some isolated marshy areas that become connected to the river during high flows (Glenn-Lewin et al. 1992). In contrast to the upper reach, residential and commercial development is prominent along the shorelines.

Trapping

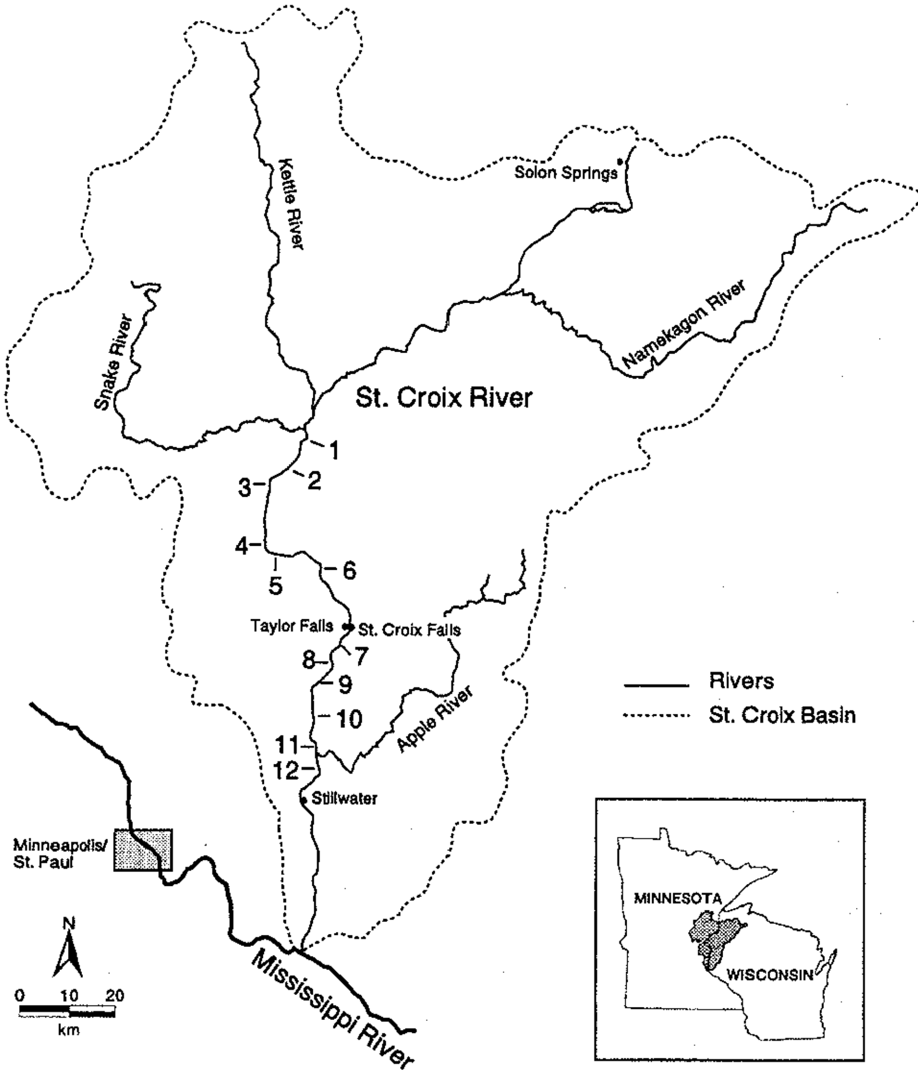
Twelve study sites, each 1.61 km in thalweg length ("river mile"), were established throughout the study area (Fig. 1). At each study site, an equal number of traps (four in June, seven in July–August) were set and run simultaneously during June–August in 1994 and 1995. Traps were initially set at even intervals within each study site, but often had to be moved because of variable water levels or vandalism. When moved, however, traps were set in the same general location and placed in approximately the same location in both 1994 and 1995 to maintain effort within each site. Turtles were trapped with commercial nylon hoop nets (1.5 m long × 0.8 m diameter hoops) with 2.5–5.0 cm nylon mesh (Lagler 1943; Legler 1960). The traps were baited every other day with canned sardines, chicken livers, and creamed corn. Overall, turtles were collected during 10 251 trap-nights (i.e., one trap set for 1 night). Traps that collapsed or were unable to capture turtles (e.g., a hole in the trap) were excluded from analysis. Trapping effort was not significantly different among study sites (ANOVA, F = 0.09, P = 1.0).

Captured turtles were aged, sexed, weighed, measured, individually marked, and released at the capture point. Maximum carapace and plastron lengths and widths were recorded to the nearest 0.1 mm using graduated calipers. Minimum carapace lengths reported in the literature were used to classify an individual's approximate age as adult (i.e., sexually mature) or juvenile (i.e., sexually immature; Vogt 1981*a*; Ernst et al. 1994). Adult turtles were sexed by examining external secondary sex characteristics (see Ernst et al. 1994). Each turtle was individually marked by notching marginal scutes (Cagle 1939) using a cordless Dremel Minimite Model 750 with a No. 199 high-speed cutter bit. Softshell turtles were marked along their shell margin using a paper hole punch (Doody and Tamplin 1992) or a triangular notch.

Habitat characteristics

To assess differences in turtle community composition in relation to river channel and physical characteristics, habitat variables were measured in August 1995. At each site, mean and maximum

Fig. 1. Study area on the St. Croix River in Minnesota and Wisconsin: numbers 1–12 represent study sites used to assess variation in composition and structure of turtle species assemblages and habitat in June–August of 1994 and 1995.



water depth, coefficient of variation (CV) for depth, channel width, bank slopes, mean stream velocity, bottom substrates, area of open sand banks/bars, number of basking locations, and site latitude were recorded. Five equally spaced transects were placed perpendicular to the river's thalweg, and 25 sampling points were equally spaced along each transect. If transects intersected islands, 25 points were measured on both sides of the island. A chart depth recorder (Eagle Mach II Computer Graph) was used to obtain a cross-sectional profile of the river along each transect, which was used to measure water depth and bottom substrate at each sampling point and to help estimate mean stream velocity for each study site. Bottom substrates were categorized as rock/gravel, sand, or muck. The river was usually shallow enough to allow substrate composition to be determined visually; however, when visibility was limited, we probed the bottom with a pole to determine texture by feel. In deeper water, we estimated substrates from the graph output: a thicker bottom was related to silt, while a thin bottom was related to gravel, based on test observations in shallow locations on the St. Croix River. Depth measurements were calibrated against known elevations at each site and adjusted for water fluctuations that occurred between habitat sampling dates. The CV of the depth measurements at each study site was used as an indicator of channel-bottom variability. Digital orthophoto quads were used to estimate the channel width along each transect and widths were then averaged for each site. Mean site velocity was calculated by dividing U.S. Geological Service stream-flow data (i.e., daily discharge) by the cross-sectional area of water determined from the transects. At each study site, available basking locations consisting of logs (i.e., snags) or rocks separated from shore were counted. Groups of fallen branches or submerged trees were counted as one basking location. During June 1995, the area of open sand banks/bars was estimated by multiplying the length of these areas by their width.

Statistical methods

Simple linear regressions were used to describe the abundance of each turtle species as a function of each habitat variable. Alpha was set at $P \leq 0.05$. To further explore the relation between the turtle community distributions and multiple habitat variables, canonical correspondence analysis (CCA) was performed using the software CANOCO (version 3.0; ter Braak 1987*a*). CCA is a direct gradient analysis method that uses species' relative abundance data (or occurrence data) and environmental data collected at different sites to derive synthetic gradients (i.e., orthogonal ordination axes) from the measured environmental variables that maximize niche separation among species (ter Braak 1986, 1987*b*; ter Braak and Verdonschot 1995). Species separation is achieved using beta diversity or the dissimilarity in community composition among sites. Ordination diagrams (biplots or triplots) are derived to help visualize patterns of community variability and main features of species distributions along environmental gradients (terBraak 1987*b*; ter Braak and Verdonschot 1995).

To better approximate a normal distribution, bottom substrates were arcsine-transformed and areas of open sandy banks/bars were square-root transformed. The remaining variables, except basking sites, slope, and velocity, which were normally distributed, were logarithmically ($\log_{10}$ + 1) transformed. A preliminary correlation matrix was examined, and highly correlated variables were excluded from the CCA analysis (DonnerWright 1997). Percent gravel was omitted because of its high correlation with latitude (r = 0.87) and inverse relationship with muck (r = –0.71). Maximum depth was omitted because of its high correlations with mean depth (r = 0.86) and bottom variability (CV of depth; r = 0.82). Percent sand was omitted because it did not vary greatly among study sites. CCA was performed with the remaining nine variables: mean water depth, bottom variability (CV of depth), channel width, bank slope, mean stream velocity, percent muck, basking sites, latitude, and area of open sandbars/banks.

Sex ratios

Heterogeneity χ^2 tests corrected for continuity were used to analyze sex ratios against a 1:1 sex ratio (Sokal and Rohlf 1969) and to determine whether proportions were homogeneous among sites. Only adult turtles whose sex could be confidently determined were used for sex-ratio comparisons. Immature females were not included; however, they were included in size comparisons.

Results

Distribution and abundance

During 2 years of sampling, we captured 1204 turtles and recaptured 165. Species caught were Blanding's (*Emydoidea blandingii*), common map (*Graptemys geographica*), common snapping (*Chelydra serpentina*), false map (*Graptemys pseudogeographica*), spiny softshell (*Apalone spinifera*), western painted (*Chrysemys picta bellii*), and wood (*Clemmys insculpta*) turtles. Spiny softshell turtles were the most frequently trapped (47%), followed by snapping turtles (20%), common map turtles (16%), painted turtles (12%), and false map turtles (4%) across all sites combined. Snapping, spiny softshell, common map, and painted turtles were distributed continuously across the entire study area. False map turtles occurred only in the lower six sites. Blanding's and wood turtles were captured on only one and five occasions, respectively.

The abundances of species varied across sites, and in most cases did not gradually increase or decrease downstream (Fig. 2). Instead, each species' distribution displayed peaks illustrating where it was more abundant along the river (Fig. 2). However, the total number of turtles (i.e., all species combined) captured in the study sites below the dam was significantly greater than in the study sites above the dam (t = 3.99, P < 0.01). For individual species, only the snapping and spiny softshell turtles (the two most common species) were caught more frequently in the lower study sites (t = 3.75, P = 0.013, and t = 3.00, P = 0.013, respectively).

Sex ratios

Overall, sex ratios of the most abundant species were significantly skewed toward males, although sex ratios varied among sites (Table 1). Significantly more female than male spiny softshell turtles were captured in one upper study site (0.36:1; χ^2 = 4.17, P < 0.05). Male:female sex ratios were as high as 4.0 for spiny softshell, 5.0 for snapping, 6.0 for painted, 3.7 for common map, and 17.0 for false map turtles.

Size–age structures

In spiny softshell, painted, common map, and false map turtles, females had significantly greater mean carapace lengths (CL) than males (Table 2). Conversely, male snapping turtles had a significantly greater mean CL than females. Frequency distributions of CLs for males of all species and for female snapping turtles were skewed toward the larger size classes, which was expected with long-lived species with continual growth. However, the length frequencies for female spiny softshell turtles, and to a lesser extent common map and painted turtles, showed a slightly bimodal distribution, with a smaller number of females in the middle size classes (Fig. 3).

Few juveniles were captured (Fig. 3). Among spiny softshell turtles, less than 2% of the captures (n = 8) were juveniles. Juveniles composed 11.5% of the overall captures of snapping turtles. However, the upper reach yielded 16.2% juveniles, while the lower reach contained only 10.5% juveniles. Common map turtle captures contained 5% juveniles. No juvenile painted or false map turtles were captured.

River habitat characteristics

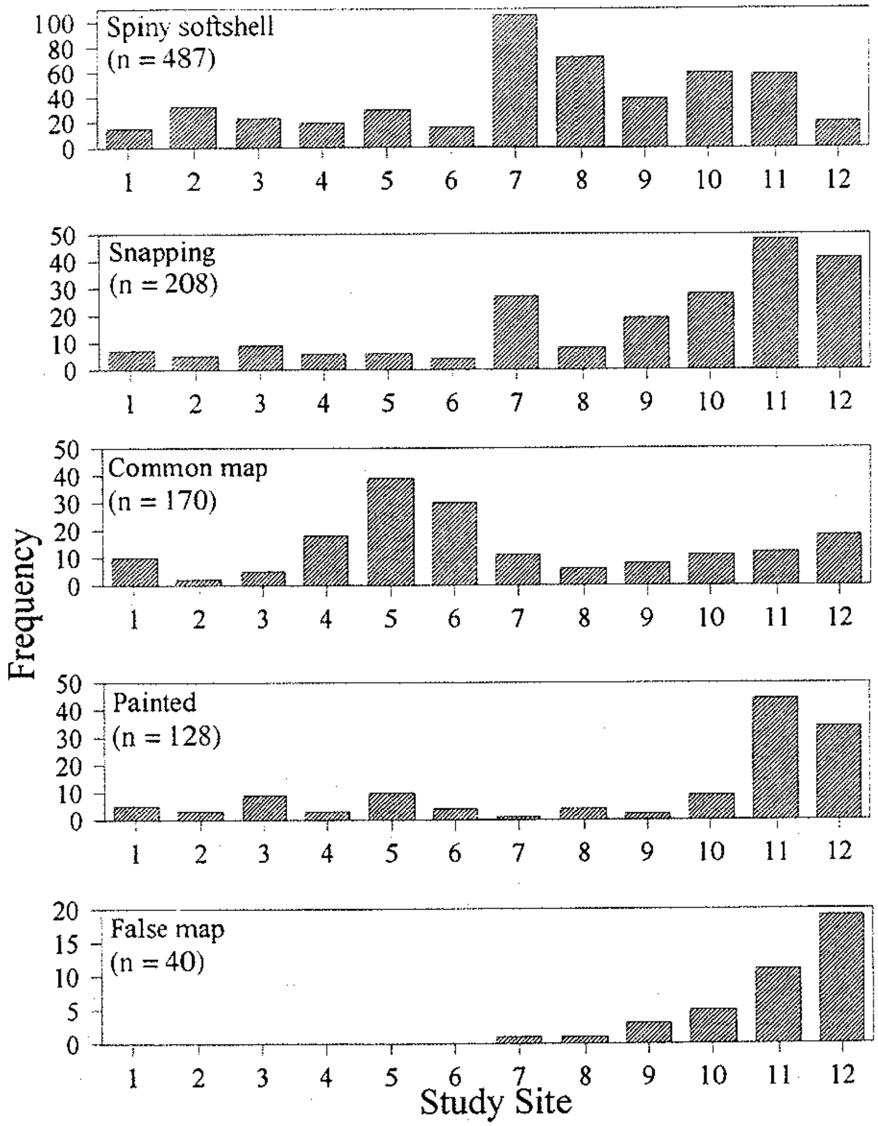
Habitat characteristics were quite variable among study sites (Fig. 4). Longitudinal trends were most noticeable for bottom substrate and number of basking sites, while profiles of several river characteristics had abrupt peaks. Bottom-substrate particle sizes became smaller downstream: gravel decreased as muck increased. The basking locations increased in number in the lower study sites and consisted mainly of fallen logs, while the basking locations in the upper study sites were mostly rocks. Maximum depth and mean channel width increased slightly downstream, except for depth at site 7 and width at site 11. The wider sections of the river (e.g., sites 11 and 12) had more muck substrates and basking locations. Water velocity decreased in these sites as well, especially at site 11.

Species–habitat relations

Linear regression showed that painted turtle abundance was positively related to percent muck, channel width, and number of basking sites (Table 3). False map turtle abundance showed significant positive relationships with latitude, bank slope, and percent muck. Significant positive relationships were also found between spiny softshell abundance and mean depth and velocity, and significant positive relationships occurred between snapping turtle abundance and percent muck, number of basking sites, and channel width (Table 3). No significant relationship was found between common map turtle abundance and any measured habitat characteristic of the St. Croix River.

For CCA, the first two axes explained 50.0 and 42.7%, respectively, of the variation in species abundance among sites. The species-conditional triplot (Fig. 5) accounted for

Fig. 2. Numbers of turtles captured using hoop nets at 12 study sites along the St. Croix River in June–August of 1994 and 1995. Sites 1–6 represent the upper St. Croix; sites 7–12 represent the lower St. Croix. Captures of Blanding's turtles (n = 1 capture) and wood turtles (n = 5 captures) are not shown.



93.6% of the variance in weighted averages of species with respect to the environmental variables: CCA axis 1 accounted for 50.5% of the variance and CCA axis 2 accounted for 43.1%. The number of basking sites and slope were strongly related to axis 1, and each was inversely related to the other (Fig. 5, Table 4). Bottom variability (CV of depth) was closely related to axis 2. Velocity and latitude were about equally associated with axes 1 and 2. The variable percent muck had the strongest gradient (most important variable), while mean depth had the weakest. Closely related to each other were latitude and the amount of open sand, mean depth and velocity, and channel width and percent muck. Furthermore, latitude and the amount of open sand were almost inversely related to channel width and percent muck.

The ordination triplot (Fig. 5) illustrates the influence of multiple habitat variables on the distribution of the five most common turtle species captured. Painted turtles were sensitive to gradients in the number of basking sites, while false map turtles were sensitive to channel width and percent muck gradients. Both species occurred more in the wider, mucky sites with numerous basking sites. False map turtles had the highest optima for all three characteristics. Larger numbers of common map turtles were found in the slower, shallow waters of the upper sites with a greater gravel component, and more open sandy areas.

Both snapping and spiny softshell turtles were positioned fairly close to the origin on both axes, indicating that they were abundant in all sites and tolerated a wide variation in habitat characteristics, as the origin represents the grand mean for all environmental variables. Both species' positions are approximately the same along the CCA axis 2 but are opposite along axis 1. Snapping turtles were sensitive to channel width and percent muck gradients, occurring more abundantly in the wider sites with muck substrates and more basking sites. Spiny softshell turtles were sensitive to mean

Table 1. Sex ratios (male:female) of turtles captured at 12 study sites along the St. Croix River, Minnesota and Wisconsin, in June–August 1994 and 1995.

Site	Spiny softshell turtle				Snapping turtle				Common map turtle				Painted turtle				False map turtle			
	M	F	Ratio	χ^2	M	F	Ratio	χ^2	M	F	Ratio	χ^2	M	F	Ratio	χ^2	M	F	Ratio	χ^2
1	6	7	0.86	0.06	5	1	5.00	2.67	6	2	3.00	1.90	3	1	3.00	0.90	–	–	–	–
2	11	18	0.61	1.64	3	1	3.00	1.00	0	1	–	1.21	3	0	–	2.80	–	–	–	–
3	9	13	0.69	0.69	5	2	2.50	1.29	3	1	3.00	0.90	4	5	0.80	0.09	–	–	–	–
4	5	14	0.36	4.17*	3	3	1.00	0.00	11	6	1.83	1.41	2	1	2.00	0.27	–	–	–	–
5	15	8	1.88	2.07	5	0	–	5.00*	22	6	3.67	9.03*	6	1	6.00	3.43	–	–	–	–
6	7	8	0.88	0.05	3	0	–	3.00	17	10	1.70	1.76	2	2	1.00	0.00	–	–	–	–
7	77	19	4.05	34.92*	15	11	1.36	0.61	7	3	2.33	1.52	0	1	–	1.21	0	1	–	0.01
8	44	22	2.00	7.27*	4	4	1.00	0.00	2	2	1.00	0.00	2	1	2.00	0.27	1	2	0.50	0.27
9	28	8	3.55	11.00*	11	6	1.83	1.47	5	2	2.50	1.20	2	0	–	1.81	1	1	1.00	0.01
10	36	19	1.89	5.19*	16	8	2.00	2.67	3	6	0.50	0.93	6	3	2.00	0.93	2	2	1.00	0.00
11	24	33	0.73	0.87	35	9	3.89	15.36*	2	7	0.29	2.67	33	11	3.00	10.90*	8	0	–	7.80*
12	10	9	1.11	0.04	24	9	2.67	6.82*	9	4	2.25	0.06	21	9	2.33	4.72	17	1	17.00	14.05*
Total	272	176	1.55	20.57*	129	54	2.39	30.74*	87	50	1.74	9.94*	84	35	2.40	20.09*	30	7	4.29	14.17*
Total for upper river	53	68	0.78	1.86	24	7	3.43	9.32*	59	26	2.27	12.81*	20	10	2.00	3.33	–	–	–	–
Total for lower river	219	108	2.03	37.68*	105	47	2.23	22.13*	24	28	0.86	0.31	64	25	2.56	17.09*	30	7	4.29	14.17*

*Sex ratios are significantly different from 50:50 (α was set at $P \leq 0.05$).

water depth and velocity gradients, occurring more abundantly in deeper, faster waters.

Discussion

This study focused on spatial and compositional changes in the turtle community (i.e., distribution and abundance) along the St. Croix River as they relate to changing channel and habitat characteristics. Congdon et al. (1986) suggested that habitat suitability was a primary factor in determining species-specific densities and biomass in turtle populations. The presence and relatively stable abundance of the common species at each study site (i.e., their ordination toward the center of the canonical axes) show that these species had wide distributions along the river and tended to be generalists. However, the abundance of each species varied along the river in association with several different river characteristics.

Spiny softshell turtles were found to occur throughout the rivers of Iowa by Williams and Christiansen (1981), illustrating their widespread nature. However, these authors suggested that spiny softshell turtles were most commonly trapped near submerged brush and fallen trees, whereas our results suggest their distribution was influenced more by water flow and depth. We found this species to be most abundant in sites with deep, fast water. Spiny softshell turtles may be drawn to the faster and deeper parts of the St. Croix River because these segments may have the hydraulic characteristics of a larger river. Spiny softshell turtles are primarily found in rivers or large lakes and have been reported to prefer a soft bottom with some aquatic vegetation and sandbars or mud flats for basking/resting (Ernst et al. 1994). Additionally, Williams and Christiansen (1981) found that females preferred open water more than males. Females were more abundant in the upper reaches of the St. Croix River than males, which also suggests that there are sex differences in habitat selection relating to behavior or food preferences.

The distribution of snapping turtles reflects their general habitat use, with a slight preference for slower waters with a soft bottom, abundant vegetation, and submerged logs, as was seen in other studies (Froese and Burghardt 1975; Major 1975; Ernst et al. 1994). Galbraith et al. (1988) found higher densities of snapping turtles in marshes and other eutrophic bodies of water and felt that higher primary production in terms of aquatic macrophytes in these areas was the primary factor influencing densities. This may explain why greater numbers of snapping turtles were captured in the lower sites, because the braided lower channel had a soft bottom and contained many log piles and marsh-like areas with abundant vegetation. Painted turtles also prefer slow, shallow water with a soft bottom and abundant aquatic vegetation, often found in ponds, marshes, and river backwaters and at lake edges (Ernst et al. 1994). Their numbers along the river reflected this preference as well, but they were not as common as snapping turtles and may not tolerate such factors as faster flow and depth in some areas of the river. Basking sites were important to both painted and snapping turtles but probably for different reasons. While painted turtles actually use these sites to bask, snapping turtles will often use the underside of logs to hide and bury themselves in the softer

Table 2. Comparison of carapace lengths of male and female turtles captured in the St. Croix River.

Turtle species	Sex	*n*	Carapace length (mm) Range	Mean ± SE	*t*	*P*
Spiny softshell	Male	272	131–223	173.5±1.1	18.1	<0.01*
	Female	206	130–412	273.5±5.4		
Snapping	Male	129	202–431	304.1±3.9	–4.88	<0.01*
	Female	54	202–345	275.6±4.3		
Painted	Male	84	90–179	143.1±1.8	2.52	0.01*
	Female	44	94–197	154.6±4.2		
Common map	Male	86	101–145	123.7±1.2	12.88	<0.01*
	Female	73	104–258	192.8±5.2		
False map	Male	29	104–143	120.5±1.7	3.08	0.01*
	Female	11	95–241	176.6±18.2		
Wood	Male	4	136–336	235.3±4.1	–	–
	Female	1	213	–		
Blanding's	Male	1	249	–	–	–
	Female	0				

*Size differences were significantly different between the sexes (α was set at $P \leq 0.05$). Immature females are included.

Fig. 3. Frequency histograms of carapace lengths of five species of turtles captured along the St. Croix River.

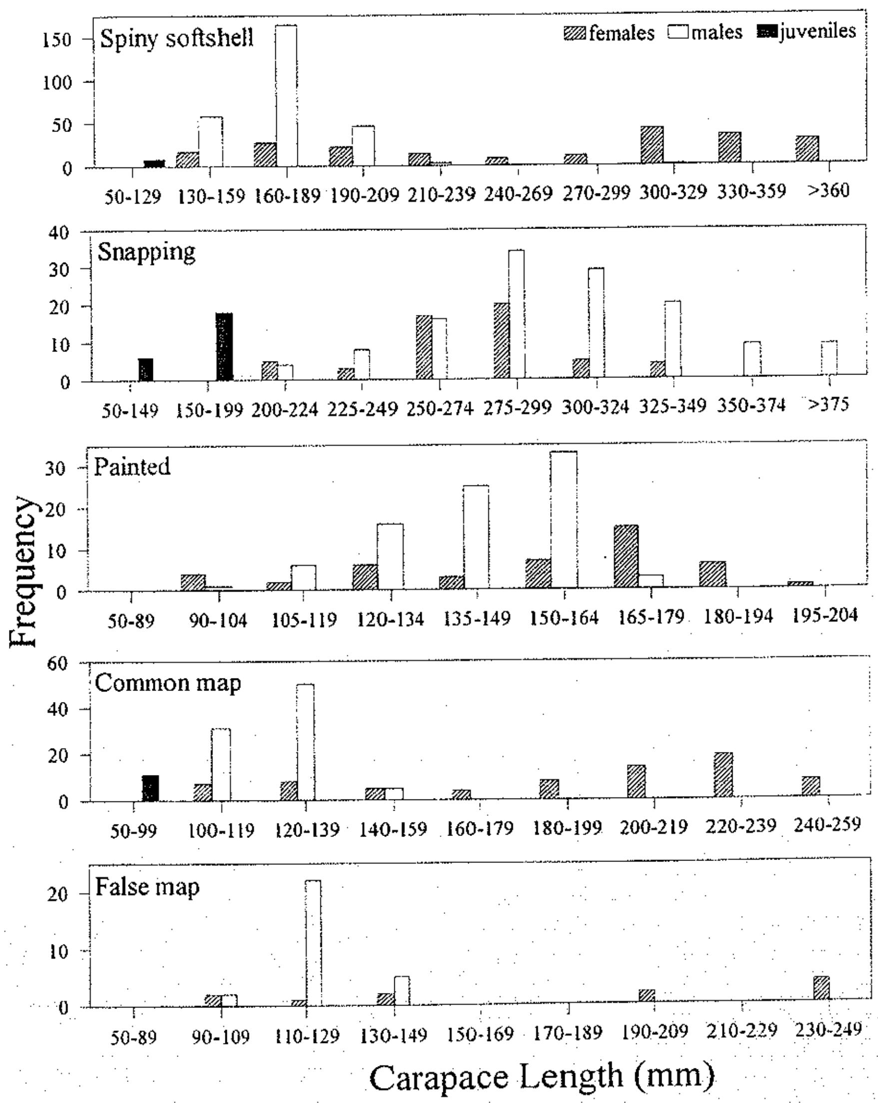


Fig. 4. Illustrations of habitat characteristics measured at 12 study sites along the St. Croix River, August 1995. Site 1 is the most upstream site; sites 6 and 7 separate the upper and lower river.

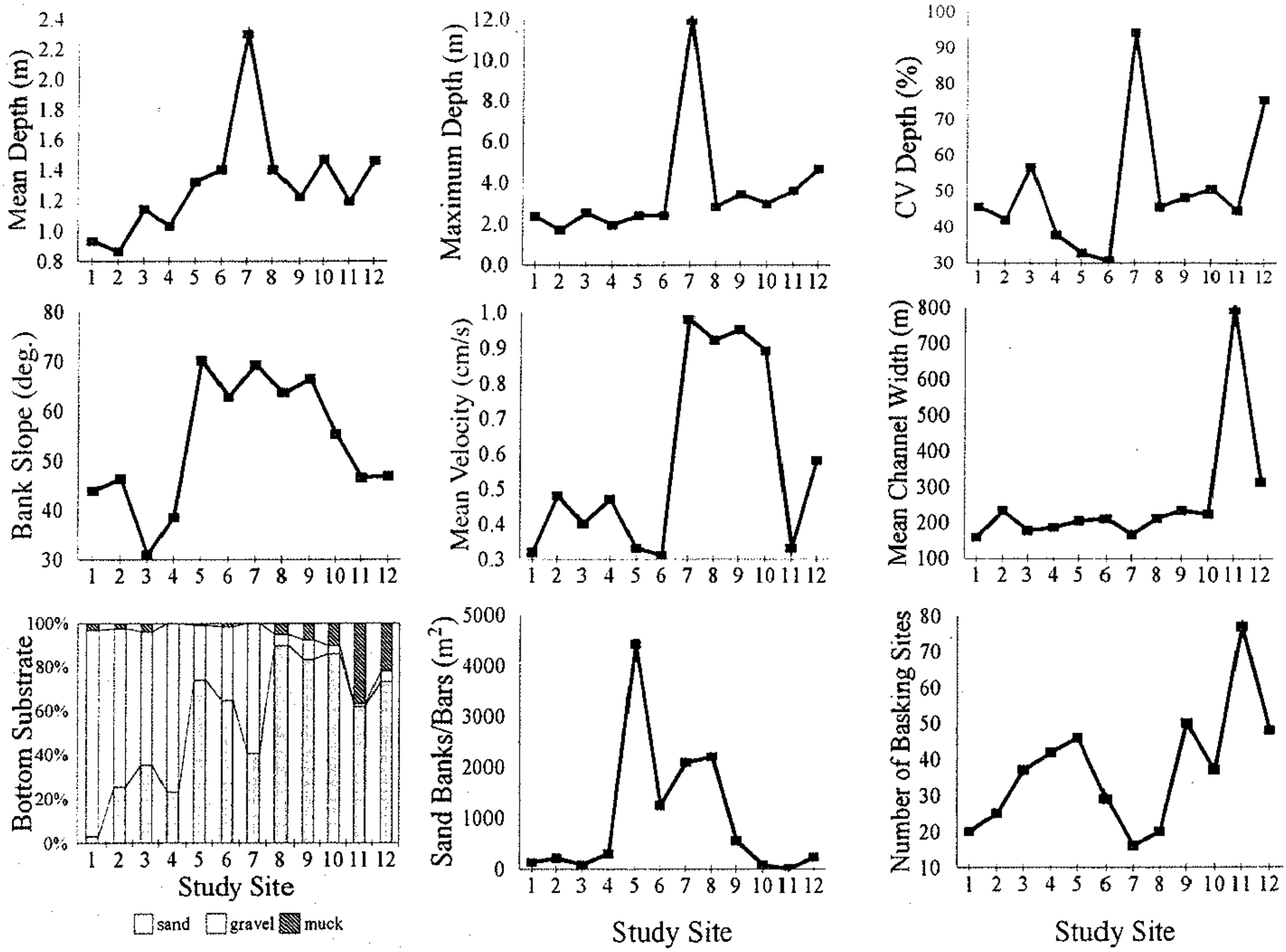


Table 3. Results of simple linear regressions by independent variables of five species of turtles captured along the St. Croix River in June–August of 1994 and 1995.

	Spiny softshell turtle		Snapping turtle		Common map turtle		Painted turtle		False map turtle	
	r^2	P	r^2	P	r^2	P	r^2	P	r^2	P
Maximum depth	0.17	0.10	0.19†	0.09	–0.09	0.78	0.01†	0.31	–0.19	0.67
Mean depth	0.52	0.01*	0.12†	0.14	–0.08	0.67	–0.03†	0.42	–0.12	0.53
CV depth	0.18†	0.65	0.20†	0.08	0.02	0.29	–0.09†	0.73	–0.24	0.85
Channel width	–0.08	0.65	0.26†	0.05*	–0.10	0.89	0.71	<0.01*	0.18†	0.22
Bank slope	0.17	0.10	–0.10†	0.91	0.03†	0.27	0.05†	0.23	0.72	0.02*
Mean velocity	0.48	0.01*	0.10†	0.17	–0.01†	0.37	0.13†	0.14	0.50	0.07
Percent muck	–0.09	0.78	0.52†	0.01*	–0.09	0.72	0.89	<0.01*	0.61†	0.04*
Percent sand	0.00	0.34	0.03	0.28	–0.09	0.46	–0.03†	0.42	–0.25	0.96
Percent gravel	–0.02	0.41	0.25†	0.06	–0.07	0.58	0.15†	0.11	0.02	0.36
Area of sand banks/bars	–0.03	0.42	0.00	0.34	0.23	0.07	–0.06†	0.54	0.29	0.16
No. of basking sites	–0.07	0.59	0.30	0.04*	–0.05	0.53	0.44†	0.01*	0.53†	0.06
Latitude	0.13	0.14	0.67	<0.01*	–0.03†	0.44	0.09†	0.18	0.86	<0.01*

*Significant relationship (α was set at $P \leq 0.05$).
†Based on $\log_{10}$ transformation of dependent variable.

Fig. 5. Canonical correspondence analysis ordination of the distributions of five turtle species along the St. Croix River. Environmental variables are represented by vectors, species are represented by circles, and sites are represented by diamonds. The diagram is interpreted by extending each arrow in the opposite direction and projecting a perpendicular line from the species or site scores to the arrow to get a point on the arrow. This point corresponds to the approximate ranking of the weighted averages of the species (site) with respect to the variable.

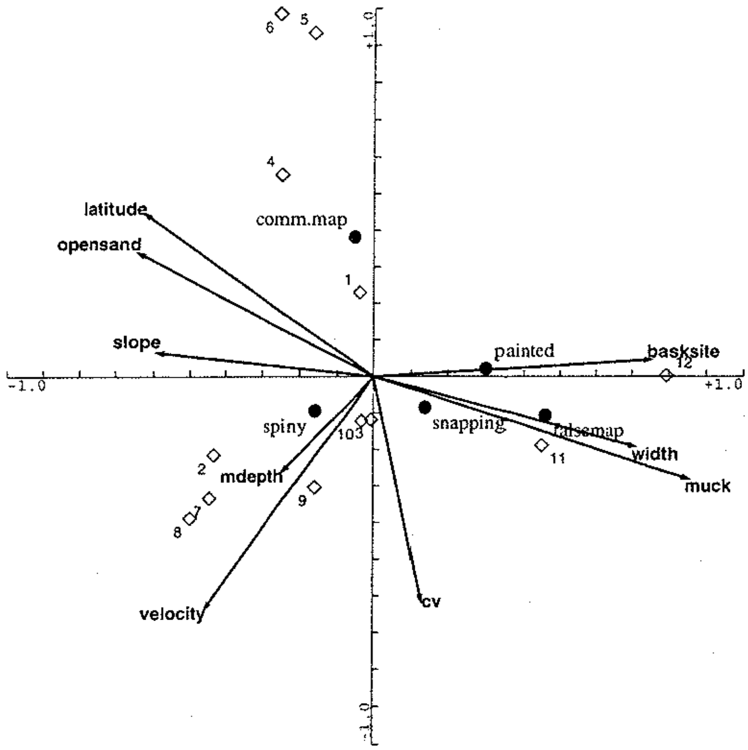


Table 4. Weighted correlation matrix of environmental variables with canonical ordination axes. Eigenvalues indicate the amount of variation explained in turtle assemblage - environmental variable gradients by each canonical axis.

	Canonical axis			
	1	2	3	4
Eigenvalue*	0.196 (50.6)	0.167 (43.1)	0.018 (4.7)	0.007 (1.8)
Percent muck	0.83	–0.28	0.20	–0.01
No. of basking sites	0.74	0.04	0.26	–0.25
Channel width	0.69	–0.19	0.37	–0.08
CV depth	0.12	–0.60	–0.37	0.04
Mean depth	–0.24	–0.24	–0.44	0.09
Area of sand banks/bars	–0.30	0.59	0.02	0.52
Mean velocity	–0.46	–0.60	–0.59	0.12
Bank slope	–0.57	0.07	–0.42	0.18
Latitude	–0.61	0.44	0.33	–0.14

*Numbers in parentheses show the percentage of variation explained.

bottom created by the debris, or hide beneath stumps and roots directly (Ernst et al. 1994), thus effectively partitioning habitat.

River characteristics associated with common map and false map turtle abundances in this study were similar to those reported by Fuselier and Edds (1994), who found common map turtles at sites with gravel substrate and bare shorelines and false map turtles at sites with mud substrate and more basking sites. As these authors noted, this differs from other findings, where common map turtles were reported to prefer areas with a soft bottom and abundant basking sites (Gordon and MacCulloch 1980; Vogt 1981*a*; Flaherty and Bider 1984; Pluto and Bellis 1986; Ernst et al. 1994). The relative unimportance of basking sites to common map turtles in our study also agrees with Flaherty and Bider (1984), who found few differences between site characteristics, including basking and nesting sites, in occupied and unoccupied bays of a lake in southwestern Quebec used by common map turtles. They hypothesized that social function determined the distribution of turtles on the basking sites used, rather than the number and quality of basking sites. The importance of open sandy areas may indicate that areas of a river which receive light for a longer period during the day are attractive to common map turtles. Light had a weak indirect effect on Sabine map turtle (*Geographica ouachitensis sabinensis*) densities by increasing densities of algae and insects, i.e., food for the turtles, and a weak direct influence by increasing basking opportunities (Shively and Jackson 1985). On the other hand, Vogt (1981*b*) felt that distributions of the common map turtle may be limited by food availability instead of habitat characteristics. He found that common map turtles were mollusk specialists, while false map turtles tended to be food generalists. The larger number of common map turtles in the upper study reach may be related to availability of their preferred food.

The occurrence of the five most common species in all sites and up to seven species at some sites suggests that some resource overlap is occurring, but to what degree is unknown. Wide degrees of resource overlap have been shown in turtle studies. In a study of three species of *Graptemys*, Fuselier and Edds (1994) found that species had wide habitat overlap, but habitats were partitioned and species could be grouped by specific habitat variables. Smooth softshell turtles (*Apalone mutica*) and spiny softshell turtles were found to have similar habitats and diet, but partitioned habitats by having different feeding strategies, with the spiny softshell turtles feeding primarily on the bottom and smooth softshell turtles feeding more in the water column (Williams and Christiansen 1981). Vogt (1981*b*) found three species of *Graptemys* occupying similar habitats, but also partitioned resources by means of different feeding strategies and food preferences. Berry (1975) found that two species of musk turtles (*Sternotherus* spp.) overlapped in habitat use, but competed for food resources where they were sympatric, since they did not spatially or temporally partition food resources. Studies carried out in the tropics have shown wide degrees of overlap in types of food eaten by different turtle species, but food types are often partitioned (Vogt and Guzman 1988; Moll 1990; Teran et al. 1995). Unfortunately, diet was not investigated in our study because of the intensive and extensive nature of our sampling.

For the common species, one species was added downstream, the false map turtle. Longitudinal gradients in the abundances of individual turtle species, however, were not evident, probably because longitudinal gradients in the habitat characteristics were not evident. A longitudinal gradient may have been evident if the study area had been extended farther upstream, where the river narrows and becomes influenced by a forest canopy, or extended downstream, where the river widens and becomes more lentic. Additionally, the small number of study sites may have precluded detection of downstream gradients in habitat characteristics.

The observed relative species abundances were subject to species-specific trapping bias and the assumption that each individual had the same probability of being sampled. Often, these assumptions are false (Ream and Ream 1966). Map and painted turtles probably occurred in higher proportions within the community but were insufficiently trapped with baited hoop nets. Both species would have been trapped more efficiently with basking traps, but using another trapping method was not feasible. Also, juveniles may have been inadequately sampled, rather than rare, owing to the trap type and reliance on baits (Ream and Ream 1966) and the placement of nets primarily in the main channel. Juveniles of many turtle species have been reported to occur somewhat apart from adults and in shallower waters (Pluto and Bellis 1986; Congdon et al. 1992) However, we assumed that because the same trapping method and effort were used among sites, trapping bias remained consistent and the observed differences in abundances for each species (i.e., species-specific variation among sites) likely reflects that species' responses to factors affecting the population.

Conservation

These data provide the first comprehensive overview of the turtle community in the St. Croix River. For five of the seven species of turtles in this river, populations are currently widespread and appear to be abundant. For the false map turtle, the downstream study sites represented the northern extent of its distributional range. The rare captures of Blanding's and wood turtles probably occurred because Blanding's turtles are specific to marsh habitats and wood turtles are restricted to scattered locations throughout the region. Their use of the river, however, illustrates the importance of riverine systems to all turtle species found within the St. Croix River basin.

The differences in numbers of the different species along the river show the influence of different channel characteristics and patterns on turtle assemblages. The meandering channel with gravel substrate in the upper sections of the river were important to common map turtles, the fast, deep waters attracted more spiny softshell turtles, and the slower, backwater areas in the lower, braided channels were preferred by snapping, painted, and false map turtles. Furthermore, the locations of the rare species identified sections of the river and associated riparian areas that were important to those species.

The lower St. Croix watershed has become a human-dominated landscape with increased forest and riparian fragmentation, roads and access points along the river, development in the riparian area, modification of geomorphological river processes, and increased human recreational use of the riverway. Changes such as these may negatively affect turtle populations, directly through increased human interactions (e.g., traffic kills, harvesting, destroying nests) and nest predation and indirectly through sedimentation, decreased water quality, removal of woody debris used as basking sites, and other shoreline riparian modifications.

Turtle life-history traits, including a long reproductive life and high adult survivorship, are tempered by high mortality rates of eggs and first-year juveniles, resulting in low annual recruitment (Ernst et al. 1994). Modeling efforts using data from long-term studies have shown that survival rates of adult turtles had the largest effect on the intrinsic rate of growth and that turtle populations cannot sustain increased adult mortality, especially when juveniles are few (Brooks et al. 1991; Congdon et al. 1993; Garber and Burger 1995; Cunnington and Brooks 1996). In this study, low numbers of juveniles of all species were captured. However, more detailed, targeted work should be conducted to estimate juvenile composition along the river more adequately. Because pressures on and disturbances of both adult and juvenile turties found in the St. Croix River are likely to increase with time, protecting diverse areas along the river with different channel characteristics and patterns, instead of only nesting areas, may be one of the most important factors contributing to the long-term viability of these turtle populations.

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