

where: chl *a* = periphyton chlorophyll *a* (mg/m<sup>2</sup>)  
TAB = total algal biovolume (cm<sup>3</sup>/m<sup>2</sup>)

Unexplained variance associated with the regression is probably attributable to differences in chl *a* content among algal species, differences in riparian shading or other factors that influence ambient light conditions (e.g., Darley 1982; Rosen and Lowe 1984), and challenges with distinguishing live and dead cells during taxonomic enumeration.

Periphyton communities were dominated by eutrophic microalgae (diatoms, blue-green algae, and green algae). Filamentous red algae (*Audouinella hermannii*) were abundant in streams with above average water clarity, velocity, and riparian-tree density (i.e., periphyton-dominated streams). Filamentous green algae were relatively uncommon on submerged woody debris; however, sparse to moderate growths of *Cladophora glomerata* were observed in flowing streams with bedrock or boulders, and moderate growths of *Spirogyra* spp. were present in pools and slow-flowing sections of streams with sand or silt bottoms. The predominance of fine streambed materials (sand and silt) in many Midwestern streams probably precluded the establishment and growth of nuisance filamentous algal species. These factors probably account for the relatively lower periphyton chl *a* values observed in this study when compared with those associated with eutrophic streams in the western U.S., that are dominated by filamentous green algae (Welch et al. 1988; Watson and Gestring 1996; Dodds et al. 1997).

#### **FACTORS ASSOCIATED WITH SESTON OR PERIPHYTON DOMINANCE IN MIDWESTERN STREAMS AND RIVERS**

Streams were classified relative to the abundance of algae (seston, periphyton, or both) as indicated by chl *a* values, and analysis of variance (ANOVA) and Tukey multiple range tests were used to determine whether water quality conditions differed significantly among stream classifications. Approximately 30 percent of the streams contained above-average (relative to this data set) concentrations of seston chl *a* and below-average values for periphyton chl *a* (seston-dominated streams). Concentrations of TON, dissolved organic carbon (DOC), and SOC were significantly higher in seston-dominated streams, suggesting organic enrichment from autotrophic (in-stream) processes. About 28 percent of streams contained below-average concentrations of seston chl *a* and above-average values for periphyton chl *a* (periphyton-dominated streams). Water clarity in periphyton-dominated streams was good, as indicated by significantly lower TSS concentrations and significantly larger euphotic-zone depths.

Stream productivity ( $P_{\max}$ ) was moderate to high in all streams with above-average amounts of algae; however, high rates of stream respiration ( $R_{\max}$ ) were associated primarily with large populations of seston. High  $R_{\max}$  conditions were associated with low DO concentrations during early morning hours, at levels that can adversely affect aquatic fauna. Stream respiration was significantly higher in streams with above-average chl *a* values for both seston and periphyton (algal-eutrophic streams; 22 percent of streams in the study). Concentrations of dissolved (but not total) nutrients were relatively lower in algal-eutrophic streams than in streams with below-average seston and periphyton chl *a* (nutrient-eutrophic streams; 20 percent of streams in the study). Stream productivity ( $P_{\max}$ ) was significantly higher in algal-eutrophic and seston-dominated streams than in nutrient-eutrophic and periphyton-dominated streams. However, periphyton chl *a* decreased significantly with modest increases in the relative abundance of macroinvertebrate scraper organisms (Harris and Porter, in review); therefore, monitoring of algal-

nutrient relations in Midwestern streams should probably consider the abundance of grazer organisms that consume benthic algae.

The abundance of algal tychoplankton (species that are loosely associated with, but not attached to, submerged benthic surfaces) in the periphyton community was a primary factor in identifying differences in community structure among Midwestern streams. These species, including *Microcystis*, *Anabaena*, other blue-green algae, and centric diatoms, are found commonly in eutrophic lakes, reservoirs, and other warm, slow-flowing water bodies such as large impounded rivers. The abundance of blue-green algae increased with the concentration of triazine herbicides (atrazine, cyanazine, and degradation products). The predominance of tychoplankton in periphyton communities in algal-eutrophic and seston-dominated streams was associated with large populations of these species in the seston, probably indicating that they had settled from the water column. Indicators of organic enrichment (SOC, DOC, TON) and stream metabolism ( $P_{\max}$  and  $R_{\max}$ ) are consistent with the large abundance of algae in these streams, whereas concentrations of dissolved nutrients were relatively low. The highest rates of stream respiration were found in algal-eutrophic streams; benthic macroinvertebrate indicators of biological integrity (e.g., EPT richness) indicated poor water quality conditions in algal-eutrophic and seston-dominated streams (Harris and Porter in review).

In contrast, algal communities in periphyton-dominated and nutrient-eutrophic streams were dominated by diatoms, blue-green algae, and red algae that grow attached to benthic surfaces. These species are found commonly in cool, flowing streams and rivers. A secondary factor in classifying differences in algal community structure in the region relates to the age of the periphyton community as inferred by the presence or dominance of certain algal species. For example, periphyton communities in streams of the Minnesota and upper Iowa River basins were characterized by diatoms (e.g., *Fragilaria vaucheriae* and *Achnantheidium minutissimum*) that are typically found in abundance on bare or recently-scoured substrates. Algae that are associated with soils (e.g., *Luticola mutica*, *Chlorococcum* sp., and *Protococcus* sp.) were also common in these streams. Periphyton community structure in these streams is consistent with recent hydrologic disturbance as indicated by relatively high rainfall, surface-water runoff, and elevated streamflow in the region (Figure A-15). Water quality in these streams is influenced by relatively low rates of stream metabolism and high concentrations of nutrients (notably TN,  $\text{NO}_2+\text{NO}_3\text{-N}$  and TP). In contrast, periphyton communities in streams of the Wapsipinicon and upper Cedar River basins consisted of species found commonly in diverse, mature algal communities (e.g., *Audouinella hermanii*, *Navicula* spp. and *Gyrosigma* spp.), which is consistent with relatively stable hydrologic conditions, ground-water discharge, and seasonally-typical streamflow (Figure A-15).

#### **SUMMARY AND IMPLICATIONS FOR ESTABLISHING AND MONITORING ALGAL-NUTRIENT CRITERIA**

Nutrient concentrations and the abundance of algae during low-flow conditions were not related directly to rates of fertilizer application or the number of livestock in Midwestern stream basins; however, rates of stream metabolism ( $P_{\max}$  and  $R_{\max}$ ) increased significantly with indicators of agricultural intensity. Algal-nutrient relations during August 1997 were more a function of landscape characteristics (riparian zones and soil properties), hydrology (ground-water and surface-water relations), and rainfall-runoff characteristics than agricultural land use, which is relatively homogeneous throughout the region. For example, average nutrient concentrations were significantly higher in the Minnesota River basin despite relatively lower agricultural intensity. Above-average rainfall and runoff from poorly drained soils, discharged through tile drains, probably explains the higher-than-expected nutrient concentrations in

these streams. Average rates of stream metabolism were relatively lower in streams in the Minnesota River basin, which is consistent with relatively higher concentrations of suspended solids and lower water clarity. Over half of these streams contained above-average seston chl *a* concentrations, which corresponds with relatively less riparian shading in Minnesota than in Illinois or Iowa. However, seston and periphyton communities were dominated by species associated with soils or those with high rates of colonization and reproduction. Benthic invertebrate and periphyton communities contained relatively fewer species; however, reduced species richness was more indicative of hydrologic disturbance (high, flashy stream flow and velocity) than organic enrichment.

In contrast, average dissolved nitrate concentrations in the Illinois River basin were significantly lower, even though agricultural intensity in those stream basins was among the highest in the region. Below-average rainfall (near drought conditions), resulting in significantly lower (surface water) nutrient yields from stream watersheds, lower stream velocities, and high rates of stream metabolism, probably explain the lower-than-expected dissolved nutrient and DO concentrations. However, concentrations of dissolved NH<sub>4</sub>-N were relatively higher, probably attributable (in part) to ground-water fluxes in basins with moderately well-drained soils. Water quality conditions in Illinois streams during August 1997 were relatively degraded, as revealed by relatively high concentrations of SOC, DOC, and TON (indicators of organic enrichment), low minimum dissolved-oxygen concentrations, high rates of stream respiration, and poor macroinvertebrate communities (low taxa and EPT richness).

Water quality in Iowa streams differed in relation to basin soil properties and riparian shading. Overall water quality was best in streams that drain basins with moderately well-drained soils and a high percentage of riparian trees (Wapsipinicon and upper Cedar River basins). These periphyton-dominated streams were characterized by low to moderate concentrations of nutrients and average stream productivity. Seston chl *a* values and rates of respiration were relatively low, and macroinvertebrate communities (e.g., EPT richness) indicated good water quality and habitat conditions.

Although phytoplankton chl *a* criteria are available to classify the trophic status of lakes and reservoirs (e.g., Carlson 1977), comparable criteria have not been established for seston or periphyton in lotic water bodies. Average chlorophyll values in the upper Midwest region are considerably lower than criteria proposed by Dodds et al. (1998) for temperate streams and rivers, whereas proposed criteria for total nutrients (TN > 1500 µg/L; TP > 75 µg/L) are exceeded in 74 percent (TN) to 89 percent (TP) of the streams in this study. Periphyton chl *a* values exceeded 70 mg/m<sup>2</sup> (proposed minimum eutrophic criterion) in only 13 percent of the streams, and seston chl *a* values exceeded 30 µg/L (proposed eutrophic criterion) in about one-third of the streams in this study. The higher recommended criteria for periphyton chl *a* (100 mg/m<sup>2</sup> to 200 mg/m<sup>2</sup>) (Welch et al. 1988; Watson and Gestring 1996; Dodds et al. 1998) was intended to protect streams and rivers from nuisance growths of filamentous algae such as *Cladophora glomerata*, other macroalgae, or other aquatic plants. These taxa require stable benthic surfaces (e.g., submerged rocks or bedrock) on which to colonize and grow to nuisance proportion. Sand and silt bottom streams of the Midwest, and submerged woody debris in these streams, do not generally provide suitable habitat to sustain nuisance filamentous algal growths. However, dense growths of microalgae (primarily diatoms and blue-green algae) on sand or woody snags in Midwestern streams could provide visible evidence of stream eutrophication during low-flow periods; the proposed minimum eutrophic criterion may be appropriate for indicating that condition.

Results from this study suggest that the abundance and composition of algal seston (phytoplankton) may be one of the better indicators of trophic conditions in streams and rivers of the upper Midwest region. Because of the highly significant correspondence between the standing crop (e.g., chl *a*) of algal seston and concentrations of total nutrients and carbon, criteria established for seston (evaluated during stable, low-flow conditions) is likely to represent total nutrient concentrations in the water and the extent to which organic enrichment is a problem for maintaining biological integrity in streams and rivers. Seston criteria would also provide an index for evaluating the clarity of streams and rivers, an important consideration relative to the public perception of trophic conditions, and water quality in general. However, criteria for total nutrients (and perhaps total suspended solids) cannot be abandoned for streams where algal growth is limited by inorganic turbidity or dense riparian-canopy shading. For example, if best-management practices (BMPs) are applied in watersheds to reduce adverse effects of sedimentation without consideration given to commensurate reductions in nitrogen or phosphorus loads to streams, excessive algal growths could ensue when productivity is no longer limited by the availability of light (e.g., in nutrient eutrophic streams and rivers). A consideration of water quality variables for establishing and monitoring the trophic condition of temperate streams and rivers is presented in Table A-3.

**Table A-3.** Summary of water quality variables for establishing criteria and monitoring the trophic condition of temperate streams and rivers.

Variable	Media (and frequency)	Relevance	Risk
Total nutrients	Water chemistry (monthly & in relation to hydrology)	chemical indicator	eutrophy
Dissolved nutrients	Water chemistry (monthly & in relation to hydrology)	chemical indicator algal-nutrient relations	eutrophy
Seston	Water samples (growing season & in relation to hydrology)	biological indicator organic enrichment food-web relations	eutrophy aquatic life biocriteria
Periphyton	Natural substrates (growing season & in relation to hydrology and aquatic herbivores)	biological indicator organic enrichment food-web relations	eutrophy; aquatic life; biocriteria
Stream metabolism	Estimates of system productivity & respiration (low flow conditions with chemical & biological measures)	biological indicator understanding	direct measure of process; aquatic life; biocriteria
Water clarity	Euphotic zone depth; water transparency; secchi depth (seasonal; with chemical & biological measures)	physical indicator understanding	aesthetic properties light availability for algal growth
Aquatic fauna	Natural substrates (low-flow conditions)	biological indicator understanding response to organic enrichment	receptor biocriteria TMDL process

Improved understanding of natural factors and algal-nutrient relations that contribute to chemical and biological indicators of eutrophication in lotic systems could enhance the development of water quality criteria within and among ecoregions in the U.S. (e.g., Level III; Omernik 1986). For example, results from this study indicate larger variance within the Western Corn Belt Plains ecoregion than between the Central and Western Corn Belt Plains ecoregions. Differences in soil drainage, ground-water/surface-water relations, and precedent rainfall-runoff conditions account for part of this variance. Improved understanding of dissolved nutrient relations with the abundance of seston and periphyton, rates of stream metabolism, and organic enrichment processes in streams could assist water managers with decisions concerning BMPs, total maximum daily load (TMDL) allocations, and the establishment of appropriate biocriteria relative to natural and human factors that contribute to the quality of streams and rivers.

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## BOW RIVER, ALBERTA

The Bow River is a documented case of recovery from point source nutrient loading rather than one of setting criteria. In contrast to lakes, cases in which the recovery of streams or rivers from nutrient reduction was thoroughly evaluated are scarce. The Bow River, Alberta, is an exception; it has been monitored for over 16 years to evaluate the effect of a reduction in first phosphorus (80%) and later nitrogen (~ 50%) from two domestic wastewater plants in Calgary (Sosiak pers. comm.). Algae and macrophytes had caused problems in the river by clogging irrigation water intakes, interfering with boating and angling, and causing low DO at night. Nitrogen removal was for the purpose of minimizing risk of ammonia toxicity rather than control of algae or macrophytes. Both periphyton and macrophytes decreased downstream in response to nutrient reduction, but the distribution and timing of the decreases were to some extent unexpected. The river's response to nutrient reduction offers pertinent implications and guidance for setting nutrient criteria in large fast-flowing, gravel-bed rivers. Median April to October flow in the Bow River over the sampling period ranged from approximately 75 to 130 m<sup>3</sup>/s.

Prior to P reduction, periphyton biomass consisted mostly of diatoms, although filamentous green algae (including *Cladophora*) were also present (Charlton et al. 1986). Biomass reached summer maximums downstream averaging approximately 300-400 mg chlorophyll *a*/m<sup>2</sup>, but occasionally up to 600 mg chlorophyll *a*/m<sup>2</sup>. Such maxima have persisted within 10 km of the effluent input since P reduction in 1983, but decreased markedly farther downstream over an approximately 90-330 km reach (Table A-4; note that data from two stations between km 304 and 533 are not shown). The decrease in periphyton occurred rather gradually over 13 years following P reduction as total dissolved P (TDP) declined to very low levels (median 10 µg/L) downstream (Sosiak pers. comm). Within 10 km downstream of the effluent input, however, TDP declined initially from a mean summer value of 111 µg/L to 19-24 µg/L and periphyton biomass exhibited no change from the high pre-treatment levels of 300-400 mg chlorophyll *a*/m<sup>2</sup>. The data upstream and downstream demonstrated that if summer TDP consistently averaged < 10 µg/L, maximum periphyton biomass typically averaged less than 100 mg chlorophyll *a*/m<sup>2</sup>. Maximum summer biomass averaged approximately 1.4 times mean values.

TDP and periphyton biomass decreased gradually over the 13-year period following treatment with the largest decline occurring after 1989, although this is not apparent from the data summary in Table A-4. The delayed decrease in TDP may have been due to declining recycling from sediments, the TP content of which declined downstream, but not upstream of Calgary (Sosiak pers. comm.).

This extensive data base also indicates that TDP was linked much closer to periphytic biomass than TP, which decreased markedly following treatment upstream (Stier's Ranch). The change was only slight downstream, in contrast to the 50% decrease in TDP (Table A-4). Note that average maximum biomass varied from 77 to 428 over a range of summer mean TP of only 40 to 59 µg/L. Periphytic biomass was also correlated with TDP (r values of -.61 to .70), but not with TP (Sosiak pers. comm.). Sosiak concluded that TDP was a much better indicator of periphytic biomass throughout the river than TP.

An interesting contrast for this case study in comparison with the Clark Fork River involves the reduced frequency of filamentous green algae and lower maximum biomass levels in the Bow River. *Cladophora* was the dominant taxa that extensively covered the bottom substrata and created the nuisance condition interfering with recreational use in the Clark Fork River. In the Bow River, the periphyton was dominated by diatoms, which can be highly visible if biomass is high. Although *Cladophora* was present

downstream from Calgary prior to nutrient reduction (Charlton et al. 1986), there was apparently not the high percent cover of filamentous greens that interferes with recreation. Part of the difference in nuisance conditions between the two rivers may be related to the higher summer flows in the Bow. Nevertheless, *Cladophora* and some other filamentous greens did largely disappear after nutrient reduction (Sosiak pers. comm.).

These data indicate that: 1) periphyton biomass in streams and rivers does respond to nutrient reduction, 2) biomass levels below nuisance levels ( $\sim 150$  mg chlorophyll *a*/m<sup>2</sup>) can be attained if P can be sufficiently reduced, 3) sufficient reductions are defined by levels approaching  $\sim 10$ - $15$   $\mu$ g/L TDP, and 4) response to nutrient reductions may not occur quickly even in rivers where water exchange is immediate. The gradual reduction in river TDP suggests that there is a long-term, slow release of P stored in (or adsorbed to) bottom sediments, even in rubble-bottom rivers.

In addition, macrophytes (mostly pond weeds) reached biomass levels of  $> 2000$  g/m<sup>2</sup> within 30 km downstream of discharges prior to effluent treatment in 1987, but declined soon after N reduction, reaching levels in 1995-1996 of  $< \sim 200$  mg/m<sup>2</sup>. The cause for macrophyte decline in response to N reduction is not clear, but was hypothesized to be due to increased N limitation at plant roots (Sosiak pers. comm., citing Barko et al. 1991). Nitrogen in the water was never considered limiting to macrophytes or algae, because DIN:TDP ratios were always well above 20:1 by weight even after N removal.

The downstream change in periphyton biomass was simulated with a model that predicts spatial and temporal biomass and nutrient (in this case SRP) concentrations in cobble/gravel-bed rivers during summer low-flow conditions. SRP was not determined in the Bow River, but TDP was converted to SRP using  $0.65 \times$  TDP. Of five years suitable for model calibration, a 4-week period in October 1997 was selected (Elswick et al. 2000). Sloughing loss was assumed negligible during this period, as has been observed in laboratory channel experiments during which periphyton is actively growing to a maximum biomass (Horner et al. 1990; Anderson et al. 1999). The model was not verified, because there was insufficient data for some processes, such as grazing, for which a constant value was used (10% of existing biomass/day).

Model simulation compared favorably with actual data (Figure A-16). The largest discrepancy was at Carsland (56 km) where biomass was overestimated by 100%. Biomass was also overestimated at all other sites, but by an average of only 25%. Part of this difference may have been related to P retention in run-of-the-river impoundments located upstream from Carsland and not included in the model. Also, grazing may have been greater than the assumed rate. Grazing rates per unit grazer biomass are available in the literature and could be used in this model if grazer biomass were available. Nevertheless, the model demonstrates the phenomenon of biomass reduction downstream following nutrient reduction at a point source. That is, while P concentrations were still too high to reduce periphyton biomass below the nuisance level ( $\sim 150$  mg chl/m<sup>2</sup>), P concentrations and biomass declined downstream and the extent of the decline can be estimated with this model.

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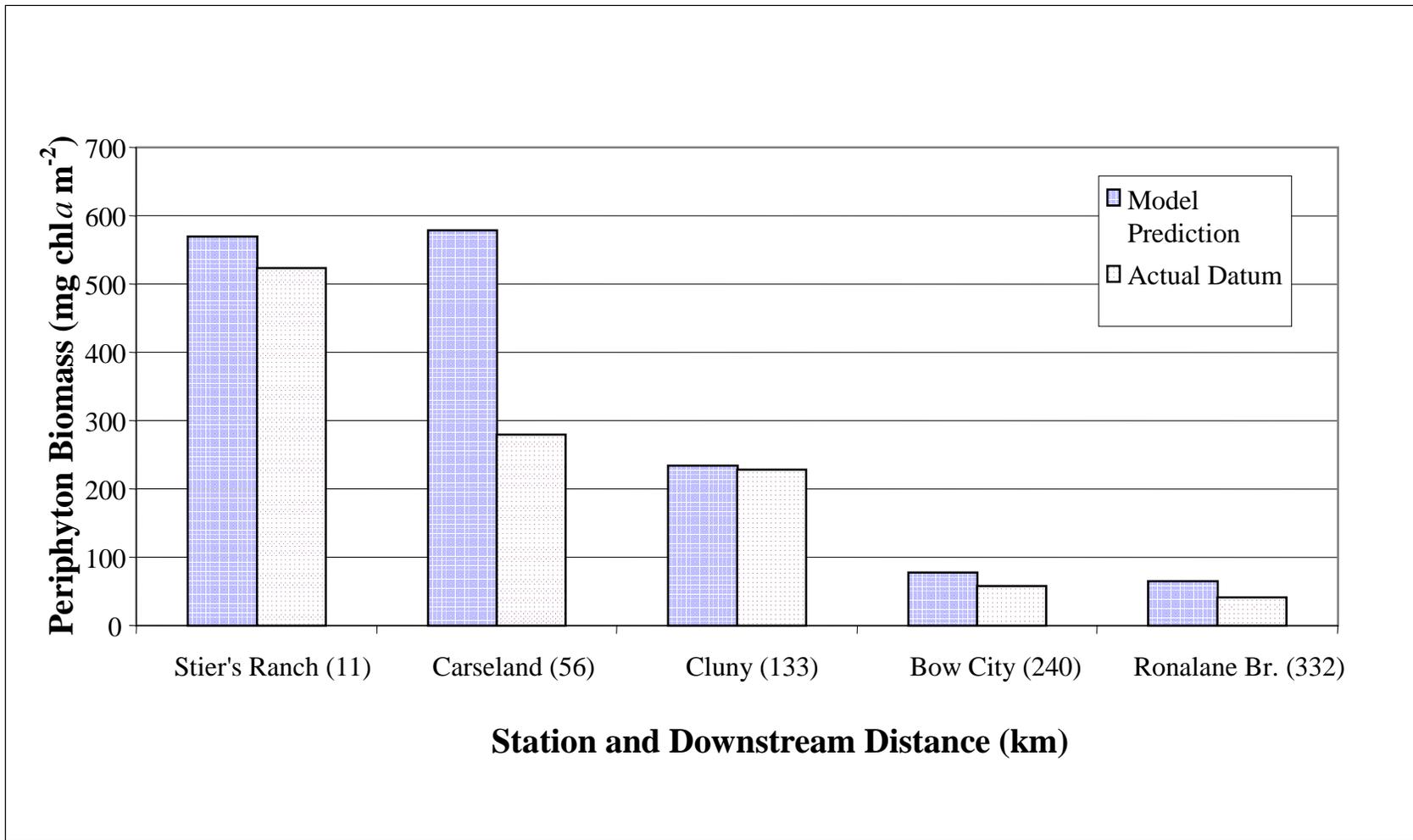
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**Table A-4. Summary of Phosphorus and Periphytic Algal Data from the Bow River, Canada<sup>1</sup>**

Station	Distance from Headwaters, km	Data type	Data years	Average summer periphytic biomass, mg/m <sup>2</sup>	Average maximum summer periphytic biomass, mg/m <sup>2</sup>	Mean summer total phosphorus, µg/L	Mean summer total dissolved phosphorus, µg/L
85 <sup>th</sup> St. bridge	254.53	post-treatment	1984-87	27	49	8.5	5.0
		post-treatment	1988-96	71	97	15.1	4.7
STP	279.14						
STP	294.03						
Stier's Ranch	304.81	pre-treatment	1981-82	248	294	147.7	110.6
		post-treatment	1984-87	189	369	52.4	18.9
		post-treatment	1988-96	225	428	59.2	24.2
Bow City	533.78	pre-treatment	1980-82	83	196	54.0	21.6
		post-treatment	1984-87	51	77	40.0	10.5
		post-treatment	1988-96	57	92	37.3	7.0
Ronlone Bridge	625.61	pre-treatment	1980-82	94	148	40.0	15.3
		post-treatment	1984-86	74	111	39.1	10.8
		post-treatment	1996-98	59	111	16.8	7.0

<sup>1</sup>Data from Sosiak, Alberta Environment Protection, personal communication

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**Figure A-16.** Model simulation of periphyton biomass during low-flow conditions in the Bow River downstream from the Fish Creek STP, Calgary, Alberta, compared with actual 1997 data.



## **NUTRIENT CRITERIA DEVELOPMENT FOR DESERT STREAMS— DETERMINANTS OF NUTRIENT DYNAMICS IN SOUTHWESTERN HOT DESERT STREAM ECOSYSTEMS**

As a class of pollutants, nutrients are unique from toxicants such as mercury or DDT, in that they have known biological functions. Macronutrients such as nitrogen and phosphorus, are at once biological necessities and, in excess quantity, agents of change to community and ecosystem attributes. As such, great care must be taken in the characterization of nutrient regimes in stream ecosystems. Streams are by their very nature dynamically changing ecosystems that must be studied at ecologically meaningful temporal and spatial scales (O'Neill et al. 1986). The characterization of "ambient" conditions with a few grab samples is inappropriate, if not reckless. The researcher must first learn what limits autotrophic productivity, the major nutrient sources and sinks and how and where nutrient transformations take place in order to make informed decisions and avoid the adoption of water quality standards that may allow or even cause shifts in stream community structure or ecosystem process.

The nutrient regime of streams in general can be complex, however, desert streams present particular complexities not found in more homogeneous, mesic landscape stream ecosystems. Spatial and temporal variability in physical structure, community composition, materials availability and the interactions between these elements strongly control nutrient processes in desert streams. Dent and Grimm (in press) found a high coefficient of variability (as high as 145%) in the spatial distribution of nutrients in Sycamore Creek, Arizona, with coefficients of variation increasing over successional time. Part of this is due to hydrologic variability, in all its temporal, spatial and amplitude scales. However, stream ecosystems are complex in time, space, composition and process, and extend beyond the limit of the wetted surface stream. These ecosystems must be considered as a whole, temporally and spatially, and not as disconnected, stand alone components in order for accurate characterization to take place.

The following discusses a number of the many determinants of nutrient regimes in desert streams. As the subject matter of this section deals with desert streams, and in particular, southwestern hot desert streams, the literature cited will concentrate on research done in those ecosystems. A hierarchical structure (sensu Stevenson 1997) will be used to organize determinants into ultimate, intermediate, and proximate categories. These hierarchical levels operate as interconnected units, with a particular level being limited by constraints imposed by higher levels with processes structured at lower levels (Pickett et al. 1989). Because of the interconnectedness of the differing hierarchical scales, it will be sometimes necessary to "mix" scales in the discussion that follows. Hydrologic variability and its effects on desert stream nutrient regimes is also discussed.

### **ULTIMATE DETERMINANTS**

Ultimately, the stream is a product of its parent geology, catchment configuration and climate. In desert streams, these structural determinants combine to organize processes at lower hierarchical levels forming ecosystems unique from more mesic ecosystems. These desert stream ecosystems consist of four interconnected and interacting subsystems, the surface stream, the hyporheic zone (zone of subsurface flow), the parafluvial zone (lateral sandbars within the active channel) and the riparian zone. These subsystems interact with and are ultimately a product of the geology and the climate/precipitation regime.

Parent geology can play a large role in the availability of nutrients to aquatic ecosystems. Because of the impermeability of desert soils and the low biomass per unit area found in terrestrial desert ecosystems, materials entrained by precipitation events readily move into aquatic ecosystems, assuring an ample supply of nutrients associated with the parent material. Soils of the arid southwest are rich in calcium phosphate (Fuller 1975) and transfer that nutrient readily to stream ecosystems. A survey of 196 sites on 157 streams in Arizona found soluble reactive phosphorus (SRP) and total dissolved phosphorus did not differ significantly among stream types (Fisher and Grimm 1983; Grimm and Fisher 1986a). This uniformity in concentration may be due to solubility equilibria (Stumm and Morgan 1981) and indicate physical rather than biological control of this nutrient. The ample supply of phosphorus coupled with the low overall input of nitrogen from the surrounding landscape has led to the condition in which nitrogen, rather than phosphorus, is the nutrient that limits primary productivity (Grimm and Fisher 1986b).

The size of the soil particles moving into and staying within the channel can also have a large impact on the nutrient dynamics of streams (Jones 1995). In Arizona desert streams, the unglaciated terrain provides little silt and clay to the stream (Fisher 1986) and the flashy hydrologic regime may cause what little sediment that makes it into the stream to be deposited either laterally or in unconstrained reaches. Valett et al. (1990) found that in Sycamore Creek, Arizona, most sediment ranged in size from coarse sand to fine gravel (0.5 -5.0mm). This paucity of fine sediments allows a relatively high rate of hydrologic conductivity within the hyporheic (Valett et al. 1990), parafluvial (Holmes et al. 1994), and riparian zone (Marti et al. in press [a]).

The hydrologically conductive sediments beneath and lateral to the wetted stream are an important zone of biologically mediated nutrient processes. Jones et al. (1995) observed significant rates of nitrification (mineralization of organic nitrogen to ammonia and a subsequent transformation to nitrate) within the hyporheic zone of Sycamore Creek. This nitrate rich hyporheic water may then exchange with nitrogen poor surface water (Dahm et al. 1987; Valett et al. 1990; Stanley and Valett 1992) where it is an important nutrient source for primary producers and may strongly influence biomass and community composition (Valett et al. 1994).

The parafluvial zone consists of sediments within the active channel but outside the wetted stream. Results from Holmes et al. (1994) indicate that the parafluvial zone can be an area of net nitrification, and increased algal productivity has been observed on the downstream edges of parafluvial sandbars. However, Holmes et al. (1996) found significant denitrification (the reduction of nitrate to nitrous oxide or dinitrogen) potential existed in hyporheic and parafluvial sediments. Conservative estimations by these authors indicated that 5-40% of nitrate produced by nitrification may be consumed by this process.

The riparian zone can also be an important area of nutrient storage and transformation. Denitrification and uptake by vegetation within riparian areas may constitute a significant sink of nutrients within a watershed (Peterjohn and Correll 1984; Pinay and Decamps 1988). Chauvet and Decamps (1989) found denitrification and nutrient retention to be important processes in these areas. Marti et al. (in press [b]) found retention of nutrients in riparian areas to be affected by the length of the interflood period rather than by the magnitude of the flood.

The overall geomorphological structure of the stream, which is a product of geology and climate, determines the pattern of the four subsystems; surface stream, hyporheic, parafluvial, and riparian. This

spatial mosaic can have a strong influence on the retention, transformation, uptake, and emission of nutrients (Fisher et al. 1998a).

The climate, while a contributing determinant of desert stream physical structure, is also an ultimate determinant of biological structure and function. Desert streams receive high rates of insolation due to the low amount of shading contributed by the relatively open riparian canopy. This open canopy itself is a product of the low precipitation rates and high pan evaporation rates found in southwestern deserts. Although precipitation rates are low in desert landscapes, this sparse precipitation may contribute substantial amounts of nitrate and ammonium to desert stream ecosystems (Grimm 1992).

### **INTERMEDIATE DETERMINANTS**

Community structure and function are shaped in part by the constraints imposed from the higher geological and climatic scale. Species composition and life history are ultimately products of the physical components of aquatic ecosystems and, in turn, alter physical structure and chemical processing at the ecosystem level. These interactions can significantly affect nutrient dynamics in aquatic ecosystems.

The change in the biotic community that occurs over time after a flood disturbance shapes and changes nutrient processing. The concept of temporal succession has been put forward to conceptualize this temporal change that occurs after a flood disturbance. Fisher et al. (1982) described the recovery of community and ecosystem attributes after flooding disturbance in Sycamore Creek, Arizona, as a model of temporal succession. In these ecosystems, biologically driven nutrient transformation, uptake, and emission can vary significantly over spatial and temporal scales.

Changes in nutrient processing and species composition over successional time can drastically alter the nutrient regime of streams in general, and, due to their open, autotrophic nature, in desert streams in particular. A flood disturbance of sufficient magnitude can scour and shuffle hyporheic and parafluvial sediments, removing attached biomass and essentially homogenizing ecosystem structure and function at the reach level. The emergent physical structure confers organization to the biotic community recolonizing the reach post flood. During the interflood period, biological processes become a progressively more prominent organizational force which, given a sufficient interdisturbance interval, can then confer organization to higher hierarchical levels.

The complexity of nitrogen processing interactions increases with successional time. Dent and Grimm (in press) found nutrient spatial heterogeneity in the surface stream to increase with time post flood. Over successional time, nitrogen uptake length decreases due to increased biological uptake (Fisher et al. 1982; Marti et al. 1997) and retention of nitrogen in the surface stream increases from early to mid successional stages and then declines during late succession (Grimm 1987). The changes seen in nutrient processing length due to disturbance may vary according to the relative resistance of the individual stream subsystem and recovery may vary over successional time due to relative resilience (Fisher et al. 1998b).

Streams by their very nature are spatially heterogeneous. In desert streams, the spatial heterogeneity of nutrients and nutrient processing is manifested in several ways. Hydrologic linkages between the surface

stream and the parafluvial and hyporheic ecosystem components vary spatially due to the underlying geomorphological structure of the stream ecosystem. As stated earlier, these are areas where important nutrient processing occurs. The extent and intensity of hyporheic upwelling and downwelling can change or even reverse in response to flooding or drying (Stanley and Valett 1992; Valett et al. 1994) considerably affecting concentrations of nitrate in the surface stream and influencing algal community composition (Valett et al. 1994).

One of the most striking successional events in desert streams is the drying and contraction of the surface stream ecosystem. This phenomena can take place either at large spatial and temporal scales, or at the scale of the reach during a 24 hour period. In Sycamore Creek, as the quantity of water delivered to the surface stream ecosystem begins to diminish after an extended wet period or post flood, drying begins to occur.

During dry periods, the wetted surface stream area can contract as much as eight fold at the scale of the entire basin. (Stanley et al. 1997). At the scale of the individual run, drying may begin at the downstream terminus and continue upstream to the area of hyporheic upwelling at the head of the run (Stanley et al. 1997). This contraction of the surface water ecosystem can strongly affect algal community composition. Nitrogen fixing cyanobacteria species inhabiting the downstream extremity of the drying run are exposed to the atmosphere long before upstream mats of filamentous green algae situated closer to the source of nitrogen rich hyporheic upwelling, potentially altering nitrogen cycling (Stanley et al. 1997). At all scales, drying of the surface stream increases the relative contribution of hyporheic processes to overall ecosystem function (Stanley and Valett 1992).

The increase in the relative proportion of the wetted stream ecosystem occupied by subsurface subsystems could have a profound effect on nitrogen processing and retention. With the decline of surface stream area available to autotrophic production and nitrogen fixation, the nitrogen transformations associated with subsurface flowpaths, nitrification, and denitrification will become proportionally more prevalent (Stanley and Valett 1992). This, coupled with the ample organic carbon available from decaying algae (Jones et al. 1995) and oxygen depletion due to respiration over extended hyporheic flowpaths, could possibly cause subsurface subsystems to become net nitrogen emitters. This emission of nitrogen gas would represent a real loss of nitrogen from the stream ecosystem.

The riparian component of the desert stream ecosystem, while ultimately a product of climate, geology, and catchment configuration, also modifies environmental factors within the ecosystem of which it is a part. At successional and reach scales, the presence of riparian vegetation is a strong determinant of the shape of the surface stream channel. Given a long period between stand destructive floods and ample surface or near surface water, fast growing woody species such as seep willow (*Baccharis salicifolia*) will progressively impinge on the surface stream. As the surface stream narrows, parafluvial ecosystem components gradually convert to riparian, considerably changing nutrient processing pathways.

The high pan evaporation rate ( $>300 \text{ cm year}^{-1}$ ) found in hot desert ecosystems coupled with high consumptive water use by phreatophytes (water-loving riparian plants) ( $1514 \text{ L day}^{-1}$ ) (Blaney and Criddle 1962) can significantly influence the size of a surface stream reach on a diel basis. Large changes in reach length during a 24 hour period have been observed on Sycamore Creek (Stanley pers. com.). This type of short term stress can effectively eliminate desiccation intolerant organisms from the benthic community of large portions of a stream reach.

In contrast to more mesic streams, many desert stream riparian zones occupy a relatively narrow band lateral to an underfit surface stream, providing minimal shading to the surface stream itself. The resultant high rate of insolation to the surface stream favors high rates of primary productivity, high relative water temperatures, and attendant increases in metabolic rates (Busch and Fisher 1981). The elevated rates of primary productivity and metabolism are controlling factors in the short uptake lengths for nitrogen covered earlier in this document.

### PROXIMATE DETERMINANTS

The nitrogen cycle, as it occurs within a desert stream, is essentially a biologically driven process. Given the physical organization conferred from higher hierarchical levels, the resultant biotic communities of the surface stream, riparian, parafluvial, and hyporheic control fixation, mineralization, nitrification and denitrification.

Nitrogen fixation by heterocystous cyanobacteria such as *Nostoc* or *Calothryx* and diatoms with phycoendosymbionts such as *Epithemia sorex* may be significant in nitrogen poor desert stream ecosystems. Grimm and Petrone (1997) measured in-situ  $N_2$  fixation rates as high as  $51 \text{ mg } N_2 \text{ m}^{-2} \text{ h}^{-1}$ . These rates were high in comparison to published values from more mesic inland systems. In this study, as much as 85% of the net nitrogen flux to the benthos was accounted for by  $N_2$  fixation on five dates for which nitrogen input/output budgets were constructed. Nitrogen fixation may be an extremely important vector of nitrogen into desert stream ecosystems, as between precipitation events, little fixed nitrogen from the surrounding uplands is transported to the stream ecosystem (Grimm and Petrone 1997).

As stated earlier, nitrification, or the biologically mediated oxidation of ammonium to nitrate takes place within hyporheic and parafluvial sediments. Jones et al. (1995) reported mean nitrification rates of  $13.1 \text{ mg } NO_3 \cdot L \text{ sediments}^{-1} \text{ h}^{-1}$  in downwelling zones in Sycamore Creek and Holmes et al. (1994) reported increases in nitrate concentrations in water moving through parafluvial flowpaths. In both studies, the highest rates of biotic activity occurred at the interface where the surface stream infiltrated into hyporheic/parafluvial sediments. This effect suggests the importance of dispersed interfaces in a heterogeneous system (Dahm et al. 1998)

Denitrification is well documented in anoxic environments such as riparian soils (Peterjohn and Correll 1984; Lowrance et al. 1984), but in well oxygenated environments such as the coarse sand/gravel hyporheic/parafluvial subsystems found in desert streams, the occurrence of denitrification is somewhat of a conundrum. Holmes et al. (1996) investigated denitrification potential in hyporheic, parafluvial and riparian sediments and found field measured rates in excess of  $150 \text{ mg } N \cdot \text{m}^2 \cdot \text{h}^{-1}$  at the stream/parafluvial interface. This study also found the highest rates of biotic activity (denitrification) at the point of infiltration at the surface-water-sediment interface.

Despite the low overall availability of the most probable limiting nutrient in southwestern hot desert streams, nitrogen, high mid-summer instantaneous standing crops of algae ( $191 \text{ mg }^{-1} \text{ m}^2$  chlorophyll a) have been measured in Sycamore Creek (Busch and Fisher 1981). The spatial distribution of algal standing crop has been linked with areas of hyporheic upwelling and downwelling. Valett et al. (1994) found significantly higher areal concentrations of chlorophyll a in upwelling zones when compared to areas of downwelling. These high quantities of algal biomass and the associated autotrophic uptake of nitrogen are the most probable cause for the declines in nitrogen concentrations of surface water found

downstream of spring sources (Grimm et al., 1981) and the lower concentrations found at points of downwelling (Valett et al., 1994).

Organic carbon released as a result of autochthonous primary production has been hypothesized as the energy source utilized in nitrification (Holmes et al., 1994; Jones et al., 1995) and denitrification (Holmes et al., 1996). However, allochthonous input of organic matter from riparian leaf litter was found to play an insignificant role in nitrogen dynamics in Sycamore Creek (Schade and Fisher 1997).

Macroinvertebrates may also significantly affect nitrogen processing in desert streams. Grimm (1988) found that during a 20 day successional period, collector gatherer invertebrate standing stock increased from 32,000 to 108,000 individuals  $\cdot$  m<sup>2</sup>. Twenty seven percent of the nitrogen ingested by the collector gatherers during this period was converted to biomass, of which only 26% (7% of total ingested nitrogen) remained in the stream as macroinvertebrate biomass. One percent of collector gatherer biomass was lost to the surrounding upland ecosystem due to the emergence of adults, 19% was lost to mortality and 9-31% was excreted as ammonia. The transformation of organic nitrogen to ammonia may be particularly significant, as the ammonia form of nitrogen is readily taken up and utilized by primary producers or available for utilization in nitrification/denitrification transformations.

#### **HYDROLOGIC VARIABILITY IN ARID LANDS STREAMS**

While hydrologic variability is an important consideration in the development of nutrient standards for all streams, the spatial and temporal heterogeneity found in arid regions, the stark contrast between wet and dry, brings this variability into sharper relief. When viewing desert catchments from above, the observer is often presented with a dry landscape of high relief bisected by the string of glistening beads that is the spatially intermittent stream. The dry arroyos or quiet, disconnected pools and short reaches of wetted stream that characterize desert streams during dry periods are in complete contrast to the raging torrents that they can become at flood stage. This hydrologic variability and the unique chemical and biological characteristics of arid lands aquatic ecosystems may make the use of broad generalizations to explain nutrient regimes impossible.

When analyzing stream nutrient regimes in the context of hydrologic variability, there is a continuum of spatial and temporal scale (sensu Pickett et al. 1989; Fisher and Grimm 1991) beyond and including discreet disturbance flows which must be considered. Ecologically important spatial and temporal scales can vary from that of a discreet patch at a single point in time, to the fluvial geomorphological and climatic factors determining the physical structure of an entire catchment. These spatial and temporal scales exist as nested hierarchies, with structure at smaller scales being influenced by higher scales (Pickett et al. 1989).

Use of a coherent hierarchical schema can confer useful organization to the analysis of nutrients and primary productivity. The heterogeneity of benthic algal assemblages is determined at several hierarchical levels, with proximate and intermediate determinants such as nutrient regime and flow stability being governed by the ultimate determinants of climate and geology (Stevenson 1997). It is important to consider the determinants of structure and function at different scales when designing ecological studies.

In arid landscapes, stream ecosystems are more dynamically linked with the surrounding upland ecosystem than streams in more mesic regions. This close linkage is due to the higher percentage of uninterrupted vectors of runoff and entrained materials from the surrounding uplands to the aquatic ecosystem. The extensive riparian buffers and dense upland terrestrial vegetation found in more mesic ecosystems are largely absent in spatially intermittent and ephemeral watercourses. The sparse vegetative cover (5-50%; Barbour et al. 1980) and high orographic relief found in the upland terrestrial catchments promote increased rates of short-term, sheetflow runoff during intense precipitation events, leading to larger, more rapid movements of precipitation and entrained materials into watercourses (see Graff 1988). This "spiky" oscillation in the hydrograph is then transferred downstream to the more perennial sections of a stream.

In desert streams, surface discharge regimes may vary from completely dry, to flows as much as three to five orders of magnitude greater than mean annual flow, all within a period of hours or days. In comparison to streams in more mesic regions, the coefficient of variation of annual flow is 467% greater in arid land streams (Davies et al. 1994). The aquatic ecosystems structured by these often catastrophic and always chaotic flow regimes exhibit spatially and temporally heterogeneous structures and functions (*sensu* Thoms and Sheldon 1996) which may not allow the application of nutrient criteria derivation techniques applicable to more homogeneous environments.

Short-term disturbance of small spatial extent may cause considerable alteration in the chemical and biological structure of a stream. Flooding may scour the benthic surface, reset the stream ecosystem to an earlier successional stage (Fisher 1983) and transport large, short-term pulses of nutrients (Fisher and Minckley 1978). Drying of a surface stream reach due to diel changes in evapotranspiration can strand algal mats (Stanley pers. com.) causing a stress disturbance (*sensu* Pickett et al. 1989). Recovery from these types of small scale disturbances may be rapid in ecosystems where the biota is disturbance adapted (Gray 1981; Grimm and Fisher 1989) and when observed in the context of larger spatial and temporal scales, these types of disturbances may represent normal oscillations in a steady state equilibrium.

Often, hydrologic regimes that effect a particular ecological structure or function may exist at spatial and temporal scales that can only be measured using multiple measurements over space and time. While the flood pulse itself may cause considerable disturbance to a stream ecosystem, the entire hydrologic regime must be considered biologically significant (Poff and Ward 1989). Variability in rates of rise and fall, timing, duration, magnitude and frequency of the flood pulse can have a significant effect on the biota of a stream (Puckridge et al. 1998). At slightly longer temporal scales, it is the relatively short interval (1.5 year) bankfull discharge that forms and maintains the physical structure of the wetted channel (Dunne and Leopold 1978) rather than the catastrophic long return interval flood.

During interflood periods, flow regimes are comparatively stable as precipitation stored within the watershed moves into the stream. The stable flow allows the control of ecosystem state variables, such as primary productivity, to shift from disturbance to morphometric/biotic controls. If the interflood period is of sufficient duration, a phase shift from wetted surface to dry occurs as flow from the watershed diminishes (Fisher and Grimm 1991). During this interval, primary productivity is a partial function of the number of days post flood (Fisher 1986; Fisher and Grimm 1988). Characterization of the interflood period is an important tool which may allow the researcher to locate the point in successional time when indexing biological data for inter or intra-stream comparison.

One portion of the hydrologic regime that is often overlooked is drying. Drying disturbance, or more specifically the contraction and fragmentation of a stream ecosystem, occurs as a spatially or temporally intermittent stream recedes after a wet period. Differing reach types (e.g., riffles, runs, constrained, unconstrained) respond to this contraction and fragmentation differentially (Stanley et al. 1997) and hyporheic, or subflow processes may come to dominate as a larger portion of the wetted volume of a stream is subsurface. (Stanley and Valett 1992; Valett et al. 1990). Drying is likely to be an important determinant of biological pattern and process (Stanley et al. 1997; Stanley and Boulton 1995), especially in streams where the dry period and extent may be greater than the wet.

Longer-term hydrologic/disturbance regimes are also an important consideration. Decadal climate variability such as the El Niño and La Niña phenomena can cause large, prolonged fluctuations in stream flow (Molles and Dahm 1990). This long return interval climate variability and the attendant change in short-term weather patterns can significantly affect the structure and function of aquatic ecosystems. The establishment, maintenance and species composition of riparian associations are strongly dependant on the seasonality, periodicity, duration, sequentiality and magnitude of storm events and subsequent flow regimes (Baker 1990; Stromberg et al. 1991).

Large, long return interval disturbances can also greatly alter the physical structure and pattern of watercourses at greater than reach scales. These large alterations may affect the physical equilibrium of the watercourse in several ways. If the system is stable or dynamically stable, internal feedback mechanisms will cause physical values such as bed load transport to return to original following a disturbance. If a system is unstable or metastable, the system may adjust to a new value causing changes in channel pattern and shape (sensu Chorley and Kennedy 1971).

In the event a large scale, destructive flood event significantly restructures a stream, changes may occur in mean particle size, pattern of reach types or the ratio of the different stream ecosystem components (surface, riparian, parafluvial, hyporheic). These changes in physical structure may significantly alter the prevailing nutrient regime (sensu Fisher et al. 1998a).

In order to properly characterize the nutrient regime of a stream ecosystem, the flow of water, surface or subsurface, flood or base flow, wet or dry must be considered at ecologically significant temporal and spatial scales. It is also important that the researcher address this hydrologic regime at the scale of the question to be answered. If a stream is dry for 75% of the average year, or 75% of its length, is it correct to characterize it from surface water data alone? If 50% of the entire annual load of a limiting nutrient passes through a stream ecosystem in three discreet storm events, what is the effect of that nutrient on the stream ecosystem itself? What is the effect to downstream ecosystems? Due to the spatial and temporal variability of flow patterns, the characterization of desert stream nutrient dynamics is an intricate undertaking. However, it is important to recognize that all stream ecosystems possess complexities that will only yield to proper inquiry.

## CONCLUSIONS

The characterization of nutrient dynamics in streams with high temporal and spatial variability, such as southwestern hot desert streams, may prove to be difficult without a commitment to addressing questions at the appropriate ecological scale. Variability in the products of climate and geology; precipitation, flow regime and physical structure, define the limits of community composition and nutrient processing. The

predictive power of any model designed to characterize nutrient dynamics without considering the ultimate determinants is extremely limited. Conversely, relying on coarse generalizations generated at the spatial and temporal scale of the ecozone to predict process at the scale of the reach is also inappropriate. Nutrient dynamics must be characterized and nutrient water quality standards developed considering the constraints and processes dictated at the different and interacting scales.

## **STEPS FOR CHARACTERIZING THE NUTRIENT REGIME OF DESERT STREAM SYSTEMS**

### **Selecting Index Sites and Periods**

As in any investigation, the researcher must remove or account for as many of the differing sources of variability as possible prior to gathering nutrient data. In streams with high spatial and temporal variability, the best case scenario would be to characterize the entire stream, source to terminus, in space and time. While this may be the most scientifically sound methodology, it is infeasible in all but the smallest basins. An alternative is to carefully choose and compare index sites (and periods) from which reasonable extrapolations can be made. This can be done using a similar hierarchical approach to that outlined above, however, extrapolation beyond the specific index is risky. The number of sights required to accurately characterize the nutrient regime in a stream type will vary with the complexity of that nutrient regime.

First, at the largest spatial scale, the position of the stream reach within the watershed must be determined. The areal extent of the basin above the sample reach, the watershed aspect (orientation to weather patterns), mean stream gradient, parent material(s) and stream order are all attributes that should be considered. At the largest temporal scale, the time since the last flood that restructured all of the stream compartments (surface, hyporheic, parafluvial, and near stream riparian) should be determined as well as any long-term fluctuations or trends in the hydrograph.

At the scale of the sample reach, the researcher should consider the landscape setting surrounding and upstream of the sampling point. It is important that the sample reach and surrounding landscape be consistent with that found for a reasonable distance upstream. This distance will depend on stream velocity, with greater distances being required in faster flowing streams. The following is a list of the major elements of a sample reach that should be addressed to characterize nutrient regime and increase data conformity between sampling sights:

### **Physical/Structural Elements**

- altitude
- terrestrial vegetation association
- terrestrial land use
- Rosgen stream type
- physical setting - constrained or unconstrained? (canyon or open plane)
- reach gradient
- solar aspect - is the sun blocked by canyon walls at times during the day or year?
- riparian association - including understory plants
- riparian cover percent
- riparian canopy density - stream shading
- stream discharge and velocity

- substrate particle size distribution
- estimated subsurface compartment volume (hyporheic, riparian and parafluvial)
- location of upwelling and downwelling zones
- water temperature

**Temporal Elements**

- season
- photoperiod
- time since last flood
- flow regime the previous 30 days
- temperature regime the previous 30 days (air and water)

**Chemistry (other than TN and TP)**

- $\text{NH}_3/\text{NH}_4$ ,  $\text{NO}_3$ , SRP
- $\text{CO}_2$
- potassium (K), calcium (Ca), magnesium (Mg), sulphur (S), boron (B), chlorine (Cl), copper (Cu), iron (Fe) manganese (Mn), molybdenum (Mo) and zinc (Zn)
- $\text{O}_2$  - dissolved and % saturation
- pH - field measured
- electrical conductivity
- total dissolved solids
- total organic carbon
- turbidity - field measured
- total suspended solids
- volatile suspended solids

**Biological Elements**

- algal community composition
- benthic chlorophyll *a*
- benthic organic matter
- benthic community productivity and respiration

When taking physical, chemical or biological samples, it is extremely important to choose the sampling point(s) and times carefully in order to accurately characterize the element in question for a particular reach at a particular time. Multiple samples taken within the reach and analyzed separately is the preferred method, however composite samples, or carefully taken grab samples can work well. The researcher should avoid or account for samples taken in areas of the stream that differ from the main body. Anoxic backwaters, upwelling or downwelling zones, highly aerated areas below waterfalls and other sections that differ physically, chemically, or biologically from the main stream, usually account for only a small portion of total stream area but may contribute significantly to materials processing. Rather than characterizing these sections individually, a point can be chosen that integrates these areas into the greater flow. A fast “run” with relatively uniform flow, biological, and bank characteristics for 20 meters that has neutral subsurface hydraulic head may be a good selection. Insolation rate (solar

energy per unit area per unit time) and diel curve should also be considered, although a viable alternative would be careful consideration of time of day, time of year, riparian shading, and cloud cover.

It is extremely important that *enough* data be gathered to characterize a nutrient regime. While the ancillary data requirement may seem large, lack of one or more of these data points may preclude accurate interpretation of the nutrient data.

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