

2014

A Review of the Hyporheic Zone, Stream Restoration, and Means to Enhance Denitrification

Leanne Merrill
SUNY Stony Brook, leanne.merill@stonybrook.edu

David J. Tonjes
SUNY Stony Brook, david.tonjes@stonybrook.edu

Follow this and additional works at: <https://commons.library.stonybrook.edu/techsoc-articles>



Part of the [Biogeochemistry Commons](#), [Environmental Chemistry Commons](#), [Environmental Engineering Commons](#), [Environmental Health and Protection Commons](#), [Environmental Indicators and Impact Assessment Commons](#), [Environmental Monitoring Commons](#), [Fresh Water Studies Commons](#), [Hydrology Commons](#), [Natural Resources Management and Policy Commons](#), [Sustainability Commons](#), and the [Water Resource Management Commons](#)

Recommended Citation

Merill, Leanne and Tonjes, David J., "A Review of the Hyporheic Zone, Stream Restoration, and Means to Enhance Denitrification" (2014). *Technology & Society Faculty Publications*. 5.
<https://commons.library.stonybrook.edu/techsoc-articles/5>

This Article is brought to you for free and open access by the Technology and Society at Academic Commons. It has been accepted for inclusion in Technology & Society Faculty Publications by an authorized administrator of Academic Commons. For more information, please contact mona.ramonetti@stonybrook.edu, hu.wang.2@stonybrook.edu.

1 A Review of the Hyporheic Zone, Stream Restoration, and Means to Enhance Denitrification

2

3 Leanne Merrill (1)

4 David J. Tonjes (2) *

5

6 (1) Department of Ecology and Evolution

7 Stony Brook University

8 Stony Brook, NY 11794-5245

9 631-632-8600

10 leanne.merill@gmail.com

11

12 (2) Department of Technology and Society

13 Stony Brook University

14 Stony Brook, NY 11794-3760

15 631-632-8518

16 david.tonjes@stonybrook.edu

17

18 * Corresponding author

19

20 Abstract

21 The hyporheic zone is the subsurface area below and adjacent to a stream where groundwater
22 mixes with stream water, through vertical, lateral, and longitudinal flows. The hyporheic zone
23 connects the stream to uplands and other terrestrial environments. It is a zone of distinct faunal
24 communities, high biological diversity and ecological complexity, and is the site of chemical
25 processing and transformations of ground- and stream waters. The hyporheic zone is important to
26 the overall ecosystem ecology of the stream, and it can influence stream water chemistry. Flows,
27 reactions, and biota in the hyporheic zone are heterogeneous and patchy, making it difficult to
28 clearly describe the ecotone in a straightforward, general way. Nitrogen processing, especially
29 denitrification, appears to be widespread in the hyporheic zone.

30 The hyporheic zone, as with most aquatic systems, is often impacted by human activities.
31 Stream restorations rarely consider potential effects on the hyporheic zone, but careful project
32 choices can enhance the condition of the hyporheic zone, and so increase uptake of nitrogen by
33 stream-associated environments as partial mitigation of continuing and increasing releases of
34 reactive nitrogen, potentially reaping short-term benefits to estuarine environments that might
35 not be as quickly realized from source control measures.

36

37 1. The Hyporheic Zone: Definition

38 The hyporheic zone is the area below and adjacent to the streambed where surface water and
39 groundwater mix (Fig. 1). It is not at one single, easily defined place, but rather is a diverse set of
40 elements (Boulton et al. 2010) that define an ecotone (Williams et al. 2010), and its attributes
41 vary considerably over time and space (Williams 1993; Poole et al. 2006; Kaser et al. 2009;
42 Zlotnik et al. 2011), so that its defining attribute may be its dynamism (Boulton et al. 2010). It is
43 also difficult to monitor so as to produce data with wide applicability (O'Connor and Harvey
44 2008). Because the hyporheic is an often overlooked, underappreciated element of the
45 environment, we begin with a general discussion of the traits of this ecologically important area.
46 This lengthy exposition of hyporheic zone attributes and its ability to host denitrification will
47 support details of hyporheic zone impairments, and the means by which the hyporheic zone can
48 be remediated, especially to promote denitrification. Other reviews in this journal (Birgand et al.
49 2007; Garcia et al. 2010; Kadlec 2012) have addressed aspects of the growing aquatic nitrogen
50 pollution problem, and it is our intention to supplement this literature. Potentially, this body of
51 work will affect management decisions relating to restorations, although it has been noted that
52 few stream restorations are directly shaped by scientific research and reports (Bernhardt et al.
53 2007).

54 The hyporheic zone has been described differently in terms of its hydrology, geochemistry,
55 and ecology. Hydrologically, the hyporheic zone is the interstitial spaces adjacent to the stream
56 bank and below the streambed that are saturated and contain some portion of channel water
57 (White 1993), especially when modified to “<98% stream water and >10% groundwater” (Triska
58 et al. 1989b; Boulton et al. 2010). Water quality that results from mixing stream and groundwater
59 in the subsurface can be distinct from both (Fraser and Williams 1998; Hill et al. 1998; Hayashi

60 and Rosenberry 2002), and can be further modified by biologically-mediated redox reactions
61 (Jones and Holmes 1996; Storey et al. 1999). The hyporheic zone was first identified as a region
62 with unique biota (Orhigdan 1959), some associated with streams or groundwater (Boulton
63 2007), but many others that are distinctive (Boulton et al. 2010). The sum of conditions create a
64 transition area between two distinct ecological regions, and it has been suggested (Williams et al.
65 2010) that it fits the definition of an “ecotone” (Odum 1971). Water flow is the dominant driver
66 of most processes, and so here the hyporheic zone is almost always considered as the mixing
67 zone for groundwater and stream water.

68 **2. Hyporheic Zone Attributes**

69 **2.1 Hyporheic Zone Hydrology**

70 A useful simplification is to consider that essentially all baseflow of streams was once
71 groundwater (Williams 1993; Winter 2000; Hayashi and Rosenberry 2002; Sophocleous 2002),
72 although it is clearly not true in all particulars (e.g., Seitzinger et al. 2006). The subsurface is key
73 for stream flows and, generally, flow through the hyporheic zone is from groundwater to surface
74 water. At some point bankward and downward from the stream, all flow is classified as being
75 "groundwater;" but, at the stream-sediment boundary, assuming permeable sediments create
76 hydraulic conductivity, there is bidirectional flow between stream and sediments (Triska et al.
77 1993), even if only driven by diffusive flows.

78 Any small difference in pressure between subsurface and surface water causes interchange
79 between them: upwelling zones where subsurface water enters into the stream; and, downwelling
80 zones where stream water enters the hyporheic zone. These zones can range from cm^2 to km^2 in
81 area (Reidy and Clinton 2004), although most are limited in extent (Runkel et al. 2003). Under
82 steady-state conditions, discharge dominates at stream banks and the streambed closest to the

83 bank, so that downward hyporheic flow is most likely near the center of the streambed; residence
84 time in the subsurface is less near banks and greatest at the streambed center (Boano et al. 2009).
85 Most stream reaches are comprised almost entirely of discharging zones (Conant 2004), although
86 continuous areas of discrete upward and downward flows increase downstream (Gooseff et al.
87 2006).

88 Flows originating in the stream can be oriented longitudinally (along the stream path) or
89 laterally into the stream bank. Small vertical head differences between the stream and the
90 subsurface waters create longitudinal flows (Williams, 1993; Holmes et al. 1996; Olsen and
91 Townsend 2003). The standard model for steady-state flows has head-driven inflows at the top of
92 riffles and outflows (including groundwater discharges) concentrated at the foot of riffles and the
93 head of pools (Williams 1993; Hill et al. 1998; Hayashi and Rosenberry 2002; Kaser et al. 2009).
94 Transitory changes in stream conditions (including flooding of previously dry areas) from
95 phenomena including run-off from precipitation, snow-melt, larger scale flooding, and/or spates
96 from dams, can create significant head differences over larger areas (Poole et al. 2006; Boano et
97 al. 2007; Kaser et al. 2009; Maier and Howard 2011). Such “event flows” may actually define
98 most flow conditions in many streams.

99 Longitudinal flows can be also initiated by flow-driven pressure differences on bedforms,
100 with upstream faces serving as points where surface water enters the subsurface (Thibodeaux and
101 Boyle 1987); this is called “advective pumping” (Worman et al. 2002), and was first described
102 by Vaux (1968) analytically. Thus, increased flow rates in the stream can drive greater exchange
103 (Fraser and Williams 1998), without any changes in surface water-subsurface water head
104 differences. Pressure variations associated with turbulent flow can be sufficient to cause
105 hyporheic exchange even in the absence of substantial bedform relief (Packman et al. 2004). The

106 frequency of bed sediment reworking means particular bedform conditions may not be
107 maintained at any one location over any long period of time (Dole-Olivier et al. 1997; Fowler
108 and Death 2001; Fischer et al. 2005; Poole et al. 2006; Boulton et al. 2010; Robertson and Wood
109 2010; Stubbington 2012), underscoring the dynamic nature of the phenomenon.

110 Lateral flows may be driven by transitory elevated stream heights (creating "bank storage"),
111 follow paleochannels across flood plains, or be created by head differences between meanders in
112 the stream path (Triska et al. 1993, Wroblicky et al. 1998; Sophocleous 2002; Cardenas 2008,
113 2009). Hill et al. (1998) also attributed lateral flows to head differences stemming from riffle-
114 pool sequences (which create differences between stream and subsurface water elevations) and
115 considerable flow appears to occur parallel but outside of stream channels – in the “alluvial”
116 aquifer (Poole et al. 2008). Lateral flows have been less studied due to their longer residence
117 times (Runkel et al. 2003). Most studies of lateral hyporheic flows focus on meander-driven
118 flows, which appear to be greatest from hinge points, and may be persistent even in settings with
119 large groundwater discharge rates (Cardenas 2009). Channel sinuosity leads to variable and
120 irregular flows through point bars, too (Cardenas 2008). Horizontal flow rates, whether lateral or
121 longitudinal, span a wide range from 1 cm d⁻¹ to 43 m d⁻¹ (Kaplan and Newbold 2000).

122 Bank storage is a special kind of hyporheic zone feature. Bank storage is created when
123 stream water absorbs into side sediments, often because stream levels rise faster than water
124 tables following precipitation (Gulley et al. 2011). This dynamic storage returns stored water as
125 water levels fall in the stream, buffering stream flow rates. Some bank storage can be formed
126 through subsurface flows in the vadose zone associated with precipitation. Although bank
127 storage is often connected to the water table, it is more a stream than groundwater feature

128 (Brunke and Gonser 1997). More bank storage occurs when stream flows are larger and where
129 sediment hydraulic conductivity is greater (Wroblicky et al. 1998).

130 Most flow in the subsurface is downstream (Poole et al. 2006) with a hierarchical mixture of
131 long and short flow paths that have different residence times in the subsurface (Fig. 2) (Poole et
132 al. 2008). These paths result from the synchronous mixtures of processes that are primarily
133 vertical (along the flowpath of the stream) or horizontal (across meanders) and result from the
134 heterogenous distributions of sediments (Liao and Cirpka 2011). This means that “mean” or
135 “median” measures of residence may be misleading, as the range (minutes to months to years)
136 (Harvey and Wagner 2000; Reidy and Clinton 2004) is affected by whether flow is through, say,
137 a ripple or across a major meander.

138 The amount of stream water in a reach that enters the hyporheic zone has been estimated over
139 several orders of magnitude, from <<1% to as much as 460% (Jones and Holmes 1996;
140 Burkholder et al. 2008), partially because of the undefined length of a "reach", but also because
141 factors affecting hyporheic exchange are so variable. High sediment conductivity, streambed
142 roughness, and low groundwater pressures result in more surface water exchange, and fine bed
143 sediment and high groundwater pressures result in much less exchange (Duff et al. 2008).
144 Surface water tracer experiments often generate substantial “tails” (retarded tracer not advected
145 with general stream flows), which has been interpreted as evidence of much mixing between the
146 stream and subsurface (Worman et al. 2002). A model of a New England river estimated 50% of
147 run-off entered the hyporheic zone at least 2.5 times, but also found a 3:1 ratio for time in the
148 main channel to time in the hyporheic zone (Stewart et al. 2011).

149 **2.2 Hyporheic Zone Geochemistry**

150 Interactions between surface waters and the subsurface can lead to geochemically-driven
151 changes in important stream attributes (Bencala 1983). Redox chemistry, the set of reactions
152 requiring electron acceptors (these molecules become “reduced”) and electron donors (these
153 molecules become “oxidized”), is key. Carbon (C) in its various forms plays a key role in redox
154 reactions in biologically active systems. In the presence of oxygen (O_2), the compound most
155 likely to become reduced (accept electrons) is O_2 . In the absence of O_2 (lower redox states), other
156 compounds act as terminal electron donors. As redox potentials decrease, the electron acceptors
157 that become thermodynamically favored are, in order: nitrate (NO_3^-) to dinitrogen (N_2) or
158 ammonia (NH_3); manganese from valence state +4 to valence state +2; iron from valence state
159 +3 to +2; sulfate (SO_4^{2-}) to sulfide (HS^-); and carbon dioxide (CO_2) to methane (CH_4). Most
160 redox reactions are microbially-mediated (Hedin et al. 1998).

161 In shallow flow groundwater systems, the groundwater usually has short residence in the
162 subsurface and typically is well-oxygenated (Gold et al. 2001; Storey et al. 1999) because it
163 usually does not contain great enough dissolved organic carbon (DOC) concentrations to support
164 sufficient metabolism to consume much O_2 over short periods of time (Gold et al. 2001).
165 Therefore, it is often only older groundwater associated with longer, deeper flow paths that may
166 be anoxic (Malcolm et al. 2003; Robertson and Wood 2010) and can support redox reactions
167 using terminal electron acceptors other than O_2 .

168 It is generally assumed that stream waters are well-oxygenated (Robertson and Wood 2010),
169 although low dissolved oxygen (DO) surface water conditions can be created behind natural or
170 artificial dams or in backwaters and channels, where organic matter accumulates and water
171 advection is low (Baker et al. 2000). Therefore, absent any local biological consumption of O_2 ,

172 downwelling zones (stream water) are usually better oxygenated than upwelling zones
173 (groundwater).

174 Hyporheic flow paths are thought to encounter enough organic C to support sufficient
175 respiration to deplete O₂ in the shallow subsurface (Jones and Holmes 1996); generally,
176 hyporheic zone O₂ concentrations are inversely related to residence time (Findlay 1995). This,
177 combined with increased contributions from groundwater, means upwelling water is often much
178 lower in DO than downwelling water.

179 The location of the hyporheic zone at the interface between the upland and the stream
180 suggests it will affect stream chemistry, especially nutrient dynamics. The hyporheic zone is a
181 transition from open water to water-sediment conditions; in it, electron donors and acceptors
182 change over a patchy mosaic; and, parcels of water appear to cycle back and forth in and out of
183 the zone. These factors produce effects on overall stream chemistry (Hedin et al. 1998; Dahm et
184 al. 1998; Baker et al. 2000). The assumed presence of a redox gradient associated with DO
185 depletion allows the hyporheic zone to be considered a geochemical “hot spot,” where changes
186 in redox conditions in the presence of diverse chemical substrates (associated with sediments or
187 in solution) fosters chemical transformations (Hedin et al. 1998), particularly denitrification
188 (Baker et al. 2000). One by-product of respiration is CO₂, and so pH values in the hyporheic
189 zone are often different from both groundwater and the stream (other reactions, many enhanced
190 by sediment-water connectivity, can also result in pH changes) (Runkel et al. 2003). The
191 distribution of reaction sites is spotty over both time and space (Hedin et al. 1998); shifts in
192 subsurface flows due to changes in stream or groundwater flows can cause relocation of reaction
193 sites. These shifts may be predictable, especially if seasonal patterns (flood, drought,
194 precipitation) are the drivers of changes in flow (Dahm et al. 1998).

195 **2.3 Hyporheic Zone Biology**

196 It is difficult to disentangle the chemistry of the hyporheic zone from its biology; in addition,
197 stream remediation project managers often focus on biological attributes, including invertebrate
198 populations which depend on hyporheic conditions (Bernhardt et al. 2007; Lake et al. 2007).
199 Thus, we will briefly discuss some of the more notable biological attributes of the hyporheic
200 zone.

201 The hyporheic zone serves two important, overt ecological purposes for stream fauna: refuge
202 for invertebrates in times of disturbance; and prime egg incubation sites. Both stem from the
203 perceived greater environmental stability of the hyporheic zone compared to open waters
204 (Orghidan 1959), a function of water velocity and temperature. Water velocity decreases upon
205 entering the hyporheic zone, by factors as much as 10^{-3} , compared to surface water (Brunke and
206 Gonser 1997), creating shelter for stream invertebrates when water column currents increase
207 (Boulton et al. 1998). Krause et al. (2011) describe temperature as the “master variable” that
208 controls all other hyporheic zone processes. Water temperature fluctuation is generally less than
209 in surface waters, and its variability decreases with increasing depth and distance from stream
210 water infiltration sites (Brunke and Gonser 1997). Thus, the asynchronous pulses of water from
211 the hyporheic moderate stream water temperatures: on short time scales night time lows are
212 warmed, and daytime highs are reduced; on longer flow paths, hyporheic flows equilibrate with
213 groundwater temperatures, further mitigating daily or seasonal temperature fluctuations (Poole et
214 al. 2008). Careful measurements of temperature changes in streams have even been used to
215 quantify hyporheic exchange rates (Westhoff et al. 2011). Consistent temperatures are
216 advantageous for salmonid spawning, and subsurface temperatures are more constant in
217 upwelling zones (van Grinsven et al. 2012).

218 Organism sheltering generally occurs in downwelling areas, allowing benthic populations to
219 rapidly recover from events (Dole-Olivier et al. 1997), although major floods require longer
220 recovery periods (Maier and Howard 2011). Stubbington (2012) notes refuge utility is a function
221 of interactions between sediment types, taxon, the kind of disturbance, and whether the flight
222 from disturbance is active or passive, so that *which* organisms seek refuge *where* and *when*,
223 while determinable, is not consistent. In addition, at least some of these disturbance events affect
224 the hyporheic environment, altering the refuge and its functionalities (Boulton 2007; Robertson
225 and Wood 2010).

226 Changes in sediments, water flows, and associated conditions make the hyporheic zone a
227 patchwork of small, differentiated habitats. Broad generalizations of benthic sediment patterns,
228 for instance, might include downwelling gravel patches at the head of a riffle, upwelling gravel
229 areas dominated by hyporheic flows at the riffle foot, with upwelling groundwater immediately
230 adjacent (although perhaps associated with finer sediments of the pool), and other areas of
231 sediment and flows associated with meander erosion (Boulton 2007).

232 Hyporheic zone organisms include microbes (Findlay and Sobczak 2000), meiofauna
233 (Hakenkamp and Palmer 2000), and macrofauna (Boulton 2000). Most faunal characterizations
234 concentrate on insect instars (transient members of the ecosystem) (Boulton et al. 2010). For
235 many biologists, the hyporheic zone is defined by the class of micro- and macro-invertebrates
236 called “hyporheos”: crustaceans, segmented worms, flatworms, rotifers, water mites, and
237 juvenile stages of aquatic insects (Williams and Hynes 1974). The eggs and alevin of salmonid
238 fish are also members, and often are the focus of hyporheic zone management programs; the
239 areas they live, excavated and then backfilled by adults, are “redds” (Environment Agency
240 2009). Differences in overall hyporheos distributions are a function of DO (Hakenkamp and

241 Palmer 2000), but also are affected by grain size variations and vertical flow patterns (Olsen and
242 Townsend 2003).

243 Bacteria are important elements of the hyporheic zone ecology, and can create biofilms.
244 Biofilms foster the creation of micro-environments – small anaerobic zones in otherwise
245 oxygenated settings, for instance – that appear to be required for reactions such as denitrification
246 (Storey et al. 1999). Biofilms create specialized environments due to expressed enzymes and the
247 restricted size of pore space environments, but the supply of nutrients and dispersion of wastes is
248 controlled by the rate of advected waters passing them (Findlay and Sobczak 2000).

249 **3.0 Hyporheic Zone Nitrogen Transformations: Research Findings**

250 Krause et al. (2011) summarized current research on N in streams, finding it can be
251 transformed, mobilized, or returned to the atmosphere at different rates over relatively small
252 scales, and that these processes differ for particular streams. The concept of nutrient “spiraling”
253 (Webster and Patten 1979) is helpful: it illustrates, in this case, N moving from organisms to a
254 variety of reservoirs, and being carried (predominantly) downstream via diverse pathways,
255 including subsurface routes, with repetitive cycling of flows, forms, mineralization, and
256 organism uptake. The retention of nutrients for at least some time is necessary in order to
257 maintain ecosystem processes in streams, and so the spiraling concept illuminates stream
258 ecological dynamics (Triska et al. 1989a, Ensign and Doyle 2006). In headwater streams,
259 groundwater is the primary source of N, although much N enters the system as organic N from
260 leaf litter and sediment inputs (Duff and Triska 2000). Transformation from organic to inorganic
261 forms is expected, along with considerable lags due to incorporation into organisms or sorption
262 onto sediments, so that the transport of N is considerably delayed along each stream reach
263 compared to a non-reactive tracer (like chloride). Nitrogen spiraling (Mulholland and DeAngelis

264 2000) describes the repeated transformation of N from inorganic to organic forms, and its track
265 from the main body of the stream into sediments. The spiral has “uptake length” (the distance an
266 atom travels before being biologically retained) and “turnover length” (the distance traveled by
267 the atom as organic matter) (Duff and Triska 2000). Hyporheic exchange should reduce uptake
268 length and increase turnover length by increasing interaction between sediments and the water
269 column (Mulholland and DeAngelis 2000). Denitrification is, in a sense, a form of completion of
270 the spiraled pathway as the N-atoms are thus lost to the system.

271

272 **3.1 Denitrification**

273 Denitrification measurements are affected by the development of techniques that accurately
274 capture data but are not universally used. Direct measurements of N₂ creation can be made in
275 aquatic systems using gas chromatography, and changes in N₂:argon (Ar) ratios can be measured
276 using membrane inlet mass spectrometry (Davidson and Seitzinger 2006). However, many often-
277 cited papers used the acetylene inhibition technique, which often understates denitrification rates.
278 Acetylene inhibition has great advantages in that it is simple to conduct and can support many
279 measurements over small spaces, which is useful to measure a patchy, inconsistent phenomenon.
280 The method can be confounded by slow diffusion into fine sediments, the presence of sulfide,
281 and insensitivity to low concentrations of NO₃⁻. Wide testing of cores and other disturbed
282 samples instead of making in situ measurements also affects the usability of many acetylene
283 inhibition results (Groffman et al. 2006; also see Powell and Bouchard 2010). Use of N¹⁵ tracer
284 techniques to track denitrification result in higher estimates of denitrification than would be
285 “expected” for acetylene inhibition approaches, given understandings of how site conditions
286 affect denitrification (Mulholland et al. 2004). Another approach is to track potential

287 denitrification by inducing conditions that lead to denitrification and measuring losses of N from
288 the system, which lead to overestimates of actual denitrification.

289 The necessary elements for hyporheic zone denitrification are subsurface organic C, low O₂
290 concentrations, and bacterial biofilms to metabolize the organic matter. Surface-subsurface
291 exchange flows create organic C pools from DOM and particulate organic matter (POM).
292 Entrained dissolved inorganic nitrogen (DIN) is then transformed by hyporheic bacteria into N₂
293 (Boyer et al. 2006; Harvey et al. 2011; Zarnetsky et al. 2011). The hyporheic zone is not uniform
294 in sediment size, O₂ availability, temperature, and other parameters, creating discrete zones of
295 denitrification instead of the entire zone being a NO₃⁻ sink (Craig et al. 2010). The controls on
296 denitrification have been found to be different under differing conditions. Sometimes a particular
297 factor (nitrate concentration or carbon availability or grain size) is the variable that best describes
298 differences in rates of denitrification, but often there is a complicated interplay among the factors
299 so that no one parameter can predict changes in nitrogen concentrations.

300 So, for instance, hyporheic zone hydrology and stream N export are linked, but not in a
301 consistent manner (Zarnetske et al. 2011). Generally, increased water residence time in stream
302 environments with suitable denitrification conditions results in increased denitrification rates
303 (Seitzinger et al. 2006; Flewelling et al. 2012; Mayer et al. 2010), a relationship characterized as
304 the Damkohler number (the residence time:reaction time ratio) (Gu et al. 2008a). Thus, at five
305 low gradient, high N concentration streams, residence time correlated with denitrification
306 (Puckett et al. 2008), and comparisons across differing stream conditions found hydrologic
307 residence time increased denitrification rates (Kaushal et al. 2008). Flowpaths where at least 2
308 days were needed to traverse a 30 cm thick zone where denitrifying activity was greatest had
309 complete N-removal; shorter residence times resulted in less N-removal (Flewelling et al. 2012).

310 Generally, it is expected that long hyporheic zone residence times will increase denitrification
311 (Hill et al. 1998), and in many sedimentary environments residence time correlates to flowpath
312 lengths, and the effect of increasing flowpaths is often to reduce N concentrations. Still,
313 denitrification of injected N into a gravel bar was largely completed in 1 hr travel time; very little
314 measurable denitrification occurred farther along the flow paths (Pinay et al. 2009). Most river
315 NO_3^- (60-80%) was removed in the first 50 m of hyporheic flowpaths for a river in a boreal
316 forest floodplain (Cliverd 2008). In the Platte River, depletion of DO occurred not in shallow
317 sediments but 30 cm below the subsurface-stream interface, which was assumed to be the result
318 of denitrification (in part) (Duff and Triska 2000).

319 A process-free model, the transient storage model, has been used for more than 25 years to
320 estimate water retained rather than advected in stream reaches. Strictly speaking, it simulates in-
321 stream storage (such as pools and back flows); but its results have been interpreted as including
322 some flow through the hyporheic zone (typically, shorter duration shallow-flow pathways)
323 (Bencala and Walters 1983; Boano et al. 2007). Use of a fluorescent tracer (resazurin) that is
324 transformed by microbial respiration into another fluorescent tracer (resorufin) can differentiate
325 between biologically active and inactive storage areas, and help interpret the degree of hyporheic
326 exchange associated with transient storage (Haggerty et al. 2008; Gonzalez-Pinzon et al. 2012).
327 For some, transient storage poorly explains N processing (Hall et al. 2002; Lautz and Siegel
328 2007) but it has produced good correlations (although these N-reductions may have resulted
329 from benthic not hyporheic functions) (Ensign and Doyle 2005). Denitrification rates were found
330 to be greatest at “separation zones”: still pools found in the lee of point bars, where water storage
331 occurs, and greater residence time in contact with fine, organic-rich sediments apparently leads
332 to more sediment denitrification (Opdyke et al. 2006). Alternately, increased flow causes less

333 contact time and creates smaller sediment surface:water volume ratios, and so must result in less
334 denitrification (Ranalli and Macalady 2010). Slowed stream flow was responsible for greater N-
335 uptake in a restored stream compared to pre-alteration conditions, with the greatest rates
336 observed in a side pool (Bukaveckas 2007). Conversely, observations at human-impacted
337 streams in the southwest U.S. found that denitrification at these sites was greater than that
338 measured at reference sites, although connectivity and interchange with the hyporheic zone was
339 greater at reference streams (Crenshaw et al. 2010). Thus, Botter et al. (2010) argue that factors
340 other than sediment contact times are also important in determining N-removal efficiencies.

341 One of these is sediment quality. Decreasing sediment grain size theoretically adds to 1)
342 surface area availability for bacteria; 2) overall residence time; 3) in particular, slower transport
343 rates of dissolved N and C through potential reaction sites; and 4) retention of C to fuel reactions
344 (Baker et al. 2000). Fine-grained sediments were associated with greater denitrification in one
345 study (Opdyke et al. 2006), and residence time in the denitrification zone controlled N-reduction
346 extent, with residence time being inversely proportional to sediment hydraulic conductivity
347 (Flewelling et al. 2012). Sediment surface area:stream volume ratios predicted denitrification in
348 small streams (Peterson et al. 2001) and were used to explain N-uptake dynamics (Ranalli and
349 Macalady 2010), under the assumption that benthic processes control denitrification reactions.
350 Stream flow rate variations across seasons (greater in spring, less in winter) controlled
351 denitrification because more water and faster flows decreased contact time with sediments
352 (Alexander et al. 2009).

353 Alternately, availability of NO_3^- was said to be the major control on denitrification (Duff and
354 Triska 1990); denitrification in high flow downstream areas of the Elbe River were greater where
355 NO_3^- concentrations in the river were higher (Fischer et al. 2005). More commonly,

356 denitrification rates are related but not proportional to available NO_3^- concentrations. The Lotic
357 Intersite Nitrogen experiment (LINX II) at 72 streams in 8 US regions used N^{15} tracers and found
358 that denitrification increased with NO_3^- concentrations, but the efficiency of the reactions
359 decreased, meaning the relative proportion of N removed was less in higher NO_3^- streams.
360 Smaller streams lost efficiency more rapidly than larger streams, perhaps because they remove a
361 "maximal amount" of N, so that downstream larger order streams have unfilled assimilative
362 capabilities (Mulholland et al. 2008). The absolute amount of NO_3^- denitrified comparing
363 seasonal flows in two streams was greater under higher NO_3^- concentration conditions – but not
364 proportionally to increases in inputs (Alexander et al. 2009). Nitrate concentrations in streams,
365 when comparing agricultural, urban, and forested land uses, were greatest in the agricultural
366 areas, and denitrification rates were also greatest in agricultural area stream sediments. But,
367 increases in denitrification did not compensate for increases in N, so stream reaches leaving
368 agricultural and urban areas had higher NO_3^- concentrations (Inwood et al. 2005).

369 Carbon is essential to denitrification, but it may not be the rate-determining factor, either
370 considered theoretically (Bardini et al. 2012) or through extensive measurements (Bohlke et al.
371 2009). Generally, the amount of C in sediments has been found to regulate denitrification, as C
372 is needed to fuel reactions that consume DO. It is also needed for the metabolic reactions that
373 cause denitrification, so that C concentrations were the best correlation for denitrification in one
374 urban setting (Mayer et al. 2010). Augmenting subsurface C where both groundwater and stream
375 water had low NO_3^- concentrations increased denitrification rates (Triska et al. 2007). Sediment
376 instability in the Elbe River meant C concentrations were well distributed with depth, and so
377 high denitrification rates were measured throughout the hyporheic zone. Denitrification rates
378 were lower outside of the main channel where sediment C concentrations were lower (Fischer et

379 al. 2005). When stream NO_3^- concentrations exceeded half of the saturation concentration,
380 sediment C content was a good predictor of denitrification rates. At less than half-saturation
381 concentrations, stream NO_3^- concentrations best predicted denitrification rates (Arrango et al.
382 2007).

383 At least one study concluded denitrification was controlled by temperature (Alexander et al.
384 2007) but no temperature effect was found by Triska et al. (2007). Because the hyporheic zone
385 buffers temperatures, most likely temperature is usually not a dominant factor affecting
386 denitrification processes. Nonetheless, seasonal effects (seasons correlate to temperature
387 changes) were found where lateral flow through a gravel bar resulted in some denitrification,
388 especially in summer (Deforet et al. 2009). However, flow rate variations and/or groundwater
389 inputs appeared to be the underlying cause of a seasonal component in denitrification rate
390 differences for two streams draining agricultural areas (Bohlke et al. 2009). A seasonal effect
391 was associated with snowmelt flooding, which had been expected to increase N exports from a
392 high gradient mountain stream, but because the higher flow rates increased hyporheic exchange,
393 NO_3^- removal rates were much higher during floods. Although the mass of N exported was
394 greater, it was not proportional to the increase in flow (Hall et al. 2009). Seasonal differences in
395 flows and nitrate inputs, based on a regression on 300 published measurements, were found to
396 explain differences in N removal (low flow and low N-inputs resulted in higher N-removal rates)
397 (Alexander et al. 2009). Daily fluctuations in N-removal in open waters were found, but this was
398 related to fluctuations in both NO_3^- and C concentrations due to photosynthetic organism
399 elemental cycling (Heffernan and Cohen 2010) rather than diurnal temperature patterns; open
400 water conditions often affect subsurface conditions with a time delay.

401 Some studies have tried to capture the apparent interplay among multiple factors. So, a
402 forested area had increased denitrification; this was linked due to increased debris inputs, which
403 slowed stream flows and increased organic matter content on the stream bottom (although it was
404 not determined if the N was lost at the stream-surface sediment interface or in the hyporheic
405 zone) (Weigelhofer et al. 2012). A study of 18 streams found links among seasonality, NO_3^-
406 concentrations, sediment C content, and denitrification rates. Sediment C was the best predictor
407 of denitrification rates, but stream NO_3^- concentrations were highest in winter, when the greatest
408 denitrification rates were measured. Agricultural land uses resulted in higher stream NO_3^-
409 concentrations compared to urban areas (Arrango and Tank 2008). Biological activity was
410 increased with warmer water in summer, but denitrification was greater in winter due to
411 increased available N from greater groundwater discharge rates. The flux of denitrified N per
412 unit streambed area was inversely related to hyporheic flow rates, suggesting that residence time
413 was important, and, denitrification was higher for areas with finer sediments (which also
414 contained more C) (Bohlke et al. 2009).

415 Denitrification mechanisms create some of these complications. Biofilms generate zones
416 where local conditions can vary tremendously from bulk water states. This is a potential
417 mechanism for patchy biochemistry, such as denitrification; this is true even though there are
418 general oxidizing states in the overall flow line (Mulholland et al. 2004). Variations at these
419 small scales fit with accounts of sudden changes in NO_3^- concentrations over distances <1 m
420 (Storey et al. 1999); if small, idiosyncratic single sites are determinants of reactions, notions like
421 the Damkohler number that apply to bulk conditions (Gu et al. 2008a) would not be pertinent,
422 although remaining descriptive of changes in water quality at the reach scale.

423 Downwelling zones are hotspots for denitrification (Holmes et al. 1996). Highest
424 denitrification rates were found in these areas, although rates can be inhibited by higher DO
425 concentrations associated with downwelling, and short residence times make it difficult for
426 microbial respiration to deplete the available DO. Denitrification was minimal in upwelling
427 zones due to a lack of NO_3^- (Storey et al. 2004). In an N-rich agricultural stream, downwelling
428 areas resulted in losses of DO and NO_3^- , while more anoxic upwelling areas transported NH_4^+
429 from groundwater to the stream (albeit in reduced concentrations), so that the hyporheic zone
430 was a sink for NO_3^- and a source of NH_4^+ for the stream (Hill et al. 1998). Similarly, in a gravel
431 bed of an NO_3^- -rich stream denitrification rapidly commenced as DO was reduced below 1 mg L^{-1}
432 ¹, and NH_4^+ concentrations increased (Peyrard et al. 2011).

433 Floods enhance denitrification, as they increase flow through the hyporheic zone and expand
434 its extent (Cliverd 2007); however, they also have the potential to reduce reactions by changing
435 biochemical conditions – “washing out” the needed redox state (Gu et al. 2008a), which also
436 may occur with high flow-high groundwater conditions (Ranalli and Macalady 2010). Low flow
437 conditions correlated well with higher denitrification rates in Baltimore. The water table was
438 closely linked to stream flow rates, so that head in the aquifer decreased with decreased flow,
439 causing less hyporheic discharge, and greater hyporheic zone residence time – thus, greater
440 denitrification (Mayer et al. 2010).

441 In a desert stream, nitrification and denitrification occurred in the subsurface; denitrification
442 rates were higher in the banks than the sub-benthic hyporheic sediments (Holmes et al. 1996). A
443 modeling solution of bedform-induced flows suggested that in the flow cells created by
444 hyporheic exchange, the shallower portion of each cell would be a nitrifying area and the deeper
445 portion would denitrify. Consumption of DO (due to available C) would determine the relative

446 proportions of each (Bardini et al. 2012). And, at one stream where denitrification occurred in
447 the hyporheic zone, the hyporheic zone (as determined by comparisons to groundwater
448 chemistry) was very shallow and was not the locus for most denitrification of the incident
449 groundwater. More denitrification occurred below the hyporheic zone, as O₂-rich groundwater
450 became depleted of DO, after coming into contact with buried organic C. Therefore, only
451 tracking hyporheic zone processes may lead to underestimates of total subsurface reactivity
452 (Stelzer et al. 2011).

453 Generally, despite recent advances in theory (Botter et al. 2010) and field techniques
454 (Haggerty et al. 2009), because hyporheic exchange rates are often not well-defined over larger
455 scales, quantifying the impact of the hyporheic zone on N-attenuation is difficult beyond single
456 site evaluations (Krause et al. 2011). Reports of large reductions include 12 mg N L⁻¹ to 0.1 mg
457 L⁻¹ over 30 cm of flow path (Gu et al. 2008b), 21% removal of total inorganic N over the entire
458 river network (nearly 75% removal by all river processes) (Stewart et al. 2011), 30% of NO₃⁻
459 additions removed in a 300 m reach (Triska et al. 1989b), differences of >80% between
460 groundwater N concentrations (approximately 15 mg N L⁻¹) and stream water concentrations
461 (mean of 2 mg N L⁻¹) (Gu et al. 2007), and overall losses of N in the subsurface in the vicinity of
462 90% (by various mechanisms that varied with depth) (Lansdowne et al. 2012). High
463 denitrification rates (2.0-16.3 mg m⁻² h⁻¹) were reported for agricultural streams in three varying
464 settings (but note NO₃⁻ concentrations increased over the reaches due to larger inputs from
465 groundwater) (Duff et al. 2008).

466 **3.2 Nitrification**

467 Nitrification occurs when bacteria oxidize NH₃ to NO₃⁻ (Hedin et al. 1998); conditions that
468 allow for nitrification include the presence of: 1) O₂; 2) NH₄⁺; and 3) a carbon source (to allow

469 for bacterial growth and reproduction) (Triska et al. 1993). However, nitrifying bacteria are
470 relatively inefficient, and so on theoretical grounds alone will only constitute a small portion of
471 microbial production compared to other heterotrophs (Storey et al. 1999). There have been
472 reports that the hyporheic zone is an area of net nitrification, transforming organic N or $\text{NH}_3\text{-N}$
473 to NO_3^- (Boulton et al. 1998).

474 Generally, subsurface waters have higher NH_4^+ concentrations than surface waters do. This
475 suggests, given overall subsurface to surface transport, that the hyporheic zone generally nitrifies
476 some NH_4^+ (Baker et al. 2000). Triska et al. (1993, 2007) describe the organic-rich subsurface
477 therefore as a patchwork of zones where nitrification and denitrification occurred discretely,
478 depending on the species of N and the redox status of the sediments.

479 Nitrification requires relatively large amounts of O_2 to occur, and so nitrifiers may be an
480 important link in the reduction of DO that may allow for denitrification. Coupled nitrification-
481 denitrification will only occur with a substantial change in redox potential (from +200 mV to -
482 200 mV), which implies a change in time and distance; however, these kinds of coupled
483 reactions appear to occur across short distances in sewage plant trickling filters, which use
484 biofilms to treat sewage, and so it has been hypothesized similarly linked reaction sites could
485 exist in the interstices of the hyporheic zone (Storey et al. 1999). This apparently was the case
486 for one stream where pressure dynamics changed the extent of the hyporheic zone so that it often
487 extended beyond its “permanent” depth. When the zone was extended, NO_3^- concentrations
488 sometimes increased in the stream, and sometimes decreased – suggesting that the particular
489 relations between nitrification and denitrification were contingent on small local variability
490 (Krause et al. 2009). A modeling study suggested that the upper portion of flow in the hyporheic

491 zone would support nitrification, while deeper flows would be more likely to result in
492 denitrification (assuming needed distributions of N-species, C, and DO) (Bardini et al. 2012).

493 In an anthropogenically-impacted, N-limited, losing, desert stream, NO_3^- concentrations
494 increased following hyporheic zone residence, with the largest increases in NO_3^- concentrations
495 being found in the summer at the head of the flowpath (Holmes et al. 1994). The hyporheic zone
496 was also found to be a net source of NO_3^- in the alluvial system of an arctic tundra stream
497 (Greenwald et al. 2008). In a stream with low DIN concentrations, organic N (as DOM and
498 POM) was first ammonified and then nitrified; there was no measurement of denitrification,
499 although DO concentrations decreased along the hyporheic flowpaths. All reactions appeared to
500 occur within the first 10 cm of flow (Harvey et al. 2011). Nitrification was found to be affected
501 by temperature, much more so than denitrification, so that with low temperatures, net
502 denitrification was found, and high temperatures led to a net increase in NO_3^- (Triska et al.
503 2007). Concurrent nitrification and denitrification were measured in the Elbe River; nitrification
504 occurred in sediments closest to the bank, and declined with sediment depth due to decreasing
505 DO concentrations (Fischer et al. 2005).

506 Jones and Holmes (1996) suspected that hyporheic zones in N-poor streams are generally a
507 NO_3^- source, and hyporheic zones in N-rich streams act as an N sink. Duff and Triska (2000)
508 agreed nitrification is more important in low-N streams, but thought nitrification was a pathway
509 to transform organic N to forms that could subsequently be denitrified, as part of subsurface
510 metabolic processes. Arrango and Tank (2008) measured substantial nitrification in agricultural
511 streams with high NO_3^- concentrations, and the occurrence of peak nitrification did not accord
512 with peak denitrification, suggesting no explicit linkages.

513 **4. The Riparian Zone and the Hyporheic Zone**

514 Although the riparian zone is imprecisely defined, for many it excludes classic wetlands with
515 open water (swamps and marshes) (*sensu* Mitsch et al. 2012). Rather, it is characterized by
516 specific vegetation communities and is physically located between uplands and the stream.
517 Underground water flow in the riparian zone tends to be dominated by groundwater (surface
518 water inputs from bank storage or infiltrating flood water can be important at times), and riparian
519 zone water tables tend to be very shallow (within 1-2 m of the ground surface) (Dahm et al.
520 1998; Hill 2000; Kaplan et al. 2010). The hyporheic zone is not defined by any surface
521 vegetation features, and so there can be some overlap between these two features. Typically,
522 some bank storage and lateral flows between meanders have been classified as both hyporheic
523 and riparian zone waters (Duval and Hill 2007; Pinay et al. 2009); some prefer not to distinguish
524 between the two processes (Vidon et al. 2010).

525 Riparian zones are often found at the base of hills, where the surface topography intercepts
526 the water table, or, at least, comes close to doing so. There is often an accumulation of fine, C-
527 enriched sediments at the base of the slopes (Hill et al. 2004). The flatter portion of the riparian
528 zone should accumulate C-rich sediments from flood overflows, which should increase closer to
529 the riverbank (Kellogg et al. 2005). Riparian zones have been identified as hot spots for
530 denitrification (Holmes 2000), although these denitrification zones are often only meters wide
531 (McClain et al. 2003), often at the uphill edge of the zone (Schipper et al. 1993), and at or near
532 the groundwater discharge point into the stream, as well (McClain et al. 2003; Flewelling et al.
533 2012). Hydric (low redox state) soils, created by high organic content, low O₂ transfer rates from
534 the ground surface, and saturated conditions, support denitrification, and are a signature element
535 of riparian zones (Gold et al. 2001). Nitrogen removal from groundwater can be as much as
536 100% for riparian zones (Dosskey 2002), but conditions that lead to substantial denitrification

537 are patchy and are not found in all shallow groundwater transition zones near streams (Stutter et
538 al. 2012).

539 **5. Hyporheic Zone Management Issues: Research Findings**

540 **5.1 Degradation of the Hyporheic Zone**

541 Anthropogenic degradation of the hyporheic zone results because it lies between surface
542 water and groundwater, two resources exploited by humans and both intentionally and
543 inadvertently affected by their activities. Impacts to the hyporheic zone often affect water
544 exchange and may poison bacteria and invertebrates (Hancock 2002). Direct changes to streams
545 and groundwater flows, such as through water withdrawals and discharges, or to physical
546 morphology such as with dams, channeling, and shoreline and bottom hardening cause impacts
547 to chemical and biological functions, too (Pringle and Triska 2000). Indirect effects come with
548 mining activities, urban and industrial discharges, changes in land use, and agriculture and
549 forestry practices, including removal of sediment and/or water, impairment of surface and/or
550 groundwater quality, disruption of hydrological connectivity between the hyporheic zone and the
551 surface and groundwater systems, and changes in hyporheic biota (Boulton 2007).

552 Changing stream flow or groundwater heads will affect the hyporheic zone. Flow patterns are
553 generally defined by head differences (Sophocleous 2002), which are affected by changes in
554 stream conditions and groundwater levels (Packman and Bencala 2000; Gu 2008a). Advective
555 pumping can be increased by higher flow rates (Fraser and Williams 1998). Flooding across
556 previously dry areas (Maier and Howard 2011) or drying of previously flowing areas (Gu et al.
557 2008a, b) can reverse or substantially change hyporheic flow patterns. Lateral flows are also
558 affected by changes in the stream flow or groundwater head, as these will change bank storage

559 and may affect the head differences between meanders (Triska et al. 1993; Wroblicky et al.
560 1998; Sophocleous 2002; Cardenas 2009).

561 Constructing dams can induce channel migration and bank erosion, moving the stream away
562 from its original course, and, as a result, changing relationships with the hyporheic zone.
563 Downstream erosion, a common feature for dams, could reduce the size of the hyporheic zone
564 (Hancock 2002). Dams change sedimentation rates and sediment flushing, which can affect the
565 interstitial spaces of the hyporheic zone. If particulates are trapped by the dam, there may be
566 fewer inputs of organic matter downstream, which could affect microbial respiration rates and
567 geochemical reactions (Environment Agency 2009). Dams can either increase or decrease
568 temperatures downstream, with the controlling factors being the size of the impoundment and its
569 management (Webb et al. 2008); temperature is a key element in hyporheic ecological processes
570 (Krause et al. 2011). Releases of water from dams also change rates by which surface-subsurface
571 exchange occurs; rapid changes resulting from dam spates may not allow organisms to
572 accommodate to the new conditions. In addition, subsurface residence time may be substantially
573 reduced under higher flows (Maier and Howard 2011). Dams also affect general downstream
574 groundwater head levels, and the biology and geochemistry of water from reservoirs can be very
575 different from that in native streams (Pringle and Triska 2000).

576 Simplification of bedforms and channels due to canalization or other channeling and
577 constraining of stream flows reduces exchange potentials between the stream and the subsurface.
578 A smooth stream bottom minimizes advective pumping (Packman et al. 2004; Poole et al. 2006).
579 A stream with fewer meanders had less lateral flow (Cardenas 2009) and overall less
580 connectivity with the subsurface (Crenshaw et al. 2010); all of these lead to a reduced portion of
581 stream water entering the hyporheic zone (Dahm et al. 1998). Fewer stream obstacles mean

582 decreased transient storage (Ensign and Doyle 2005). Straightening channels decreases the
583 overall amount of sediment area per linear distance traversed by the stream, and so decreases
584 water exchange and associated subsurface reactions (Opdyke et al. 2006). In addition,
585 canalization of waterways changes subsurface entry points into the stream, so groundwater may
586 not flow through the riparian zone (Gold et al. 2001). Urban environments are characterized by
587 altered stream channels; in one, Groffman et al. (2005) found that although substantial
588 denitrification appeared to occur, a lack of debris accumulations limited the number of locations
589 where proper reaction conditions could occur. Streams where channels have been modified often
590 have greater erosion rates; locations with higher erosion rates or where flows were constrained
591 and/or straightened, were characterized as being less likely to retain nutrients (Dahm et al. 1998).

592 Mining in a stream basin can add excess silt, introduce heavy metals, and change channel
593 morphological features. Runoff can introduce additional silt to the hyporheic zone leading to
594 colmation (the clogging of interstitial spaces), which limits surface water exchange, and so
595 decreases hyporheic zone O₂ and nutrients. Mining that occurs directly in a stream increases
596 colmation by causing sediment resuspension (Hancock 2002). Overall, the occurrence and
597 amount of colmation is affected by stream bed transport properties, as small differences in
598 velocity affect settling and resuspension (Rehg et al. 2005). Mining activities that change stream
599 pH (by exposing sulfidic minerals) increase dissolved metals concentrations, and could prove to
600 be toxic to the hyporheos (Hancock 2002). The hyporheic zone was shown to immobilize
601 manganese from copper mining in Arizona (Harvey and Fuller 1998) and, because changes in
602 redox zonation occur generally in hyporheic zones and residence time in reactive sediments
603 promotes sorption, generally the hyporheic zone does a fair job in removing many metals of
604 concern from mining waste-impacted groundwater and surface water (Gandy et al. 2007).

605 Changes in channel geomorphology associated with in-stream mining, such as widening or
606 deepening of the channel with the removal of sediments, can cause loss of riffle-pool sequences
607 and river bends, and lower floodplain water levels, thus also changing hyporheic flows (Hancock
608 2002).

609 Negative impacts to the hyporheic zone from urban and industrial activities come from
610 effluents, stormwater, and other discharges, as well as from groundwater pollution, and general
611 colmation effects. Nutrients from effluents and stormwaters increase N concentrations;
612 discharged metals and organics may affect the hyporheos; and colmation results from excess
613 sediment inputs (Hancock 2002). High levels of sewage-polluted groundwater prompted a faunal
614 composition change in one hyporheic zone (Mallard et al. 1994), a finding which does not
615 support a more general hypothesis that the hyporheic zone can serve as a refuge from pollution
616 for stream invertebrates (Hancock 2002). Inputs of sewage-derived DOM into groundwater
617 systems caused a change in invertebrate community structure to more pollutant-tolerant
618 organisms (Hartland et al. 2011). It is thought that urban environments support a less diverse
619 hyporheic biology that has less production (Environment Agency 2009). Overall, however,
620 determining impacts to biota from pollution is hampered by a lack of detailed information for
621 many subsurface taxa (Hakencamp and Palmer 2000); nonetheless, it has been proposed that
622 larger hyporheic zone organisms would be suitable for use as biomarkers, as their distributions
623 are affected by pollutants in streams (Boulton 2000).

624 Water quality impairments in many streams correlate to the amount of agriculture in the
625 surrounding basin. Agriculture (including range activities which often affect fluvial landscapes)
626 and forestry introduce excess nutrients and silt to stream ecosystems, change vegetation
627 distributions and the physical landscape (including stream morphology and positioning),

628 discharge pollutants of various kinds, and also alter flows in the hyporheic zone through
629 groundwater and surface water extraction (Pringle and Triska 2000). Unregulated forestry has
630 been found to reduce inputs of large wood, alter riparian zone vegetation (leading to hyporheic
631 zone effects), and increase sedimentation (Environment Agency 2009). Any residual poor
632 practices will also have some impacts similar to these. Nutrients may be introduced to aquatic
633 systems through fertilizers, waste from livestock, and ash from forestry waste management.
634 Augmented nutrient levels in streams lead to reduced DO and can change hyporheic conditions
635 from oxidizing to reducing (Hancock 2002). In many agricultural areas adjacent to streams, the
636 streams are physically modified (channelized and tiled) to drain high water tables or encourage
637 run-off to prevent saturated soils; this was found to diminish riparian and hyporheic cycling of N
638 (Triska et al. 2007), and also affected the general ecology of the impacted streams (Freeman et
639 al. 2007). Anoxic conditions associated with stream degradation may increase denitrification, a
640 potential environmental benefit, but only if net N removal equals or exceeds N inputs (Boulton et
641 al. 1997).

642 Agriculture and forestry can increase colmation. Generally, the loss of riparian vegetation
643 (from field expansion or livestock browsing or trampling) can lead to bank collapse, burying the
644 hyporheic zone and limiting parafluvial exchange. Native riparian vegetation was found to
645 support a more diverse and abundant hyporheos than pasture land (Boulton et al. 1997).
646 Deforested riparian areas have narrower streams with less bed roughness and higher stream
647 velocities. This was thought to lead to lower denitrification rates because of less connectivity to
648 subsurface processes (Sweeney et al. 2004). Livestock moving through streams can affect the
649 hyporheic zone by contributing nutrients through waste, compacting gravel and clogging
650 interstitial spaces, resuspending sediments, and consuming or trampling riparian vegetation

651 (Hancock 2002). Sediment inputs are also increased by near-stream construction (Hester and
652 Gooseff 2010). Erosion generally changes bedform conditions; the introduction of substantial
653 sediments into streams can lead to sand slugs, which, while comprising new hyporheic habitat,
654 are not natural features, and have not proved amenable to restoration projects intending to restore
655 habitat heterogeneity (Lake et al. 2007). Generally, agricultural impacts to streams are thought to
656 result in simplified hyporheic population structures that have less overall production
657 (Environment Agency 2009).

658 **5.2 Stream Restoration, Nitrogen Dynamics, and the Hyporheic Zone**

659 Environmental management requires making selections from a suite of goals, which are
660 developed from identified and sought values and functions for the restoration site. Natural
661 systems do not have such pre-selected goals, per se, although our analyses often impute
662 intentions and directions to them. However, when we take steps to undo our effects on a system,
663 we must choose the directions and aims for the project, as our general alterations of the world
664 make it impossible to simply return to pre-anthropogenic conditions.

665 The most common explicit goal for stream restoration projects is to improve habitat for one
666 or more commercial fish species; this is closely related to project rationales to improve habitat
667 for stream macroinvertebrates, either as habitat indicator species or to support the charismatic
668 fish species (Bernhardt et al. 2007; Lake et al. 2007). Often these goals are achieved through
669 alteration of stream morphology (Bond and Lake 2003) – what has been described as the “field
670 of dreams” hypothesis (“if you build it, they will come”) (Palmer et al. 1997). Although
671 management programs seeking to increase salmonid fish populations sometimes specifically seek
672 to improve the hyporheic zone, as these species lay eggs and have young fish that live in the top
673 5-50 cm of stream sediments (Environment Agency 2009), even comprehensive stream

674 restoration designs usually do not explicitly address any subsurface hydraulic connectivity issues
675 (e.g., Shields et al. 2003).

676 General restoration efforts for stream and benthic habitats can also enhance the hyporheic
677 zone and affect its ability to transform N, even if not implicitly included in project planning, as
678 hyporheic zone improvements are a byproduct of efforts aimed at other goals (Welti et al. 2012).
679 For instance, one common stream restoration approach to improve fish habitat is to flush fine
680 sediment from benthic gravel areas (Arthington and Pusey 2003), which should also improve
681 connectivity into the hyporheic zone. Adding woody debris to streams is another common
682 surface water ecosystem rehabilitation technique that also helps hyporheic zones. If the log is
683 partially embedded in sediment, across a flowpath, this will create two downwelling areas: one
684 just before the water hits the log and another right at the downstream plunge pool. There will
685 also be an upwelling area shortly after the plunge pool (Fig. 3). This should also reduce
686 colmation, which will improve connectivity (Boulton 2007).

687 If the hyporheic zone is a foundation for overall stream health, then its significance in
688 restoration plans is thought to be severely underappreciated (Boulton et al. 2010). To address this
689 failing, the British Environment Agency issued a 250 page handbook on science issues
690 associated with the hyporheic zone. One chapter discussed how common stream restoration
691 efforts affect the hyporheic zone. The addition of in-stream deflectors and large wood was
692 identified as the most common activity (43% of projects). This increases hyporheic exchange,
693 increases subsurface DO, and generally enhances subsurface chemical reactions. It tends to
694 redistribute fauna because of habitat changes. Plantings to enhance fish cover was the second
695 most common restoration technique affecting the hyporheic zone (18% of projects), and was
696 thought to create very local changes in flows, chemistry, and habitats. Bed raising and substrate

697 changes (8% of all projects) increases stream connectivity, could enhance chemical reactions,
698 and could have a major effect on habitat types and distributions. Increasing the sinuosity of the
699 stream (6.5% of all projects) increases lateral hyporheic flows and tends to increase subsurface
700 residence time, and creates more diversity of benthic and hyporheic habitats. Removing
701 dams/weirs (6% of all projects) increases lotic environments and may increase exchange
702 processes but probably decreases overall storage times; it causes major shifts in fauna due to
703 habitat change. Removing artificial banks and beds (5% of all projects) causes a substantial
704 increase in exchange and adds the subsurface-banks as potential habitat zones. Creating riffles
705 (4.5% of all projects) increases exchange rates and subsurface residence time, increasing the
706 potential for chemical reactions, and, at a minimum, relocates subsurface habitats (Environment
707 Agency 2009). Although not explicitly mentioned in the handbook, other improvements to
708 riparian zone conditions, such as plantings or vegetation restoration should also indirectly
709 improve hyporheic zone functions.

710 However, increased connectivity with surface water or groundwater can have negative
711 consequences. Contaminated groundwater can degrade surface water if it is transmitted through
712 the hyporheic zone (Hancock 2002) or contaminated surface water can affect groundwater or
713 hyporheic zone water quality (Environment Agency 2009). Restoring connectivity can also allow
714 invasive species to spread and expose endemic species to new competitors, changing community
715 dynamics (Kondolf et al. 2006). Even increased hyporheic zone denitrification (see below) can
716 have negative consequences: one estimate is that the equivalent of 10% of anthropogenic
717 emissions of nitrous oxide (a potent greenhouse gas) are generated from river denitrification
718 processes (Beaulieu et al. 2011).

719 One broad stream restoration review identified vertical connectivity with the hyporheic zone
720 as an important element in creating proper ecological functions, but no explicit actions were
721 identified to achieve the connectivity goal (Lake et al. 2007). However, a similar review included
722 specific design elements to improve hyporheic zone functions: creating features such as pools,
723 riffles, steps, log dams, bars, meanders, and side channels, along with in-stream placement of
724 debris dams and large wood, and increasing bed complexity (or at least matching historical
725 patterns), coarsening sediments, and restoring the riparian zone (Hester and Gooseff 2010).

726 Stream restoration projects aiming to increase bedform heterogeneity will strengthen
727 connections in longitudinal, lateral, and vertical dimensions and increase surface-subsurface
728 exchange flowpaths, although predictive capabilities for such efforts were said to be lacking
729 (Boulton et al. 2010). Several weir variants (cross vanes and J-hooks) were installed in a New
730 York mountain stream to reduce stream erosion, and also to increase hyporheic zone
731 connections. Temperature testing largely corresponded with modeling of the project, suggesting
732 that design water exchange patterns can be largely achieved in practice (Crispell and Endreny
733 2009). A Nevada project undertaken to restore riparian functions by elevating downcut sections
734 and adding riffles and pools was found to have greater transient storage, as measured by
735 retention time, compared to unrestored areas. Modeling supported longer flow intervals in the
736 hyporheic zone, which suggested denitrification would have also increased (Knust and Warwick
737 2009). Several small weirs (1.5 m high) were constructed in another stream to mimic beaver
738 dams; a complex flow pattern of shallow pools, plunge pools, glides, and riffles with a variety of
739 sediment distributions and bedforms resulted. Indirect measurements (temperature and water
740 chemistry) along with modeling found distinct areas of inhibited and enhanced hyporheic
741 exchange, with evidence of much denitrification found in downwelling zones, and some more in

742 upwelling areas (Fanelli and Lautz 2008). Conversely, installation of a flat gravel bed, although
743 conformed to the preferred depths used by salmon for spawning, did not replace lost habitat from
744 dam construction. Salmon did not use the artificially formed sediments, and it was suggested that
745 the lack of bedform definition impeded hyporheic flows. Salmon possibly found the space subpar
746 due to the absence of hyporheic environmental modifications (particularly temperature control)
747 (Kondolf et al. 2006).

748 Instead of proposing in-stream modifications, Vaux (1968), using analytical solutions of flow
749 equations, determined that subsurface flows could be enhanced by changing hydraulic
750 conductivity in sediments (explicitly intended to increase DO availability for salmon alevins).
751 Structural changes included various high or low conductivity blocks of material, or sheet pilings.
752 Ward et al. (2011) simulated the structural changes proposed by Vaux, and, using reasonable rate
753 values derived from high gradient streams, estimated the impacts on processes such as
754 denitrification, respiration, and temperature buffering from various designs. A template to
755 achieve various effects was proposed. It was noted, on a practical note, that high conductivity
756 subsurface features can be difficult to retain as they will have their effectiveness reduced by
757 sediment clogging, but that some of the same results could be achieved through selection of
758 various low conductivity structures (the functions of which are unlikely to be easily degraded).

759 Currently, there are few broad guides focusing on improving stream N-management, as there
760 are for increasing bank stability and some other stream attributes. One explicit management
761 approach suggested an emphasis on 2nd and 3rd order streams with low flow rates, calling for
762 enhanced C availability and increased transient storage and interchanges with surrounding
763 terrestrial environments (Craig et al. 2008). The program targeted in-stream N, not subsurface
764 concentrations. The low order streams were preferred in accord with N-removal efficiencies

765 identified by Ensign and Doyle (2006). Carbon enhancement was not selected based on any cited
766 studies, but rather to ensure stream metabolism was maintained to allow for denitrification.
767 However, Hartland et al. (2011) determined that enhancing DOM in subsurface environments
768 caused a change in invertebrate populations to more pollution tolerant species, and so this
769 remedial approach for N may have unintended consequences.

770 A stream restoration project in Maryland that was intended to decrease stormwater-driven
771 erosion also led to improved N-removal rates. Cobbles and boulders and coarse sediments were
772 set into the stream, and features such as point bars, pool-riffle sequences, and meanders were
773 constructed. The riparian zone had trees planted, and banks were cut to be closer to the stream
774 surface in places. Tracer tests found that mean denitrification rates were twice as high for
775 restored areas as unrestored areas, and groundwater and stream water NO_3^- concentrations were
776 lower in the upstream restoration areas. Low bank riparian reaches had greater overall
777 denitrification rates, which was attributed to wider channels and less stream incision creating
778 greater overall system hydrological connections (for both the hyporheic and riparian zones)
779 (Kaushal et al. 2008). Approximately 40% of nitrate loadings were removed, due to “greater
780 whole stream connectivity” and especially to increased residence time (especially in the
781 hyporheic zone, where most denitrification was assumed to occur) (Klockner et al. 2009).

782 A long-time (ca. 100 yr) channelized stream in Kentucky was relocated to its former
783 floodplain. Its flow patterns were altered by creating meanders and pool-riffle sequences; the
784 restored segment was wider and shallower and approximately 15% longer than the channelized
785 segment had been. Significantly slower flow rates, higher temperatures, greater transient storage
786 areas, and more connectivity with the hyporheic zone were created. Nitrogen uptake was
787 estimated to be 30 times greater than the channelized segment used to have, and approximately

788 an order of magnitude greater than a reference site (which had a thriving, forested riparian zone)
789 (Bukaveckas 2007).

790 Constructing artificial riffles (adding stones or cobbles) or gravel bars, or recreating
791 meanders are also common habitat restorations. Constructed riffles and a constructed step in N-
792 rich agricultural and urban streams induced additional hyporheic exchange, with clear
793 downwelling and upwelling trends (Fig. 4). The hyporheic zone at the restored sites was a NO_3^-
794 sink; the streams had steeper longitudinal hydraulic head gradients and coarser substrates than
795 reaches with natural riffles and steps, suggesting the restored sites had enhanced NO_3^- removal
796 capabilities (Kasahara and Hill 2006). At another site, a constructed gravel bar and re-meandered
797 stream reach caused enhanced lateral hyporheic exchange flow. Vertical exchange was increased
798 at the gravel bar by adding a riffle-pool sequence. The need to manipulate sediments in
799 restorations was underlined, especially in agricultural and urban settings where fine-grained
800 sediments predominate and cause colmation (Kasahara and Hill 2007). Construction of baffles
801 also lead to increased denitrification – however, the effect was thought to be due to increased
802 transient storage due to stream velocity decreases, and not increased hyporheic zone exchange
803 (Ensign and Doyle 2005). Adding debris dams and gravel bars to streams in urban and suburban
804 settings caused greater denitrification rates, more than other management steps, even when
805 compared to forested reference sites. These sites supported organic-rich matrices, which seemed
806 to be the key factor for added N-losses (Groffman et al. 2005).

807 Indirect effects on the hyporheic zone may be achieved through alternative restoration
808 efforts. Forested riparian zones, for instance, were associated with greater hydrologic retention
809 times in stream reaches, apparently from slowing stream flows through debris additions. The
810 debris may have increased hyporheic zone inputs or created surface backwaters. In any case, N-

811 reductions greater than degraded, non-forested areas were measured (Weigelhofer et al. 2012).
812 Stream fencing can be useful in preventing cattle from encroaching on the riparian zone (Vidon
813 et al. 2010); not only might that lead to indirect hyporheic zone benefits from a restored riparian
814 buffer, but keeping cattle out of a stream is a good direct hyporheic zone remediation activity. In
815 the Danube River, changes to channels to restore more natural flow conditions increased surface-
816 subsurface connectivity, and resulted in greater rates of denitrification (among other enhanced
817 hyporheic zone functions) (Welti et al. 2012). It has also been suggested that restoring variable
818 flow conditions in controlled streams can improve nutrient uptake, as this may increase contact
819 with subsurface C pools (Faulkner 2008).

820 Agricultural drains are designed to have flat bottoms and steep, unvegetated sides to facilitate
821 water flows. These ditches lose functionality as they erode and with increasing plant
822 colonization, and the narrow-bottomed, vegetated, and often benched ditches that result have
823 been called “2-stage” ditches. Testing of sediments found that the benches in 2-stage ditches
824 function like floodplains, and have good denitrification potential (greater than sediments in 1-
825 stage ditches). Although this potential decreases some effects associated with excessive fertilizer
826 use, drains also foster direct transport of excess N from fields to streams; overall, it is likely that
827 areas with drains have quicker transport of more N to surface waters than areas that are not
828 drained (Powell and Bouchard 2010). In one setting, a bioreactor was installed in a ditch instead
829 of relying on natural deterioration of the ditch structure. The woodchip bioreactor generated
830 impressive denitrification rates, estimated to exceed those associated with natural wetlands in the
831 region by a factor of 40 (Robertson and Merkley 2009).

832 There appear to be correlations among land use, channelization, and the hyporheic zone’s
833 ability to retain NO_3^- , but the exact linkages have not been made yet (Robertson and Wood

834 2010). Although some studies have quantified the effect of stream restoration on nutrient
835 dynamics, it is difficult to determine general effects that extend beyond the specific examples
836 (Bukaveckas 2007). Clearly, understanding denitrification better is an important element in the
837 construction of accurate watershed nutrient management plans (Davidson and Seitzinger 2006).
838 Because denitrification is limited in time and space within the hyporheic zone, meeting the
839 definition of “hot spots”/“hot moments,” it may not be possible to manage specific stream
840 elements to create increased denitrification rates. Instead, increasing overall stream-hyporheic
841 zone connectivity may be the most feasible means of achieving the desired end (McClain et al.
842 2003), although such a restoration approach becomes a "black box" solution, resistant to further
843 analysis.

844 **6. Conclusions**

845 Regional mass balances (e.g., Howarth et al. 1996; van Breeman et al. 2002) find that sources
846 of N to the environment exceed identified sinks, and so denitrification is assumed to account for
847 the lost N, based on data collected in experimentation over physically small spaces and short
848 durations (Grimm et al. 2003). Use of N₂:Ar ratios and very precise direct measurements of N₂
849 appear to be resolving some of the analytical issues (Laursen and Seitzinger 2002; McCutchan et
850 al. 2003). However, historically, it has very difficult to measure denitrification well at any scale,
851 from the regional to site-specific. This has led to the invocation of “hot-spots,” variable over
852 time and space, to account for inabilities to repeat measurements or to find the expected
853 phenomenon that is predicted by mass-balance and other modeling (Boyer et al. 2006).
854 Denitrification of groundwater N in the hyporheic zone has been consistently found for streams
855 across the U.S.; the amount of denitrification is site specific, but generally relates to residence
856 time in the reaction zone beneath the stream (Puckett et al. 2008). The absolute impact of the

857 hyporheic zone is a function of still poorly determined relationships defined by Findlay (1995):
858 short residence times with high reaction activity lead to as much alteration of water chemistry as
859 longer residence times with slower reaction rates. Long residence times imply that not very much
860 water volume can be processed through the subsurface. Short reaction times allow for greater
861 volumes to be treated, but then require resolution of conundrums such as quick depletion of DO
862 (which appears to require residence time), DOC availability to fuel reactions, and whether small
863 biofilm zones can suffice to explain how otherwise well-oxygenated sediments can host
864 denitrification. Denitrification in the hyporheic zone occurs in spatially discrete zones, and
865 requires specific geologic and nutrient conditions. Although best estimates are that river basins
866 are the site of significant denitrification (for instance, van Breeman et al. 2002), a skeptical
867 analysis of extent of hyporheic conditions could conclude that there is often not enough
868 upwelling and downwelling relative to the size of the stream to generally create meaningful
869 effects on stream N-cycling.

870 Riparian zones cannot be separated from the hyporheic zone, given their close spatial and
871 functional proximity in many streams. Riparian zones have been described as poor “end-of-pipe
872 solutions” for increasing nutrient content in run-off and groundwater; where conditions are
873 suboptimal (deep groundwater flow paths, non-hydric sediments), only minor (<10%) N-
874 reduction can be expected (Stutter et al. 2012). The strongest correlations for N reductions in
875 streams have been found to wetlands acreage, not riparian or hyporheic conditions (McClain et
876 al. 2003). In fact, factors other than denitrification potential (such as land use, population
877 density, soil quality, and N atmospheric deposition rates) correlate much better with stream N
878 concentrations (Smith et al. 2008).

879 This supports the proposition that augmenting subsurface denitrification is unlikely to be
880 more effective at reducing stream N-concentrations than reducing input N concentrations
881 (Ranalli and Macalady 2010). Various land use programs have been proposed to achieve lower
882 N-inputs (Howarth 2005; Silgram et al. 2005; Hiscock et al. 2007), with one estimate being that
883 major changes in N-loading in 25% of headwater streams could “easily” lead to 10-15%
884 reductions in river discharge N loadings (Alexander et al. 2007). However, most input control
885 programs have not been able to achieve their goals (Boesch et al. 2001; Howarth 2005). One of
886 the few clear reductions in the delivery of N to coastal waters occurred in the Black Sea in the
887 1990s. This was not due to management success, but rather reflected the substantial, negative
888 impacts of economic chaos on agriculture in the former Soviet Union (Howarth 2005).

889 General prescriptions to reduce world-wide releases of reactive N by 25-30% include
890 controlling emissions from fossil fuel combustion, increasing efficiency of N applications to
891 crops, improving animal waste management, and, in cities without sewage treatment, treating at
892 least half of all human septic wastes (Galloway et al. 2008). Howarth (2005) identified steps to
893 be taken in the U.S. that could reduce coastal impacts from increased N releases. These included
894 source reduction steps, and additional treatment possibilities including:

895 1) changing agricultural drainage systems so as to improve nutrient uptake

896 This has been identified as feasible and generally creating few impacts to overall agricultural
897 output. Mostly this kind of project appears to require changes in perception of desired aesthetics
898 and some changes in general ditch management (Birgand et al. 2007), although more substantial
899 projects are also feasible (Robertson and Merkley 2009). Agricultural drainage systems do not
900 affect N that was exported directly to groundwater, however.

901 2) adding wetlands to riverine systems wherever feasible and desired.

902 It has been argued that above-ground, flow-through marshes are the most effective means of
903 reducing NO_3^- concentrations, especially if flow short-circuiting is avoided through careful
904 design (Kadlec 2012). Greater removal efficiencies (although greater space requirements are
905 needed too) can be achieved using constructed subsurface wetlands (Garcia et al. 2010), although
906 subsurface treatment is most beneficial when pathogen exposure is a major concern (Kadlec
907 2012). Marsh projects like these can be monitored and assessed more easily than less intrusive
908 changes to foster subsurface NO_3^- removal in riparian and/or hyporheic zones. Marsh
909 construction requires large expanses of space, however, and may not be the landscape feature
910 that is possible, needed, or desired in all settings.

911 3) restoring riparian areas as is possible.

912 A nation-scale modeling exercise in England suggested that substantial attenuation of N-inputs
913 through subsurface reactions is possible in many lotic environments (although certainly not all)
914 (Smith et al. 2009). Bayesian simulations using literature search denitrification values suggested
915 that basic riparian restoration techniques would lead to approximately 25% more N-assimilation
916 in restored reaches compared to impacted reaches (Faulkner 2008). Still, although higher
917 concentrations of NO_3^- lead to higher denitrification rates, the increase in denitrification is not
918 proportional to increases in inputs (Alexander et al. 2009), and so only mitigates (not resolves)
919 the issue of increasing N-releases.

920 The degree that restoration efforts should focus on the hyporheic zone and its potential for
921 denitrification is not clear. Estuarine N-loads are a function of prior loadings in the upriver
922 region: e.g., water quality in the Gulf of Mexico is closely linked to historical fertilizer
923 applications throughout the Mississippi-Missouri River basin (Alexander et al. 2007).
924 Degradation and alteration of headwater streams (in particular) was identified as a major element

925 in coastal hypoxia due to a loss of nutrient processing capabilities (Freeman et al. 2007). This
926 seems to imply that restoration efforts in these areas, assuming that denitrification potential is
927 part of the selected approach, could be effective in improving a major regional problem. But,
928 determining the impact of a potential denitrification zone depends on the degree and reliability of
929 the connection between N-source and the denitrification zone (McClain et al. 2003). There is
930 good evidence that denitrification occurs in the riparian and hyporheic zones, reducing
931 groundwater N inputs and mitigating stream NO_3^- concentrations. Denitrification in riparian
932 zones requires groundwater to be funneled through particular small regions of the streamside
933 environment, and many groundwater pathways do not intersect these zones. Hyporheic processes
934 depend on generating micro-scale patches of favorable conditions, or appear to be governed by
935 Freundlich reaction kinetics: denitrification increases as ambient concentrations of NO_3^-
936 increase, but denitrification rate increases are not fast enough so as to keep pace with the
937 increases in the stream water NO_3^- . Slower flow rates through sediments compared to flow rates
938 in the stream and the relatively small volume of the hyporheic zone imply that, in most settings,
939 water in a particular reach cannot have much residence time in the subsurface. Thus, there can
940 only be a limited role for these environments as checks on increasing stream NO_3^- content and
941 deliveries to marine systems. Increasing treatment of water through wetlands appears to return
942 greater dividends than enhancing subsurface NO_3^- treatment potentials.

943 Incorporating better knowledge of these ecotones into stream remediation plans is not
944 pointless, however; understanding the functionalities of these zones better could lead to better
945 crafting of environmental initiatives. On Long Island (New York, U.S.), management concerns
946 regarding NO_3^- concentrations in a shallow lagoonal estuary have focused on direct groundwater
947 discharges to the estuary (Kinney and Valiela 2011). However, although the fresh water entering

948 the estuary is derived from groundwater, most enters the estuary via short stream systems. A
949 focus on improving riparian and hyporheic zone processes in these canalized, heavily altered
950 streams, where sufficient space for wetland construction appears to be lacking, might pay a
951 greater short-term dividend than trying to change overall N-inputs to groundwater (where 20-50
952 year residence times have been modeled). In this way, rehabilitation of hyporheic zones could
953 reduce estuarine N-loadings within timescales appreciated by funding agencies and politicians.

954 Therefore, there is virtue in addressing the hyporheic zone, and improving its connectivity
955 with surface waters as stream modifications are made. Even greater returns might be realized by
956 treating the hyporheic and riparian zones together. Although source controls on NO_3^- appear to
957 be the most effective means of reducing NO_3^- inputs to sensitive marine environments, greater
958 water flows through subsurface zones will help to ameliorate increases in NO_3^- releases from
959 agriculture and other human endeavors, especially if short-term effects are desired.

960

961 **Acknowledgements**

962 Jessica Gurevitch was extremely helpful with her comments, both on the MS project that was
963 the genesis of this paper, and on early drafts of this work. Comprehensive, careful, and
964 thoughtful peer review of the paper enhanced nearly all aspects off our initial submission.

965

966

967

968

969 **References**

- 970
971 Alexander, R.B., E.W. Boyer, R.A. Smith, G.E. Schwarz, and R.B. Moore. 2007. The role of
972 headwater streams in downstream water quality. *Journal of the American Water Resources*
973 *Association* 43(1):41-59.
- 974 Alexander, R.B., J.K. Bohlke, E.W. Boyer, M.B. David, J.W. Harvey, P.J. Mulholland, S.B.
975 Seitzinger, C.R. Tobias, C. Tonitto, and W.M. Wollheim. 2009. Dynamic modeling of
976 nitrogen losses in river networks unravels the coupled effects of hydrological and
977 biogeochemical processes. *Biogeochemistry* 93:91-116.
- 978 Arrango, C.P., J.L. Tank, J.L. Schaller, T.V. Royer, M.J. Bernot, and M.B. David. 2007. Benthic
979 organic carbon influences denitrification in streams with high nitrate concentration.
980 *Freshwater Biology* 52:1210-1222.
- 981 Arrango, C.P., and J.L. Tank. 2008. Land use influences the spatiotemporal controls on
982 nitrification and denitrification in headwater streams. *Journal of the North American*
983 *Benthological Society* 27(1):90-107.
- 984 Arrigoni, A.S., G.C. Poole, L.A.K. Mertes, S.J. O'Daniel, W.W. Woessner, and S.A. Thomas.
985 2008. Buffered, lagged, or cooled? Disentangling hyporheic influences on temperature cycles
986 in stream channels. *Water Resources Research* 44:W09418 (doi:10.1029/2007WR006480).
- 987 Arthington, A.H., and B.J. Pusey. 2003. Flow restoration and protection in Australian rivers.
988 *River Research and Applications* 19:377-395.
- 989 Baker, M.A., C.N. Dahm, and H.V. Valett. 2000. Anoxia, anaerobic metabolism, and
990 biogeochemistry of the stream-water-groundwater interface. pp. 259-283, *In* J.B. Jones and
991 P.J. Mulholland (Eds.). *Streams and Ground Waters*. Academic Press, San Diego. 425 pp.

992 Bardini, L., F. Boano, M.B. Cardenas, R. Revelli, and L. Ridolfi. 2012. Nutrient cycling in
993 bedform induced hyporheic zones. *Geochimica and Cosmochimica Acta* 64:47-61.

994 Beaulieu, J.J., J.L. Tank, S.K. Hamilton, W.M. Wollheim, R.O. Hall, Jr., P.J. Mulholland, B.J.
995 Peterson, L.R. Ashkenas, L.W. Cooper, C.N. Dahm, W.K. Dodds, N.B. Grimm, S.L.
996 Johnson, W.H. McDowell, G.C. Poole, H.M. Valett, C.P. Arango, M.J. Bernot, A.J. Burgin,
997 C.L. Crenshaw, A.M. Helton, L.T. Johnson, J.M. O'Brien, J.D. Potter, R.W. Shiebley, D.J.
998 Sobota, and S.M. Thomas. 2011. Nitrous oxide emissions from denitrification in stream and
999 river networks. *Proceedings of the National Academy of Science* 108(1):214-219.

1000 Bencala, K.E. 1983. Simulation of solute transport in a mountain pool-and-riffle stream with a
1001 kinetic mass transfer model for sorption. *Water Resources Research* 19(3):732-738.

1002 Bencala, K.E., and R.A. Walters. 1983. Simulation of solute transport in a mountain pool-and-
1003 riffle stream – a transient storage model. *Water Resources Research* 19(3):718-724.

1004 Bernhardt, E.S., E.B. Sudduth, M.A. Palmer, J.D. Allen, J.L. Meyer, G. Alexander, J. Follastad-
1005 Shah, B. Hassett, R. Jenkinson, R. Lave, J. Rumps, and L. Pagano. 2007. Restoring rivers
1006 one reach at a time: Results from a survey of U.S. river restoration practitioners. *Restoration*
1007 *Ecology* 15(3):482-493.

1008 Birgand, F., R.W. Skaggs, G.M. Chescheir, and J.W. Gilliam. 2007. Nitrogen removal in streams
1009 of agricultural catchments – A literature review. *Critical Reviews in Environmental Science*
1010 *and Technology* 37(5):381-487.

1011 Boano, F., R. Revelli, and L. Ridolfi. 2007. Bedform-induced hyporheic exchange with unsteady
1012 flows. *Advances in Water Research* 30:148-157.

1013 Boano, F., R. Revelli, and L. Ridolfi. 2009. Quantifying the impact of groundwater discharge on
1014 the surface-subsurface exchange. *Hydrological Processes* 23:2108-2116.

1015 Boesch, D.F., R.B. Brinsfield, and R.E. Magnien. 2001. Chesapeake Bay eutrophication:
1016 Scientific understanding, ecosystem restoration, and challenges for agriculture. *Journal of*
1017 *Environmental Quality* 30:303-320.

1018 Bohlke, J.K., R.C. Antweiler, J.W. Harvey, A.E. Laursen, L.K. Smith, R.L. Smith, and M.A.
1019 Voytek. 2009. Multi-scale measurements and modeling of denitrification in streams of
1020 varying flow and nitrate concentration in the Upper Mississippi River basin, USA.
1021 *Biogeochemistry* 93:117-141.

1022 Bond, N.R., and P.S. Lake. 2003. Local habitat restoration in streams: Constraints on the
1023 effectiveness of restoration for stream biota. *Ecological Management & Restoration*
1024 4(3):193-198.

1025 Botter, G., N.B. Basu, S. Zanardo, P.S.C. Rao, and A. Rinaldo. 2010. Stochastic modeling of
1026 nutrient losses in streams: Interactions of climatic, hydrologic, and biogeochemical controls.
1027 *Water Resources Research* 46(8):W08509 (doi: 10.1029/2009WR008758).

1028 Boulton, A. 2000. The subsurface macrofauna. pp. 337-361, *In* J.B. Jones and P.J. Mulholland
1029 (Eds). *Streams and Ground Waters*. Academic Press, San Diego. 425 pp.

1030 Boulton, A.J. 2007. Hyporheic rehabilitation in rivers: Restoring vertical connectivity.
1031 *Freshwater Biology* 52:632-650.

1032 Boulton, A.J., M.R. Scarsbrook, J.M. Quinn, and G.P. Burrell. 1997. Land-use effects on the
1033 hyporheic ecology of five small streams near Hamilton, New Zealand. *New Zealand Journal*
1034 *of Marine and Freshwater Research* 31(5):609-622.

1035 Boulton, A.J., S. Findlay, P. Marmonier, E.H. Stanley, and H.M. Valett. 1998. The functional
1036 significance of the hyporheic zone in streams and rivers. *Annual Review of Ecology and*
1037 *Systematics* 29:59-81.

1038 Boulton, A.J., T. Datry, T. Kasahara, M. Mutz, and J.A. Stanford. 2010. Ecology and
1039 management of the hyporheic zone: Stream-groundwater interactions of running waters and
1040 their floodplains. *Journal of the North American Benthological Society* 29(1):26-40.

1041 Boyer, E.W., R.B. Alexander, W.J. Parton, C. Li, K. Butterbach-Bahl, S.D. Donner, R.W.
1042 Skaggs, and S.J. Del Gosso. 2006. Modeling denitrification in terrestrial and aquatic
1043 ecosystems at regional scales. *Ecological Applications* 16(6):2123-2142.

1044 Brunke, M., and T. Gonser. 1997. The ecological significance of exchange processes between
1045 rivers and groundwater. *Freshwater Biology* 37:1-33.

1046 Bukaveckas, P.A. 2007. Effects of channel restoration on water velocity, transient storage, and
1047 nutrient uptake in a channelized stream. *Environmental Science and Technology* 41(5):1570-
1048 1576.

1049 Burkholder, B.K., G.E. Grant, R. Haggerty, T. Khangaonkar, and P.J. Wampler. 2008. Influence
1050 of hyporheic flow and geomorphology on temperature of a large, gravel-bed river, Clackmas
1051 River, Oregon, USA. *Hydrological Processes* 22:941-953.

1052 Cardenas, M.B. 2008. The effect of river bend morphology on flow and timescales of surface
1053 water-groundwater exchange across pointbars. *Journal of Hydrology* 362:134-141.

1054 Cardenas, M.B. 2009. Stream-aquifer interactions and hyporheic exchange in gaining and losing
1055 sinuous streams. *Water Resources Research* 45:W06429 (doi:10.1029/2008WR007651).

1056 Cleorn, J.E. 2001. Our evolving conceptual model of the coastal eutrophication problem. *Marine*
1057 *Ecology Progress Series* 210:223-253.

1058 Cliverd, H.M. 2007. Surface-subsurface hydrologic exchange and nitrogen dynamics in the
1059 hyporheic zone of the Tanana River. MS Thesis, University of Fairbanks, AK. 66 pp.

1060 Cliverd, H.M. 2008. Nitrogen retention in the hyporheic zone of a glacial river in interior Alaska.
1061 *Biogeochemistry* 88:31-46.

1062 Conant, B., Jr. 2004. Delineating and quantifying ground water discharge areas using streambed
1063 temperatures. *Ground Water* 42(2):243-257.

1064 Craig, L.S., M.A. Palmer, D.C. Richardson, S. Filoso, E.S. Bernhardt, B.P. Bledsoe, M.W.
1065 Doyle, P.M. Groffman, B.A. Hassett, S.J. Kaushal, P.M. Mayer, S.M. Smith, and P.R.
1066 Wilcock. 2008. Stream restoration strategies for reducing river nitrogen loads. *Frontiers in*
1067 *Ecology and the Environment* 6(10):529-538.

1068 Craig, L., J.M. Bahr, and E.E. Roden. 2010. Localized zones of denitrification in a floodplain
1069 aquifer in southern Wisconsin, USA. *Hydrogeology Journal* 18:1867-1879.

1070 Crenshaw, C.L., N.B. Grimm, L.H. Zeglin, R.W. Shelbly, C.N. Dahm, and A.D. Pershall. 2010.
1071 Dissolved inorganic nitrogen dynamics in the hyporheic zone of reference and human-altered
1072 southwestern U.S. streams. *Archiv fur Hydrobiologie* 176(4):391-405.

1073 Crispell, J.K., and T.A. Endreny. 2009. Hyporheic exchange flows around constructed in-
1074 channel structures and implications for restoration design. *Hydrological Processes* 23:1158-
1075 1168.

1076 Dahm, C.N., N.B Grimm, P. Marmonier, and P. Vervier. 1998. Nutrient dynamics at the
1077 interface between surface waters and groundwaters. *Freshwater Biology* 40:427-451.

1078 Davidson, E.A. and S. Seitzinger. 2006. The enigma of progress in denitrification research.
1079 *Ecological Applications* 16(6):2057-2063.

1080 Deforet, T., P. Marmonier, D. Rieffel, N. Crini, P. Giraudoux, and D. Gilbert. 2009. Do
1081 parafluvial zones have an impact in regulating river pollution? *Spatial and temporal*

1082 dynamics of nutrients, carbon, and bacteria in a large gravel bar of the Doubs River (France).
1083 *Hydrobiologia* 623:235-250.

1084 Dole-Olivier, M.-J., P. Marmonier, and J.-L. Beffy. 1997. Response of invertebrates to lotic
1085 disturbance: Is the hyporheic zone a patchy refugium? *Freshwater Biology* 37:257-276.

1086 Dosskey, M.J. 2002. Setting priorities for research on pollution reduction functions of
1087 agricultural buffers. *Environmental Management* 30(5):641-650.

1088 Duff, J.H., and F.J. Triska. 1990. Denitrification in sediments from the hyporheic zone adjacent
1089 to a small forested stream. *Canadian Journal of Fisheries and Aquatic Sciences* 47:1140-
1090 1147.

1091 Duff, J.H., and F.J. Triska. 2000. Nitrogen biogeochemistry and surface-subsurface exchange in
1092 streams. pp. 197-220, *In* J.B. Jones and P.J. Mulholland (Eds.). *Streams and Ground Waters*.
1093 Academic Press, San Diego. 425 pp.

1094 Duff, J.H., A.J. Tesoriero, W.B. Richardson, E.A. Strauss, and M.D. Munn. 2008. Whole-stream
1095 response to nitrate loading in three streams draining agricultural landscapes. *Journal of*
1096 *Environmental Quality* 37:1133-1144.

1097 Duval, T.P., and A.R. Hill. 2007. Influence of base flow stream bank seepage on riparian zone
1098 nitrogen biogeochemistry. *Biogeochemistry* 85:185-199.

1099 Ensign, S.H., and M.W. Doyle. 2005. In-channel transient storage and associated nutrient
1100 retention: Evidence from experimental manipulations. *Limnology and Oceanography*
1101 50(6):1740-1751.

1102 Ensign, S.H., and M.W. Doyle. 2006. Nutrient spiraling in streams and river networks. *Journal of*
1103 *Geophysical Research* 111:G04009 (doi:10.1029/2005JG000114).

- 1104 Environment Agency. 2009. *The Hyporheic Handbook: A Handbook on the Groundwater-*
1105 *Surface Water Interface and Hyporheic Zone for Environment Managers*. Environment
1106 Agency, Bristol, UK. 264 pp.
- 1107 Fanelli, R.M., and L.K. Lautz. 2008. Patterns of water, heat, and solute flux through streambeds
1108 around small dams. *Ground Water* 46(5):671-687.
- 1109 Faulkner, B.R. 2008. Bayesian modeling of the assimilative capacity component of nutrient total
1110 maximum daily loads. *Water Resource Research* 44:W08415 (doi:10.1029/2007WR006638).
- 1111 Findlay, S. 1995. Importance of the surface-subsurface exchange in stream ecosystems: The
1112 hyporheic zone. *Limnology and Oceanography* 40:159-164.
- 1113 Findlay, S., and W.V. Sobszak. 2000. Microbial communities in hyporheic sediments. pp. 287-
1114 306, *In* J.B. Jones and P.J. Mulholland (Eds.). *Streams and Ground Waters*. Academic Press,
1115 San Diego. 425 pp.
- 1116 Fischer, H., F. Kloep, S. Wilzcek, and M.T. Pusch. 2005. A river's liver – microbial processes
1117 within the hyporheic zone of a large lowland river. *Biogeochemistry* 76:349-371.
- 1118 Flewelling, S.A., J.S. Herman, G.M. Hornberger, and A.L. Mills. 2012. Travel time controls the
1119 magnitude of nitrate discharge in groundwater bypassing the riparian zone to a stream on
1120 Virginia's coastal plain. *Hydrological Processes* 26:1242-1253.
- 1121 Fowler, R.T., and R.G. Death. 2001. The effect of environmental stability on hyporheic
1122 community structure. *Hydrobiologia* 445:85-95.
- 1123 Fraser, B.G., and D.D. Williams. 1998. Seasonal boundary dynamics of a groundwater/surface-
1124 water ecotone. *Ecology* 79(6):2019-2031.

1125 Freeman, M.C., C.M. Pringle, and C.R. Jackson. 2007. Hydrologic connectivity and the
1126 contribution of stream headwaters to ecological integrity at regional scales. *Journal of the*
1127 *American Water Resources Association* 43(1):5-14.

1128 Galloway, J.N., A.R. Townsend, J.W. Erisman, M. Bekunda, Z. Cai, J.R. Freney, L.A.
1129 Martinelli, S.P. Seitzinger, and M.A. Sutton. 2008. Transformation of the nitrogen cycle:
1130 Recent trends, questions, and potential solutions. *Science* 320:889-892.

1131 Gandy, C.J., J.W.N. Smith, and A.P. Jarvis. 2007. Attenuation of mining-derived wastes in the
1132 hyporheic zone: A review. *Science of the Total Environment* 373:435-446.

1133 Garcia, J., D.P.L. Rousseau, J. Morato, E. Leage, V. Matamoros, and J.M. Bayona. 2010.
1134 Contaminant removal processes in subsurface-flow constructed wetlands: A review. *Critical*
1135 *Reviews in Environmental Science and Technology* 40(7):561-661.

1136 Gold, A.J., P.M. Groffman, K. Addy, D.Q. Kellogg, M. Stolt, and A.E. Rosenblatt. 2001.
1137 Landscape attributes as controls on ground water nitrate removal capacity of riparian zones.
1138 *Journal of the American Water Resources Association* 37(6):1457-1464.

1139 Gonzalez-Pinzon, R., R. Haggerty, and D.D. Myrold. 2012. Measuring aerobic respiration in
1140 stream ecosystems using the resazurin-resorufin system. *Journal of Geophysical Research*
1141 117:G00N06 (doi:10.1029/2012JG001965).

1142 Gooseff, M.N., J.K. Anderson, S.M. Wondzell, J. LaNier, and R. Haggerty. 2006. A modeling
1143 study of hyporheic exchange pattern and the sequence, size, and spacing of stream bedforms
1144 in mountain stream networks, Oregon, USA. *Hydrological Processes* 20:2443-2457.

1145 Greenwald, M.J., W.B. Bowden, M.N. Gooseff, J.P. Zarnetske, J.P. McNamara, J.H. Bradford,
1146 and T.R. Brosten. 2008. Hyporheic exchange and water chemistry of two arctic tundra

1147 streams of contrasting geomorphology. *Journal of Geophysical Research* 113:G02029, doi:
1148 10.1029/2007JG000549.

1149 Grimm, N.B., S.E. Gergel, W.H. McDowell, E.W. Boyer, C.L. Dent, P. Groffman, S.C. Hart, J.
1150 Harvey, C. Johnston, E. Mayorga, M.E. McClain, and G. Pinay. 2003. Merging aquatic and
1151 terrestrial perspectives of nutrient biogeochemistry. *Oecologia* 137:485-501.

1152 Groffman, P.M., A.M. Dorsey, and P.M. Mayer. 2005. N processing within geomorphic
1153 structures in urban streams. *Journal of the North American Benthological Society* 24:613-
1154 625.

1155 Groffman, P.M., M.A. Altabet, J.K. Bohlke, K. Butterbach-Bahl, M.B. David, M.K. Firestone,
1156 A.E. Giblin, T.M. Kana, L.P. Nielsen, and M.A. Voytek. 2006. Methods for measuring
1157 denitrification: Diverse approaches to a difficult problem. *Ecological Applications*
1158 16(6):2091-2122.

1159 Gu, C., G.M. Hornberger, A.L. Mills, J.S. Herman, and S.A. Flewelling. 2007. Nitrate reduction
1160 in streambed sediments: Effects of flow and biogeochemical kinetics. *Water Resources*
1161 *Research* 43:W12413 (doi:10.1029/2007WR006027).

1162 Gu, C., G.M. Hornberger, J.S. Herman, and A.L. Mills. 2008a. Effects of freshets on the flux of
1163 groundwater nitrate through streambed sediments. *Water Resources Research* 44:W05415
1164 (doi:10/1021/2007W006488).

1165 Gu, C., G.M. Hornberger, J.S. Herman, and A.L. Mills. 2008b. Influence of stream-groundwater
1166 interactions in the streambed sediments on NO_3^- flux to a low-relief coastal stream. *Water*
1167 *Resources Research* 44:W11432 (doi:10/1021/2007W006739).

1168 Gulley, J., J.B. Martin, E.J. Screaton, and P.J. Moore. 2011. River reversals into karst springs: A
1169 model for cave enlargement in eogenetic karst aquifers. *GSA Bulletin* 123(3/4):457-467.

1170 Haggerty, R., A. Argerich, and E. Marti. 2008. Development of a “smart” tracer for the
1171 assessment of microbiological activity and sediment-water interaction in natural waters: The
1172 resazurin-resorufin system. *Water Resources Research* 44:W00D01
1173 (doi:10.1029/2007WR006670).

1174 Haggerty, R., E. Marti, A. Argerich, D. von Schiller, and N.B. Grimm. 2009. Resazurin as a
1175 “smart” tracer for quantifying metabolically active transient storage in stream ecosystems.
1176 *Journal of Geophysical Research* 114:G03014 (doi:10.1029/2008JG000942).

1177 Hakencamp, C.C., and M.A. Palmer. 2000. The ecology of the hyporheic meiofauna. pp. 307-
1178 336, *In* J.B. Jones and P.J. Mulholland (Eds.). *Streams and Ground Waters*. Academic Press,
1179 San Diego. 425 pp.

1180 Hall, R.O., Jr., E.S. Bernhardt, and G.E. Likens. 2002. Relating nutrient uptake with transient
1181 storage in forested mountain streams. *Limnology and Oceanography* 47(1):255-265.

1182 Hall, R.O., Jr., M.A. Baker, C.D. Arp, and B.J. Koch. 2009. Hydrological control of nitrogen
1183 removal, storage, and export in a mountain stream. *Limnology and Oceanography*
1184 54(6):2128-2142.

1185 Hancock, P.J. 2002. Human impacts on the stream-groundwater exchange zone. *Environmental*
1186 *Management* 29(6):763-781.

1187 Hartland, A., G.D. Fenwick, and S.J. Bury. 2011. Tracing sewage-derived organic matter into a
1188 shallow groundwater food web using stable isotope and fluorescence signatures. *Marine and*
1189 *Freshwater Research* 62:119-129.

1190 Harvey, L.W., and C.C. Fuller. 1998. Effect of enhanced manganese oxidation in the hyporheic
1191 zone on basin-scale geochemical mass balance. *Water Resources Research* 34:623-636.

1192 Harvey, J.W., and B.J. Wagner. 2000. Quantifying hydrologic interactions between streams and
1193 their subsurface hyporheic zones. pp. 4-44, *In* J.B. Jones and P.J. Mulholland (Eds.). *Streams*
1194 *and Ground Waters*. Academic Press, San Diego. 425 pp.

1195 Harvey, B.N., M.L. Johnson, J.D Kiernan, and P.G. Green. 2011. Net dissolved inorganic
1196 nitrogen production in hyporheic mesocosms with contrasting sediment size distributions.
1197 *Hydrobiologia* 658:343-352.

1198 Hayashi, M., and D.O. Rosenberry. 2002. Effects of ground water exchange on the hydrology
1199 and ecology of surface water. *Ground Water* 40(3):309-316.

1200 Hedin, L.O., J.C. von Fischer, N.E. Ostrom, B.P. Kennedy, M.G. Brown, and G.P. Robertson.
1201 1998. Thermodynamic constraints on nitrogen transformations and other biogeochemical
1202 processes at soil-stream interfaces. *Ecology* 79(2):684-703.

1203 Heffernan, J.B., and M.J. Cohen. 2010. Direct and indirect coupling of primary production and
1204 diel nitrate dynamics in a subtropical spring-fed river. *Limnology and Oceanography*
1205 55(2):677-688.

1206 Hester, E.T., and M.N. Gooseff. 2010. Moving beyond the banks: Hyporheic restoration is
1207 fundamental to restoring ecological services and functions of streams. *Environmental*
1208 *Science and Technology* 44(5):1521-1525.

1209 Hill, A.R. 2000. Stream chemistry and riparian zones. Pp. 83-110, *In* J.B. Jones and P.J.
1210 Mulholland (Eds.). *Streams and Ground Waters*. Academic Press, San Diego. 425 pp.

1211 Hill, A.R., C.F. LaBadia, and K. Sanmugadas. 1998. Hyporheic zone hydrology and nitrogen
1212 dynamics in relation to the streambed topography of a N-rich stream. *Biogeochemistry*
1213 42:285-310.

1214 Hill, A.R., P.G.F. Vidon, and J. Langat. 2004. Denitrification potential in relation to lithology in
1215 five headwater riparian zones. *Journal of Environmental Quality* 33:911-919.

1216 Hiscock, K., A. Lovett, A. Saich, T. Dockerty, P. Johnson, C. Sandhu, G. Sunnenberg, K.
1217 Appleton, B. Harris, and J. Greaves. 2007. Modelling land-use scenarios to reduce
1218 groundwater nitrate pollution: The European Water4All project. *Quarterly Journal of*
1219 *Engineering Geology and Hydrogeology* 40(4):417-434.

1220 Holmes, R.M. 2000. The importance of ground water to stream ecosystem function. pp. 137-148,
1221 *In* J.B. Jones and P.J. Mulholland (Eds.). *Streams and Ground Waters*. Academic Press, San
1222 Diego. 425 pp.

1223 Holmes, R.M., S.G. Fisher, and N.B. Grimm. 1994. Parafluvial nitrogen dynamics in a desert
1224 stream ecosystem. *Journal of North American Benthological Society* 13:468-478.

1225 Holmes, R.M., J.B. Jones, Jr., S.G. Fisher, and N.B. Grimm. 1996. Denitrification in a nitrogen-
1226 limited stream ecosystem. *Biogeochemistry* 33(2):125-146.

1227 Howarth, R.W. 2005. The development of policy approaches for reducing nitrogen pollution to
1228 coastal waters of the USA. *Science in China Series C: Life Sciences* 48 (Suppl. 2): 791-806.

1229 Howarth, R.W., G. Billen, D. Swaney, A. Townsend, N. Jaworski, K. Lathja, J.A. Downing, R.
1230 Elmgren, N. Caraco, T. Jordan, F. Berendse, J. Freney, V. Kudeyarov, P. Murdoch, and Z.
1231 Zhao-Liang. 1996. Regional nitrogen budgets and riverine N & P fluxes for the drainages to
1232 the North Atlantic Ocean: Natural and human influences. *Biogeochemistry* 35(1):75-139.

1233 Inwood, S.E., J.L. Tank, and M.J. Bernot. 2005. Patterns of denitrification associated with land
1234 use in 9 midwestern headwater streams. *Journal of the North American Benthological*
1235 *Society* 24(2):227-245.

1236 Jones, J.B., and R.M. Holmes. 1996. Surface-subsurface interactions in stream ecosystems.
1237 Trends in Ecology and Evolution 11:239-242.

1238 Kadlec, R.H. 2012. Constructed marshes for nitrate removal. Critical Reviews in Environmental
1239 Science and Technology 42(9):934-1005.

1240 Kaplan, L.A., and J.D. Newbold. 2000. Surface and subsurface dissolved organic carbon. pp.
1241 237-258, In J.B. Jones and P.J. Mulholland (Eds.). Streams and Ground Waters. Academic
1242 Press, San Diego. 425 pp.

1243 Kaplan, D., R. Munoz-Carpena, and A. Ritter. 2010. Untangling complex shallow groundwater
1244 dynamics in the floodplain wetlands of a southeastern U.S. coastal river. Water Resources
1245 Research 46:W08528 (doi:10.1029/2009WR009038).

1246 Kasahara, T., and A.R. Hill. 2006. Effects of riffle-step restoration on hyporheic zone chemistry
1247 in N-rich lowland streams. Canadian Journal of Fisheries and Aquatic Sciences 63:120-133.

1248 Kasahara, T., and A.R. Hill. 2007. Instream restoration: Its effects on lateral stream-subsurface
1249 water exchange in urban and agricultural streams in southern Ontario. River Research and
1250 Applications 23:801-814.

1251 Kaser, D.H., A. Binley, A.L. Heathwaite, and S. Krause. 2009. Spatio-temporal variations in
1252 hyporheic flow in a riffle-step-pool sequence. Hydrological Processes 23:2138-2149.

1253 Kaushal, S.S., P.M. Groffman, P.M. Mayer, E. Stritz, and A.J. Gold. 2008. Effects of stream
1254 restoration on denitrification in an urbanizing watershed. Ecological Applications 16(3):789-
1255 804.

1256 Kellogg, D.Q., A.J. Gold, P.M. Groffman, K. Addy, M.H. Stolt, and G. Blazejewski. 2005. In
1257 situ ground water denitrification in stratified, permeable soils underlying riparian wetlands.
1258 Journal of Environmental Quality 34:524-533.

- 1259 Kinney, E.L., and I. Valiela. 2011. Nitrogen loading to Great South Bay: Land use, sources,
1260 retention, and transport from land to bay. *Journal of Coastal Research* 27(4):672-686.
- 1261 Klocker, C.A., S.S. Kaushal, P.M. Groffman, P.M. Mayer, and R.P. Morgan. 2009. Nitrogen
1262 uptake and denitrification in restored and unrestored streams in urban Maryland, USA.
1263 *Aquatic Science* 71:411-424.
- 1264 Knust, A.E., and J.J. Warwick. 2009. Using a fluctuating tracer to estimate hyporheic exchange
1265 in restored and unrestored reaches of the Truckee River, Nevada, USA. *Hydrological
1266 Processes* 23:1119-1130.
- 1267 Kondolf, G.M., A.J. Boulton, S. O'Daniel, G.C. Poole, F.J. Rahel, E.H. Stanley, E. Wohl, A.
1268 Bang, J. Carlstrom, C. Cristoni, H. Huber, S. Koljonen, P. Louhi, and K. Nakamura. 2006.
1269 Process-based ecological river restoration: Visualizing three-dimensional connectivity and
1270 dynamic vectors to recover lost linkages. *Ecology and Society* 11(2):5-23.
- 1271 Krause, S., L. Heathwaite, A. Binley, and P. Keenan. 2009. Nitrate concentration changes at the
1272 groundwater-surface water interface of a small Cumbrian river. *Hydrological Processes*
1273 23:2195-2211.
- 1274 Krause, S., D.M. Hannah, J.H. Fleckenstein, C.M. Heppell, D. Kaeser, R. Pickup, G. Pinay, A.L.
1275 Robertson, and P.J. Wood. 2011. Interdisciplinary perspectives on processes in the hyporheic
1276 zone. *Ecohydrology* 4:481-499.
- 1277 Lake, P.S., N. Bond, and P. Reich. 2007. Linking ecological theory with stream restoration.
1278 *Freshwater Biology* 52:597-615.
- 1279 Lansdowne, K., H. Trimmer, C.M. Heppell, F. Sgourdis, S. Ullah, A.L. Heathwaite, A. Binley,
1280 and H. Zhang. 2012. Characterization of the key pathways of dissimilatory nitrate reduction

1281 and their response to complex organic substrates in hyporheic sediments. *Limnology and*
1282 *Oceanography* 57(2):387-400.

1283 Laursen, A.E., and S.P. Seitzinger. 2002. Measurement of denitrification in rivers: An integrated,
1284 whole reach approach. *Hydrobiologia* 485:67-81.

1285 Lautz, L.K., and D.I. Siegel. 2007. The effect of transient storage on nitrate uptake lengths in
1286 streams: An inter-site comparison. *Hydrological Processes* 21:3533-3548.

1287 Liao, Z., and O.A. Cirpka. 2011. Shape-free inference of hyporheic traveltime distributions from
1288 synthetic conservative and “smart” tracer tests in streams. *Water Resources Research*
1289 47:W07510 (doi:10.1029/2010WR009927).

1290 Maier, H.S., and K.W.F. Howard. 2011. Influence of oscillating flow on hyporheic zone
1291 development. *Ground Water* 49(6):830-844.

1292 Malcolm, I.A., A.F. Youngson, and C. Soulsby. 2003. Survival of salmonid egg in a degraded
1293 gravel-bed stream: Effects of groundwater-surface water interactions. *River Research and*
1294 *Applications* 19(4):303-316.

1295 Mallard, F., J.L. Reygrobelle, J. Mathieu, and M. Lafont. 1994. The use of invertebrate
1296 communities to describe groundwater flow and contaminant transport in a fractured rock
1297 aquifer. *Archiv fur Hydrobiologie* 131:93-110.

1298 Mayer, P.M., P.M. Groffman, E.A. Stritz, and S.S. Kaushal. 2010. Nitrogen dynamics at the
1299 groundwater-surface water interface of a degraded urban stream. *Journal of Environmental*
1300 *Quality* 39:810-823.

1301 McClain, M.E., E.W. Boyer, C.L. Dent, S.E. Gergel, N.B. Grimm, P.M. Groffman, S.C. Hart,
1302 J.W. Harvey, C.A. Johnston, E. Mayorga, W.H. McDowell, and G. Pinay. 2003.

1303 Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic
1304 ecosystems. *Ecosystems* 6:301-312.

1305 McCutchan, J.H., Jr., J.F. Saunders III, A.L. Pribyl, and W.M. Lewis Jr. 2003. Open-channel
1306 estimation of denitrification. *Limnology and Oceanography: Methods* 1:74-81.

1307 Mitsch, W.J., L. Zhang, K.C. Stefanik, A.M. Nahlik, C.J. Anderson, B. Bernal, M. Hernandez,
1308 and K. Song. 2012. Creating wetlands: Primary succession, water quality changes and self
1309 design over 15 years. *BioScience* 62(3):237-250.

1310 Mulholland, P.J., and D.L. DeAngelis. 2000. Surface-subsurface exchange and nutrient spiraling.
1311 pp. 149-166, *In* J.B. Jones and P.J. Mulholland (Eds.). *Streams and Ground Waters*.
1312 Academic Press, San Diego. 425 pp.

1313 Mulholland, P.J., H.M. Valett, J.R. Webster, S.A. Thomas, L.W. Cooper, S.K. Hamilton, and
1314 B.J. Peterson. 2004. Stream denitrification and total nitrate uptake rates measured using a
1315 field ¹⁵N tracer addition approach. *Limnology and Oceanography*, 49(3):809-820.

1316 Mulholland, P.J., A.M. Helton, G.C. Poole, R.O. Hall, Jr., S.K. Hamilton, B.J. Peterson, J.L.
1317 Tank, L.R. Ashkenas, L.W. Cooper, C.N. Dahm, W.K. Dodds, S.E.G. Findlay, S.V. Gregory,
1318 N.B. Grimm, S.L. Johnson, W.H. McDowell, J.L. Meyer, H.M. Valett, J.R. Webster, C.P.
1319 Arango, J.J. Beaulieu, M.J. Bernot, A.J. Burgin, C.L. Crenshaw, L.T. Johnson, B.R.
1320 Niederlehner, J.M. O'Brien, J.D. Potter, R.W. Shiebley, D.J. Sobota, and S.M. Thomas.
1321 2008. Stream denitrification across biomes and its response to anthropogenic nitrate loading.
1322 *Nature* 452:202-206.

1323 O'Connor, B.L., and J.W. Harvey. 2008. Scaling hyporheic exchange and its influence on
1324 biogeochemical reactions in aquatic ecosystems. *Water Resources Research* 44:W12423
1325 (doi:10.1029/2008WR007160).

- 1326 Odum, E.P. 1971. *Fundamentals of Ecology*. 3rd Ed. W.B. Saunders, Philadelphia. 574 pp.
- 1327 Olsen, D.A., and C.R. Townsend. 2003. Hyporheic community composition in a gravel-bed
1328 stream: Influence of vertical hydrological exchange, sediment structure and
1329 physicochemistry. *Freshwater Biology* 48:1363-1378.
- 1330 Opdyke, M.R., M.B. David, and B.L. Rhoads. 2006. Influence of geomorphological variability in
1331 channel characteristics on sediment denitrification in agricultural streams. *Journal of*
1332 *Environmental Quality* 35:2103-2112.
- 1333 Orghidan, T. 1959. Ein neuer Lebensraum des unterirdischen Wassers, der hyporheische Biotop.
1334 *Archiv fur Hydrobiologie* 55:392-414. (Translated and reprinted in 2010 as: A new habitat of
1335 subsurface waters: The hyporheic biotope. *Archiv fur Hydrobiologie* 176(4):291-302).
- 1336 Packman, A.I., and K.E. Bencala. 2000. Modeling surface-subsurface hydrologic interactions.
1337 pp.45-80, *In* J.B. Jones and P.J. Mulholland (Eds.). *Streams and Ground Waters*. Academic
1338 Press, San Diego. 425 pp.
- 1339 Packman, A.I., M. Salehin, and M. Zaramella. 2004. Hyporheic exchange with gravel beds:
1340 Basic hydrodynamic interactions and bedform-induced advective flows. *Journal of Hydraulic*
1341 *Engineering (ASCE)*, 130(7):647-656.
- 1342 Palmer, M.A., R.F. Ambrose, and L.N. Poff. 1997. Ecological theory and community restoration
1343 ecology. *Restoration Ecology* 5:291-300.
- 1344 Peterson, B.J., W.M. Wollheim, P.J. Mulholland, J.R. Webster, J.L. Meyer, J.L. Tank, E. Marti,
1345 W.B. Bowden, H.M. Valett, A.E. Hershey, W.H. McDowell, W.K. Dodds, S.K. Hamilton, S.
1346 Gregory, and D.D. Morrall. 2001. Control of nitrogen export from watersheds by headwater
1347 streams. *Science* 292:86-90.

1348 Peyrard, D., S. Demotte, S. Sauvage, P. Namour, M. Gerino, P. Vervier, and J.M Sanchez-Perez.
1349 2011. Longitudinal transformation of nitrogen and carbon in the hyporheic zone of an N-rich
1350 stream: A combined modeling and field study. *Physics and Chemistry of the Earth* 36:599-
1351 611.

1352 Pinay, G., T.C. O'Keefe, R.T. Edwards, and R.J. Naiman. 2009. Nitrate removal in the hyporheic
1353 zone of a salmon river in Alaska. *River Research and Applications* 25:367-375.

1354 Poole, G.C. J.A. Stanford, S.W. Running, and C.A. Frissell. 2006. Multiscale geomorphic drivers
1355 of groundwater flow paths: Subsurface hydrologic dynamics and hyporheic habitat diversity.
1356 *Journal of North American Benthological Society* 25(2):288-303.

1357 Poole, G.C., S.J. O'Daniel, K.L. Jones, W.W. Woessner, E.S. Bernhardt, A.M. Helton, J.A.
1358 Stanford, B.R. Boer, and T.J. Beechie. 2008. Hydrologic spiraling: The role of multiple
1359 interactive flow paths in stream ecosystems. *River Research and Applications* 24:1018-1031.

1360 Powell, K.L., and V. Bouchard. 2010. Is denitrification enhanced by the development of natural
1361 fluvial morphology in agricultural headwater ditches? *Journal of the North American*
1362 *Benthological Society* 29(2):761-772.

1363 Pringle, C.M., and F.J. Triska. 2000. Emergent biological patterns and surface-subsurface
1364 interactions at landscape scales. pp. 167-193, *In* J.B. Jones and P.J. Mulholland (Eds.).
1365 *Streams and Ground Waters*. Academic Press, San Diego. 425 pp.

1366 Puckett, L.J., C. Zamora, H. Essaid, J.T. Wilson, H.M. Johnson, M.J. Brayton, and J.R. Vogel.
1367 2008. Transport and fate of nitrate at the ground-water/surface-water interface. *Journal of*
1368 *Environmental Quality* 37:1034-1050.

- 1369 Ranalli, A.J., and D.L. Macalady. 2010. The importance of the riparian zone and in-stream
1370 processes in nitrate attenuation in undisturbed and agricultural watersheds: A review of the
1371 scientific literature. *Journal of Hydrology* 389:406-415.
- 1372 Rehg, K.J., A.I. Packman, and J. Ren. 2005. Effects of suspended sediment characteristics and
1373 bed sediment transport on streambed clogging. *Hydrological Processes* 19:413-427.
- 1374 Reidy, C., and S. Clinton. 2004. Delineation of the Hyporheic Zone. The Water Center Fact
1375 Sheet, University of Washington. 2 pp.
- 1376 Robertson, W.D., and L.C. Merkle. 2009. In-stream bioreactor for agricultural nitrate treatment.
1377 *Journal of Environmental Quality* 38:230-237.
- 1378 Robertson, A.L., and P.J. Wood. 2010. Ecology of the hyporheic zone: Origins, current
1379 knowledge and future directions. *Archiv fur Hydrobiologie* 176(4):279-289.
- 1380 Runkel, R.L., D.M. McKnight, and H. Rajaram. 2003. Modeling hyporheic zone processes.
1381 *Advances in Water Science* 26:901-905.
- 1382 Schipper, L.A., A.B. Cooper, C.G. Harfoot, and W.J. Dyck. 1993. Regulators of denitrification
1383 in an organic riparian soil. *Soil Biology and Biochemistry* 25(7):925-933.
- 1384 Seitzinger, S., J.A. Harrison, J.K. Bohlke, A.F. Bouwman, R. Lowrance, B. Peterson, C. Tobias,
1385 and G. Van Drecht. 2006. Denitrification across landscapes and waterscapes: A synthesis.
1386 *Ecological Applications* 16(6):2064-2090.
- 1387 Shields, F.D., R.R. Copeland, P.C. Klingeman, M.W. Doyle, and A. Simon. 2003. Design for
1388 stream restoration. *Journal of Hydraulic Engineering (ASCE)* 129(8):575-584.
- 1389 Silgram, M., A. Williams, R. Waring, I. Neumann, A. Hughes, M. Mansour, and T. Beslen.
1390 2005. Effectiveness of the Nitrate Sensitive Areas Scheme in reducing groundwater

1391 concentrations in England. *Quarterly Journal of Engineering Geology and Hydrogeology*
1392 38(2):117-127.

1393 Smith, J., M. Bonell, J. Gilbert, W.H. McDowell, E.A. Sudicky, J.V. Turner, and R.C. Harris.
1394 2008. Groundwater-surface water interactions, nutrient fluxes and ecological response in
1395 river corridors: Translating science into effective environmental management. *Hydrological*
1396 *Processes* 22:151-157.

1397 Smith, J.W.N., B.W.J. Surridge, T.H. Haxton, and D.N. Lerner. 2009. Pollutant attenuation at the
1398 groundwater-surface water interface: A classification scheme and statistical analysis using
1399 national-scale nitrate data. *Journal of Hydrology* 369:392-402.

1400 Sophocleous, M. 2002. Interactions between groundwater and surface water: The state of the
1401 science. *Hydrogeology Journal* 10:52-67.

1402 Stelzer, R.S., L.A. Bartsch, W.B. Richardson, and E.A. Strauss. 2011. The dark side of the
1403 hyporheic zone: Depth profiles of nitrogen and its processing in stream sediments.
1404 *Freshwater Biology* 56:2021-2033.

1405 Stewart, R.J., W.M. Wollheim, M.N. Gooseff, M.A. Briggs, J.M. Jacobs, B.J. Peterson, and C.M.
1406 Hopkinson. 2011. Separation of river-network-scale nitrogen removal among main channel
1407 and two transient storage compartments. *Water Resources Research* 47:W00j10
1408 (doi:10.1029/2010WR009896).

1409 Storey, R.G., R.R. Fulthorpe, and D.D. Williams. 1999. Perspectives and predictions on the
1410 microbial ecology of the hyporheic zone. *Freshwater Biology* 41:119-130.

1411 Storey, R.G., D.D. Williams, and R.R. Fulthorpe. 2004. Nitrogen processing in the hyporheic
1412 zone of a pastoral stream. *Biogeochemistry* 69:285-313.

1413 Stubbington, R. 2012. The hyporheic zone as an invertebrate refuge: A review of variability in
1414 space, time, taxa and behaviour. *Marine and Freshwater Research* 63:293-311.

1415 Stutter, M.I., W.J. Chardon, and B. Kronvang. 2012. Riparian buffer strips as a multifunctional
1416 management tool in agricultural landscapes: Introduction. *Journal of Environmental Quality*
1417 41:297-303.

1418 Sweeney, B.W., T.L. Bott, J.K. Jackson, L.A. Kaplan, J.D. Newbold, L.J. Standley, W.C.
1419 Hession, and R.J. Horwitz. 2004. Riparian deforestation, stream narrowing, and loss of
1420 stream ecosystem services. *Proceedings of the National Academy of Science* 101(39):14132-
1421 14137.

1422 Thibodeaux, L.J., and J.D. Boyle. 1987. Bedform-generated convective transport in bottom
1423 sediment. *Nature* 325:341-343.

1424 Triska, F.J., V.C. Kennedy, R.J. Avanzino, G.W Zellwegger, and K.E. Bencala. 1989a. Retention
1425 and transport of nutrients in a third-order stream: Channel processes. *Ecology* 70:1877-1892.

1426 Triska, F.J., V.C. Kennedy, R.J. Avanzino, G.W Zellwegger, and K.E. Bencala. 1989b.
1427 Retention and transport of nutrients in a third-order stream in northwestern California:
1428 Hyporheic processes. *Ecology* 70:1893-1905.

1429 Triska, F.J., J.H. Duff, and R.J. Avanzino. 1993. The role of water exchange between a stream
1430 channel and its hyporheic zone in nitrogen cycling at the terrestrial-aquatic interface.
1431 *Hydrobiologia* 252:167-184.

1432 Triska, F.J., J.H. Duff, R.W. Sheibley, A.F. Jackman, and R.J. Avanzino. 2007. DIN retention-
1433 transport through four hydrologically connected zones in a headwater catchment of the upper
1434 Mississippi River. *Journal of the American Water Resources Association* 43(1):60-71.

1435 van Breeman, N., E.W Boyer, C.L. Goodale, N.A. Jaworski, K. Paustian, S.P. Seitzinger, K.
1436 Lathja, B. Mayer, D. van Dam, R.W. Howarth, K.J. Nadelhoffer, M. Eve, and G. Billen.
1437 2002. Where did all the nitrogen go? Fate of nitrogen inputs to large watersheds in the
1438 northeastern U.S.A. *Biogeochemistry* 57/58:267-293.

1439 van Grinsven, M., A. Mayer, and C. Huckins. 2012. Estimation of streambed groundwater fluxes
1440 associated with coaster brook trout spawning habitat. *Ground Water* 50(3):432-441.

1441 Vaux, W.G. 1968. Intragravel flow and interchange of water in a streambed. *Fisheries Bulletin*
1442 66(3):479-489.

1443 Vidon, P. 2010. Riparian zone management and environmental quality: A multi-contaminant
1444 challenge. *Hydrological Processes* 24:1532-1535.

1445 Vidon, P., C. Allan, D. Burns, T.P. Duval, N. Gurwick, S. Inamdar, R. Lowrance, J. Okay, D.
1446 Scott, and S. Sebestyen. 2010. Hot spots and hot moments in riparian zones: Potential for
1447 improved water quality management. *Journal of the American Water Resources Association*
1448 46(2):278-298.

1449 Ward, A.S., M.N. Gooseff, and P.A. Johnson. 2011. How can subsurface modifications in
1450 hydraulic conductivity be designed as stream restoration structures? Analysis of Vaux's
1451 conceptual models to enhance hyporheic exchange. *Water Resources Research* 47:W08512
1452 (doi:10.1029/2010WR010028).

1453 Webb, B.W., D.M. Hannah, D. Moore, L.E. Brown, and F. Nobilis. 2008. Recent advances in
1454 stream and river temperature research. *Hydrological Processes* 22:902-918.

1455 Webster, J.R., and B.C. Patten. 1979. Effects of watershed perturbation on stream potassium and
1456 calcium dynamics. *Ecological Monographs* 49:51-72.

1457 Weigelhofer, G., J. Fuchsberger, B. Teufl, N. Welti, and T. Hein. 2012. Effects of riparian forest
1458 buffers on in-stream nutrient retention in agricultural catchments. *Journal of Environmental*
1459 *Quality* 41(2):373-379.

1460 Welti, N., E. Bondar-Kunze, G. Singer, M. Tritthart, S. Zechmeister-Boltenstern, T. Hein, and G.
1461 Pinay. 2012. Large-scale controls on potential respiration and denitrification in riverine
1462 floodplains. *Ecological Engineering* 42:73-84.

1463 Westhoff, M.C., M.N. Gooseff, T.A. Bogaard, and H.H.G. Savenije. 2011. Quantifying
1464 hyporheic exchange at high spatial resolution using natural temperature variations along a
1465 first-order stream. *Water Resources Research* 47:W10508 (doi:10.1029/2010WR009767).

1466 White, D.S. 1993. Perspectives on defining and delineating hyporheic zones. *Journal of the*
1467 *North American Benthological Society* 12:61-69.

1468 Williams, D.D. 1993. Nutrient and flow vector dynamics at the hyporheic/groundwater interface
1469 and their effects on the interstitial fauna. *Hydrobiologia* 251:185-198.

1470 Williams, D.D., and H.B.N. Hynes. 1974. The occurrence of benthos deep in the substratum of a
1471 stream. *Freshwater Biology* 4:233-256.

1472 Williams, D.D., C.M. Febria, and J.C.Y. Wong. 2010. Ecotonal and other properties of the
1473 hyporheic zone. *Archiv fur Hydrobiologia* 176(4):349-364.

1474 Winter, T.C. 2000. Interaction of ground water and surface water. pp. 15-20, *In Proceedings of*
1475 *the Ground-Water/Surface-Water Interactions Workshop*. EPA/542/R-00/007, U.S.
1476 Environmental Protection Agency, Washington, DC. 200 pp.

1477 Worman, A., A.I Packman, H. Johansson, and K. Jonsson. 2002. Effect of flow-induced
1478 exchange in hyporheic zones on longitudinal transport of solutes in streams and rivers. *Water*
1479 *Resources Research* 38(1):1001 (doi: 10.1029/2001WR000769).

1480 Wroblicky, G.J., M.E. Campana, H.M. Valett, and C.N. Dahm. 1998. Seasonal variation in
1481 surface-subsurface water exchange and lateral hyporheic area of two stream-aquifer systems.
1482 Water Resources Research 34:317-328.

1483 Zarnetske, J.P, R. Haggerty, S.M. Wondzell, and M.A. Baker. 2011. Dynamics of nitrate
1484 production and removal as a function of residence time in the hyporheic zone. Journal of
1485 Geophysical Research 116:G01025 (doi:10.1029/2010JG001356).

1486 Zlotnik, V.A., M.B. Cardenas, and D. Toundykov. 2011. Effects of multi-scale anisotropy on
1487 basin and hyporheic groundwater flow. Ground Water 49(4):576-583.

1488

1489 **List of Figures**

1490 Figure 1. The hyporheic zone

1491 Figure 2. Diverse subsurface flowpaths (adapted from Poole et al. 2008): paths range from very
1492 short and shallow (s. to min.) to those that are very long (mos. to yrs.). Temporally longer
1493 pathways tend to traverse physically longer subsurface pathways.

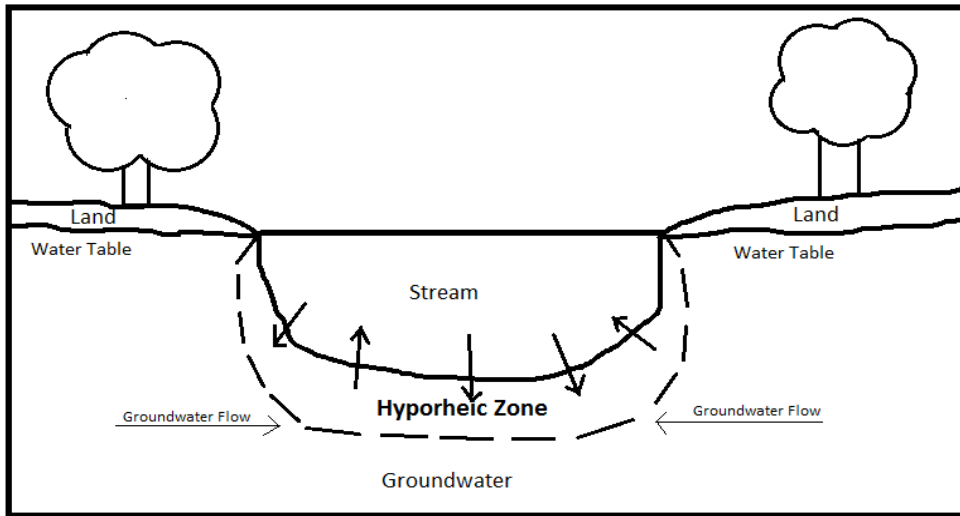
1494 Figure 3. Micro-pressure effects on hyporheic flow, caused by a partially embedded log in a
1495 gravel-bed riffle (adapted from Boulton 2007)

1496 Figure 4. Hyporheic flowpaths through a riffle (adapted from Boulton 2007)

1497

1498

1499



1500

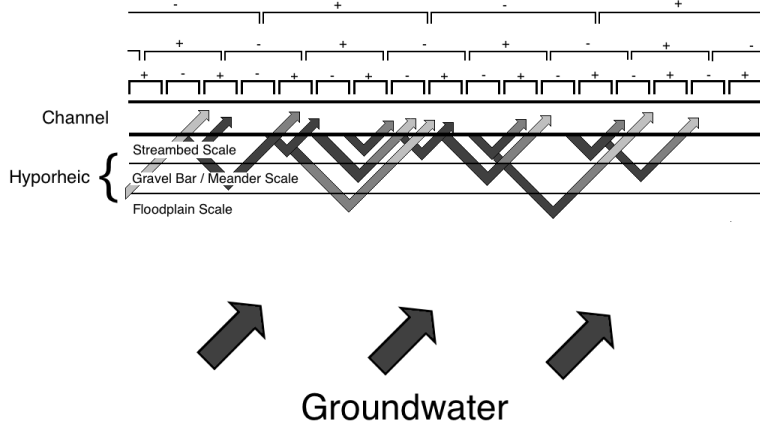
1501

1502

1503

Figure 1. The hyporheic zone

1504



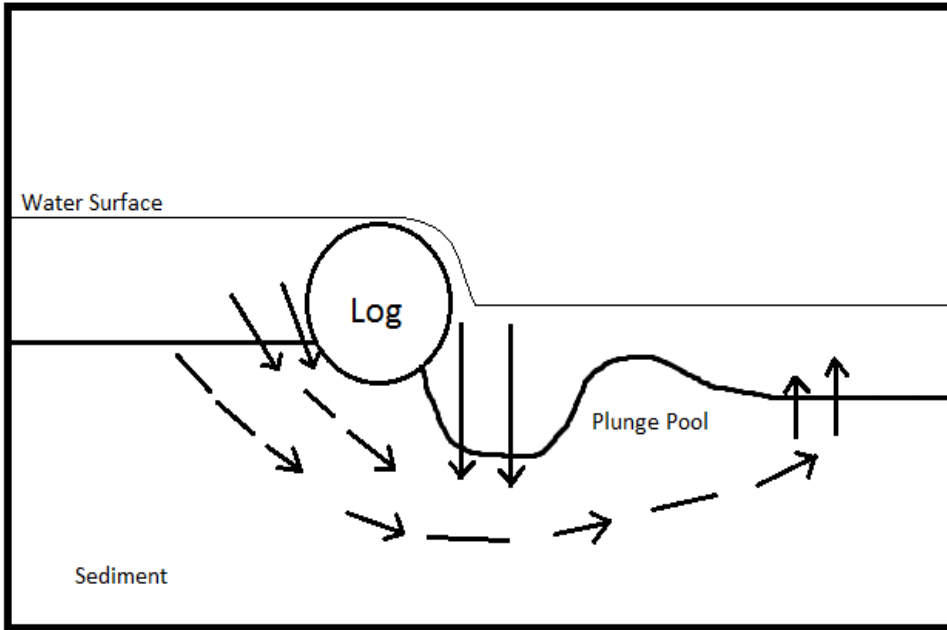
1505

1506

1507 Figure 2. Diverse subsurface flowpaths (adapted from Poole et al. 2008): paths range from very
1508 short and shallow (s. to min.) to those that are very long (mos. to yrs.). Temporally longer
1509 pathways tend to traverse physically longer subsurface pathways. Groundwater controls the
1510 overall directionality of flow.

1511

1512
1513
1514

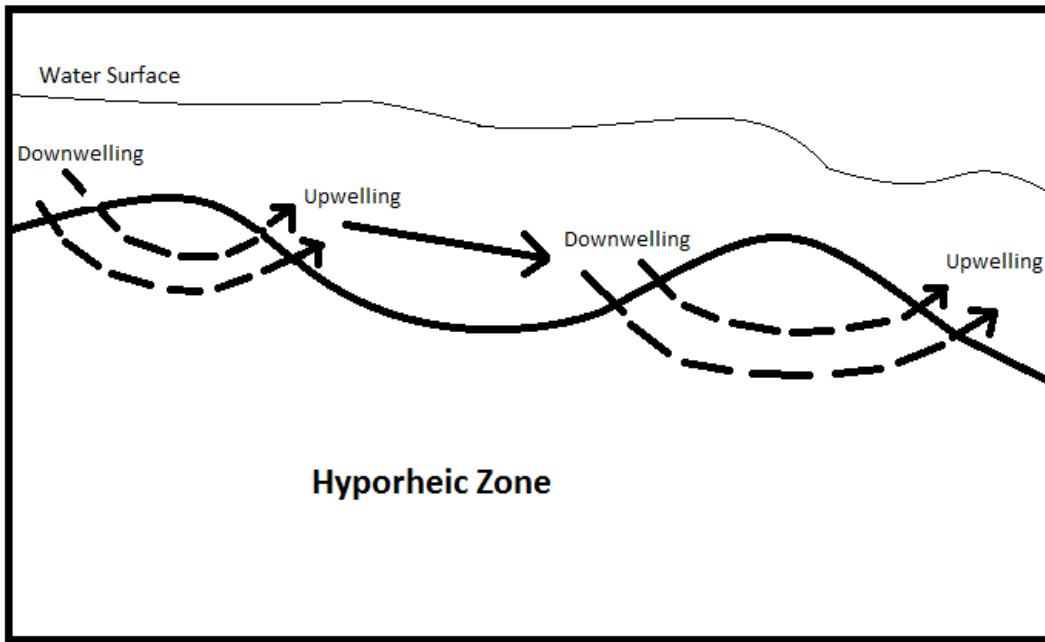


1515
1516
1517
1518
1519

Figure 3. Micro-pressure effects on hyporheic flow, caused by a partially embedded log in a gravel-bed riffle (adapted from Boulton 2007)

1520

1521



1522

1523

1524

1525

Figure 4. Hyporheic flowpaths through a riffle (adapted from Boulton 2007)