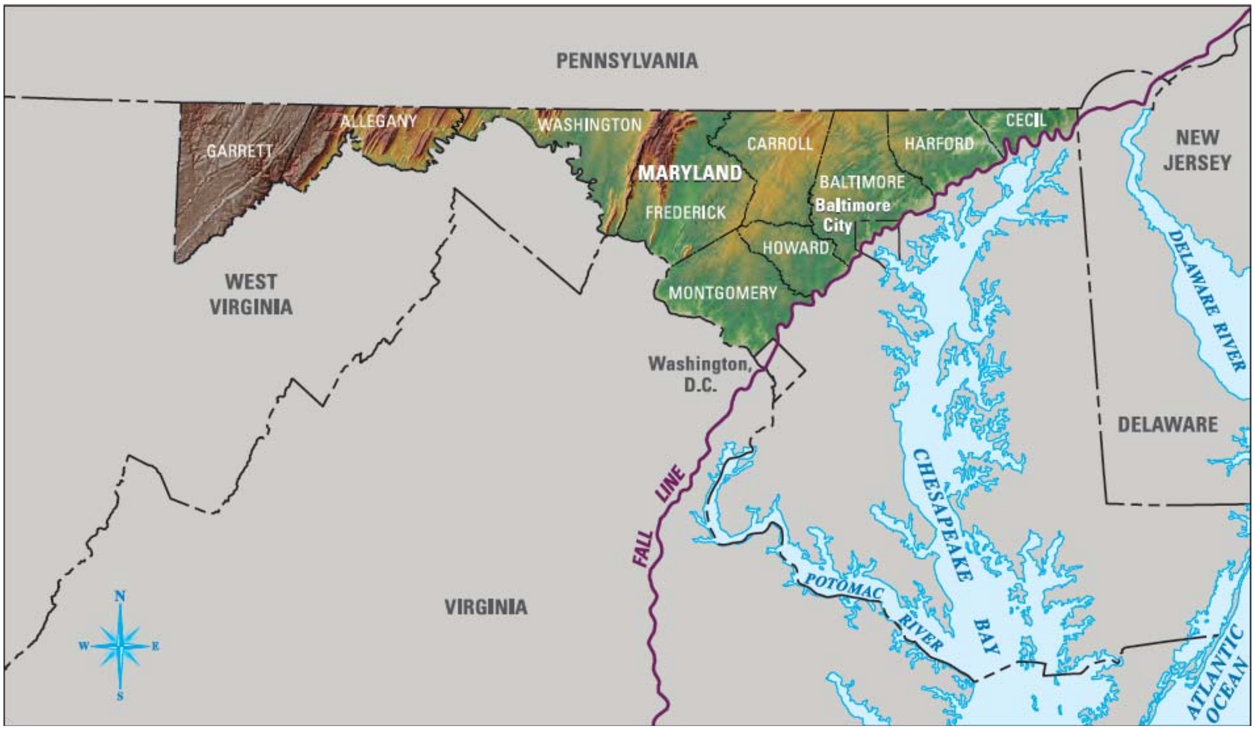
ECOLOGICAL RESPONSES TO FLOW ALTERATION: A LITERATURE REVIEW WITHIN THE CONTEXT OF THE MARYLAND HYDROECOLOGICAL INTEGRITY ASSESSMENT.

A CONTRIBUTION TO THE COMPREHENSIVE ASSESSMENT OF WATER SUPPLY IN THE REGION UNDERLAIN BY FRACTURED ROCK IN MARYLAND.



Maryland Department of Natural Resources
Resource Assessment Service
Monitoring and Non-Tidal Assessment Division
RAS-MANTA-AIM-13-01

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ECOLOGICAL RESPONSES TO FLOW ALTERATION: A LITERATURE REVIEW WITHIN THE CONTEXT OF THE MARYLAND HYDROECOLOGICAL INTEGRITY ASSESSMENT.

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EXECUTIVE SUMMARY

Literature on flow-ecology relationships, particularly as they relate to flow regime alteration from impoundments and water withdrawal, were reviewed within the context of management questions that guide Maryland's Hydroecological Integrity Assessment. Gaining insight into these questions by examining the success and shortcomings of past studies will help; 1) guide the monitoring and assessment of flow-ecology relationships, 2) interpret biological responses often influenced by multiple factors, 3) evaluate the efficacy of current flow-by standards, and 4) improve the tools available to water and natural resource managers used to conserve aquatic habitat and biota. Narrative and illustrative examples of hypothetical and empirical flow-ecology relationships are included to further elucidate probable biological responses to flow alteration.

We found 124 sources with qualitative associations or quantitative data on flow-ecology, many of which were part of literature reviews on flow alteration. Fish were the dominant response organism studied, followed by benthic macroinvertebrates and freshwater mussels, although some studies considered multiple response organisms. Physical habitat and hydrologic conditions were frequently included in studies as they related to flow alteration and biological response. Riparian vegetation and algae were excluded because regulatory triggers do not currently exist in Maryland for these faunal groups. In addition to aforementioned sources of ecological data, studies of hydrology, thermal regime, sampling design and analysis, and environmental flow techniques and recommendations were reviewed.

Overall, ecological response to anthropogenic-induced flow alteration was overwhelmingly detrimental. Stream fish and freshwater mussels appeared to respond adversely to flow alteration, regardless of the mechanism. Benthic macroinvertebrate responses were typically negative, but occasionally showed inconclusive or positive response. The predominant source of anthropogenic-induced flow alteration identified was impoundment, followed by water withdrawal, land use change, and climate. A few studies considered more than one alteration mechanism. Research into the effects of groundwater withdrawal on biological communities was more prevalent than studies of surface water withdrawals. Literature on impoundments was usually in relation to hydroelectric or flood control projects or lacked detail about its use as a public water supply. Some studies also reported experimental reductions in flow, which can be assumed to represent the potential effect of water withdrawal.

While this literature review focused on flow alteration mechanisms associated with impoundments and water withdrawals, the overall results were in accordance with the findings of other reviews that investigated biological response to flow alteration broadly. Anthropogenic alteration of the natural flow regime results in negative effects to stream biota. The magnitude of biological response typically reflects the magnitude of flow alteration, although some organisms declined regardless of the level of alteration. Sources of information on environmental flow techniques and recommendations provide a variety of prescriptive and experimental water management options that could be used to conserve streams with high ecological integrity and water supplies. In addition, sources on flow-ecology study design and analysis should be useful to inform the monitoring and assessment of streams in Maryland as the potential effects to aquatic biology from water withdrawal are investigated.

INTRODUCTION

Flow is regarded as a master variable that shapes and sustains stream habitat and biodiversity. Flow regimes vary naturally both spatially and temporally in response to climate and landscape level controls. These aspects make all flow regimes and their aquatic communities' unique (Poff et al. 1997). Stream organisms differ in their environmental tolerances and requirements, and thus any change in resource condition from altered flows can influence organism behavior and biotic interactions (Welcomme et al. 2006). Streamflow is altered at regional and local scales by human behavior, such as patterns of land use that lead to changes in infiltration and runoff rates, impoundment of streams for flood control, hydropower generation, or water supply, and water extraction for consumption (Wang et al. 1997, Poff et al.1997, Lloyd et al. 2003, Graf 2006). As a result, the condition of streams and the biota that have adapted in them are a reflection of the quantity, quality, timing, and variability of water (Bunn & Arthington 2002, Lytle & Poff 2004).

Globally and locally there is a growing interest in preserving streamflow to conserve aquatic ecosystems and biodiversity while maintaining sustainable water supplies for human use (Postel 2000, Poff et al. 2003, Arthington et al. 2006, Richter 2009). This effort has been accelerated due to the ubiquitous alteration of flowing waters and impairment to their biota due to dams, diversions, and abstractions (Dewson et al. 2007, Murchie et al. 2008), urbanization (Poff & Zimmerman 20100), water use and climate change projections (Xenopoulos & Lodge 2006, Chu et al. 2008) and advances in analysis and assessment techniques (Underwood 1994, Richter et al. 1996, Anderson et al. 2000, Poff et al. 2010). In Maryland, recent and severe droughts, in addition to population growth and water demand projections, created concern over water supply sustainability. These factors led to a series of recommendations by a multidisciplinary commission assembled to manage and protect water resources for human and aquatic resource needs (Wolman 2008). To meet the commissions' recommendations, the potential effects of water withdrawals on aquatic life and habitat are currently being assessed in concert with various studies on the hydrology of streams underlain by fractured bedrock in Maryland (Fleming et al. 2012).

Although the effects of impoundments on flow regimes have been well documented, these studies generally focused on regulated flow regimes of large dams, the response of aquatic species or communities to dam operation, and the influence of dam operation on instream habitat (Bain et al. 1988, Morgan et al. 1991, Kinsolving & Bain 1993, Layzer et al. 1993, Sheidegger & Bain 1995, Travnichek et al. 1995, Freeman et al. 2001, Marchetti & Moyle 2001, Bednarek & Hart 2005, Galbraith et al. 2010). How aquatic species and communities respond to anthropogenic-induced hydrologic alteration driven by surface and groundwater withdrawals relative to the influence exerted by other natural and anthropogenic factors is poorly understood. Therefore, an evaluation of water withdrawal impacts should include these factors while examining its influence on stream hydrology and biota. To be scientifically and socially defensible, such studies must employ rigorous sampling designs with clear objectives that can account for uncertainty while providing adequate spatial and temporal coverage (Cottingham et al. 2005, Murchie et al. 2008, Souchon et al. 2008). Additionally, an interdisciplinary approach (e.g., Jacobson et al. 2008, Waco & Taylor 2010) to the assessment of hydroecological integrity is undoubtedly necessary as the relationship between streamflow and groundwater must be defined in order to develop management strategies that minimize the stress to stream ecosystems from excessive water removal.

The primary goal of this literature review is to assimilate and describe results from previous studies as they pertain to management questions that are the framework for a assess hydroecological integrity assessment of Maryland’s streams. Gaining insight into these questions by examining past studies will help; 1) guide the monitoring and assessment of flow-ecology relationships, 2) interpret biological responses often influenced by multiple factors, 3) evaluate the efficacy of current flow-by standards, and 4) improve the tools available to water and natural resource managers used to conserve aquatic habitat and biota. Narrative and illustrative examples of hypothetical and empirical flow-ecology relationships adapted from various studies are included to elucidate the information presented in this literature review.

METHODS

Literature searches were primarily conducted using publisher databases (BioOne, Blackwell, EBSCOhost, ScienceDirect, and Wiley Online Library) and GoogleScholar. The following keywords were used in various combinations: biological integrity, environmental flow, drought, fish, flow alteration, flow regime, groundwater, hydrologic alteration, invertebrate, macroinvertebrate, minimum flow, freshwater mussel, streamflow, and withdrawal. Since management questions (Stranko et al. 2011) focus on developing better strategies to protect stream resources from the potential effects of excessive water withdrawal (Wolman 2008), literature on the response of biota to high flows was not actively sought. Other pertinent sources of information were found by inspecting the references within literature reviews (e.g., Sophocleous 2002, Lake 2003, Lloyd et al. 2003, Tharme 2003, Monk et al. 2007, Muchie et al. 2008, Poff & Zimmerman 2010, McManamay et al. 2011). When possible, we acquired electronic, full-text copies, although some literature could only be found as paper documents.

The information within all scientific articles obtained was reviewed for their applicability in providing answers to the hydroecological integrity assessment management questions (Table 1). A spreadsheet was then populated with characteristics useful to summarize and stratify literature based on ecological and hydrologic attributes. The context of flow-ecology literature was recorded in this spreadsheet to distinguish between studies focused on ecological or hydrologic responses, study design and data analysis, and environmental flows. When discernable, the primary flow component (e.g., regime, magnitude, variation) measured in each study along with the source of flow alteration (e.g., impoundment or climate) was recorded. Studies were also categorized by biological response organism. Because the objectives of this literature review did not include a quantitative evaluation of prior studies, information on spatial extent, temporal duration, or direction and magnitude of biological response was not analyzed, although it was noted where appropriate to elucidate flow-ecology relationships.

TABLE 1. PROPOSED MANAGEMENT QUESTIONS TO ADDRESS IN THE MARYLAND HYDROECOLICAL INTEGRITY ASSESSMENT.

1. Which Maryland stream species (including rare, threatened, endangered, game, invasive, and migratory species) and ecosystems are most/least sensitive to flow alterations? Are there specific biological indicators of water withdrawal?
2. Which aspects of flow regimes have the most/least influence on stream species and ecosystems? How do alterations in flow affect species and ecosystems? Can the specific mechanisms responsible for flow alterations be determined and described?
3. Which components of flow-ecology relationships are most/least affected by surface (intake and impoundment) and groundwater withdrawals?
4. What relationship between surface and groundwater withdrawals and stream ecological integrity can be established?
5. For past and future water-uses, how have/might surface and groundwater withdrawals impact individual species and ecosystems (include scenarios such as: flooding, drought, increasing population, cumulative impacts, climate change, confounding factors, etc.)?
6. What spatial and seasonal aspects of flow need to be maintained for specific streams, including under drought conditions to ensure the protection of stream species and ecosystems?
7. Is additional research/monitoring needed?

RESULTS & DISCUSSION

In addition to eight hydroecological reviews, a total of 124 sources were found that provided qualitative associations or quantitative data on flow-ecology relationships and biological responses to flow alteration (Appendix I). Fish were the predominant biological response organism (N=34) of focus in most studies, followed by benthic macroinvertebrates (N=16) and freshwater mussels (N=12) (Appendix II). Multiple response organisms were used in four studies. Biological response was measured by indicator species presence, assemblage composition and structure, or community indices. Suitability or condition of physical habitat in relation to the level of flow alteration and requirements of response organism were also commonly assessed. Minimum/low flows and flow regime were the primary component studies for all three biological groups. Few studies assessed the biological response to alteration of flow regime variability.

In addition to the aforementioned sources, studies were reviewed in the categories of stream hydrology (N=27), thermal regime (N=5), sampling design and analysis (N=17), and environmental flow techniques and recommendations (N=13) (Appendix II). Sources on hydrologic alteration primarily reported indices to quantify flow regime change and ecological response or strategies to classify streams to assess flow-ecology relationships. There were fewer studies representative of flow regime alteration, minimum/low flows and hydrologic variability. Literature categorized as sampling design and analysis generally consisted of studies not directly related to flow-ecology, but instead were common techniques to assess and establish relationships. The distinction between design and analysis literature that dealt with environmental flow assessments from studies of stream hydrology that dealt with classification for study design or indices for statistical analyses from was not entirely clear. Environmental flow literature was typically narrative and useful for proposing water management, ecosystem restoration strategies, or establishing foundational flow-ecology relationships.

The response of stream biota to anthropogenic-induced flow alterations was overwhelmingly harmful regardless of faunal group (Appedix III). Moreover, the magnitude of flow regime alteration did not appear to greatly influence the magnitude of biological response. Stream fish and freshwater mussels responded negatively to flow alteration regardless of the mechanism of alteration. Benthic macroinvertebrate responses were typically negative, but were occasionally neutral and rarely positive. These studies were generally conducted in the southeastern and western United States. Some sources were regional while others were national and international.

The mechanisms of anthropogenic-induced flow alterations were predominantly impoundments (N=31), followed by water withdrawal (N=16), landscape alteration (N=8), and climate (N=6) (Appendix IV). Some of these studies (N=8) considered more than one flow alteration mechanism. Several sources were also vague as to the type of water withdrawal or reported a reduction in streamflow as a surrogate for withdrawal. Assessments of the potential ecological effects of groundwater withdrawals were more prevalent than assessments of surface water withdrawals, even though surface water withdrawals were associated with impoundments. The effects of groundwater withdrawals were primarily evaluated in arid lands or chalk streams, while studies on impoundments and surface withdrawals were widely distributed in geographic range. Studies of impoundments rarely mentioned whether water supply was a primary or secondary use. The prevalence of flow alteration mechanisms reviewed in this study was primarily a result of the studies' scope.

MANAGEMENT QUESTION 1: Which Maryland stream species (including rare, threatened, endangered, game, invasive, and migratory species) and ecosystems are most/least sensitive to flow alterations? Are there specific biological indicators of water withdrawal?

Maryland species-specific information on sensitivity to flow alteration was represented by just a few studies, primarily in regards to larger dams and their operation in published literature. While not directly related to water withdrawal, the institution of a minimum flow from Conowingo Dam improved the condition and growth rate of white perch, yellow perch, and channel catfish downstream of the dam (Weisberg & Burton 1993). Furthermore, this change in water management strategy also drastically increased benthic macroinvertebrate density (Weisberg et al. 1990). Similarly, Morgan et al. (1991) reported that the revised operation (reduction in low and high flows) of Brighton Dam increased benthic macroinvertebrate abundance, density, and community health downstream of the dam (Figure 1).

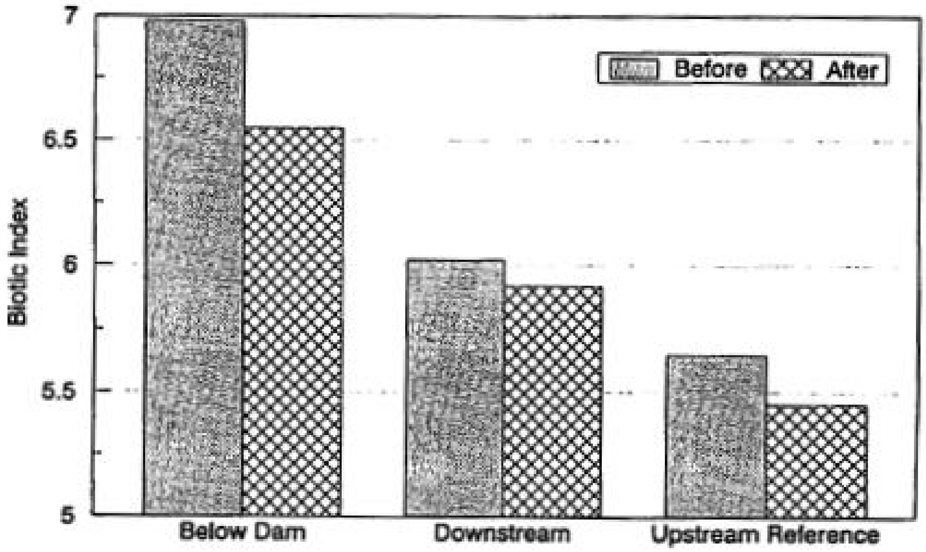

FIGURE 1. BIOTIC INDEX VALUES FOR MACROINVERTEBRATE SAMPLING STATIONS, BRIGHTON DAM. A DECLINE IN THE INDEX REPRESENTS AN IMPROVEMENT IN QUALITY. REPRODUCED FROM MORGAN, R.P., R.E. JACOBSON, S.B. WEISBERG, L.A. MCDOWELL, & H.T. WILSON. 1991. EFFECTS OF FLOW ALTERATION ON BENTHIC MACROINVERTEBRATE COMMUNITIES BELOW BRIGHTON HYDROELECTRIC DAM. JOURNAL OF FRESHWATER ECOLOGY 6: 419-429 WITH PERMISSION GRANTED BY COPYRIGHT CLEARANCE CENTER INC ON TAYLOR & FRANCIS'S BEHALF (HTTP://WWW.TANDF.CO.UK/JOURNALS).

Information on the sensitivity of rare species in Maryland to changes in flow was also lacking, likely in part because of their rarity. Species-discharge relationships were developed for most rare fish species in Maryland based on field observations of macrohabitat use versus availability (Kazyak et al. 2005). Further defining these relationships may provide an indication of a species sensitivity to flow alteration if its distribution is restricted to a narrow range of flows. Overall, the sensitivity of bass and sunfishes (Centrachidae) to flow alteration is quite variable and typically a reflection of species-specific life history traits and habitat requirements (Cooke et al. 2009). Their popularity as gamefish has in part been due to their ability to thrive in a variety of environmental conditions outside of their native range. Little detail was found on how flow regime alteration might affect migratory fishes, such as shads (Clupeidae) or American eels (but see Hightower & Sparks 2003). More general mechanisms such as dams blocking migration routes and flow reductions modifying migration timing and spawning habitat have been well documented (Cooke & Leach 2003, Jessop 2003).

Although relatively few studies have been conducted in Maryland on the potential biological affects due to flow alteration (but see Morgan & Cushman 2005), the sensitivity of species and ecosystems can be inferred in multiple ways. First, several regional hydroecological assessments investigated the response of several indicator species that are also found in Maryland (Jacobson et al. 2008, Armstrong et al. 2010, Kanno & Vokoun 2010). Secondly, wide ranging species (e.g., brook trout) with specific ecological requirements (e.g., cold water) have been studied in relation to stream hydrology (Zorn et al. 2002, Waco & Taylor 2010). Thirdly, a substantial body of literature highlights the sensitivity of traditional measures of species and communities (e.g., biological indices, functional groups, relative abundance, richness, etc.) to various types and magnitudes of flow alteration as they relate to fish (Scheidegger & Bain 1995, Freeman et al. 2001, Marchetti & Moyle 2001, Freeman & Marcinek 2006, Knight et al. 2008, Gido et al. 2010, Carlisle et al. 2010, Kanno & Vokoun 2010, Meador & Carlisle 2011), macroinvertebrates (Morgan et al. 1991, Armitage et al. 1992, Claussen et al. 1997, Wood & Armitage 2004, Bednarek & Hart 2005, Wills et al. 2006, Kennen et al. 2008, Konrad et al. 2008, DeGasperi et al. 2009, Kennen et al. 2010, Walters & Post 2011), and freshwater mussels (Hardison & Layzer 2001, Golloday et al. 2004, Gagnon et al. 2004, Haag & Warren 2008, Galbraith & Vaughn 2010).

TABLE 2. LIST OF INDICATOR SPECIES USED IN EVALUATIONS OF FLOW ALTERATION ON STREAM FISH COMMUNITIES OF THE MID-ATLANTIC.

Indicator species	Study location	Response to flow alteration
Eastern blacknose dace	Massachusetts	Decreased abundance
Brook trout	Connecticut, Mass.	None, slight decrease
Brown trout	Connecticut	Usable habitat decreased
Fallfish	Connecticut, Mass.	Usable habitat decreased, none
Tessellated darter	Connecticut	Usable habitat decreased
White sucker	Massachusetts	None

Life history traits (e.g., habitat classification) have long been used to study the effects of flow regime alteration on fish communities due to large dams (Bain et al. 1988, Kinsolving & Bain 1993, Travnichek et al. 1995, Herbert & Gelwick 2003). Life history traits provide an insightful path to study community relationships independent of species level organization and how they respond to environmental conditions, including hydrologic variation at multiple scales (Poff & Allan 1995, Welcomme et al. 2006). Unlike community-level and taxonomically-based metrics that make up indexes of biological integrity, trait classifications respond similarly to disturbance across physical and geographic boundaries (Lamaroux et al. 2002). In addition, traits provide a mechanistic approach to identifying impacts to aquatic life from anthropogenic stressors and the importance of different co-varying stressors (Wooster et al. 2011). Recently, trait-based groupings have been used as an alternative to functional groups and family-level metrics to evaluate fish community response to flow alteration due to water withdrawals with consideration to the relative influence of natural and anthropogenic factors (Freeman & Marcinek 2006, Poff et al. 2006, Armstrong et al. 2010, Kanno & Vokoun 2010). For example, Kanno & Vokoun (2010) documented fish assemblages of stream sites with high water withdrawal rates were generally composed of lower proportions of fluvial dependent fishes and greater proportions of macrohabitat generalists (Figure 2). Trait-based inquiries have also been employed to investigate the influence of flow regime on benthic macroinvertebrates and freshwater mussels (Poff et al. 2006, Galbraith et al. 2011, Wooster et al. 2011).

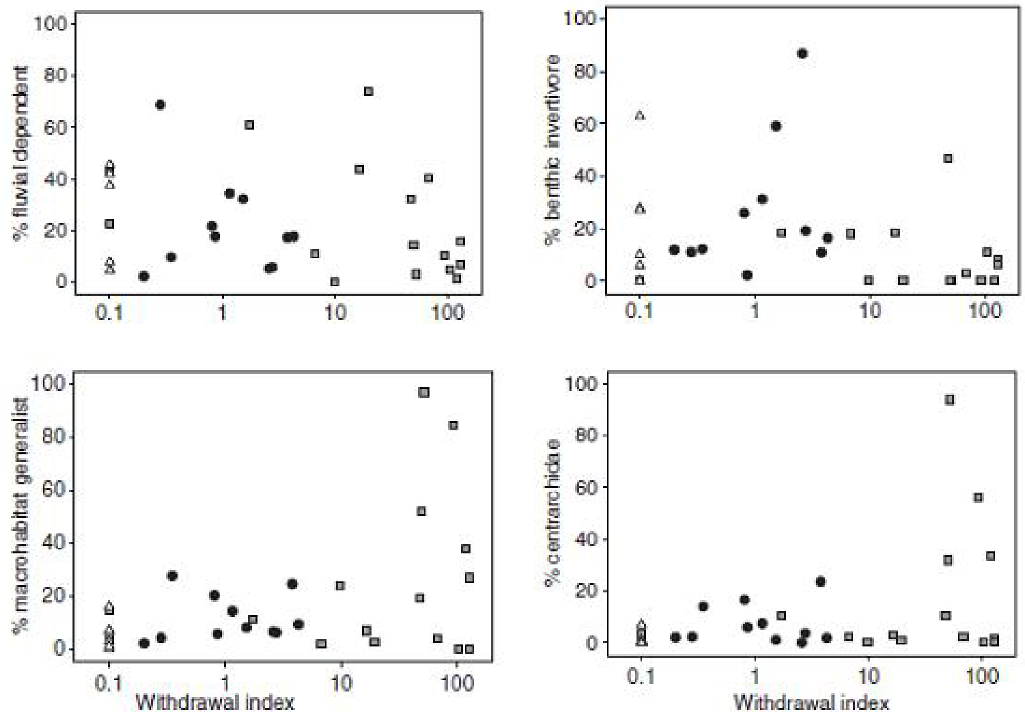

FIGURE 2. LIFE HISTORY TRAITS, FISH ASSEMBLAGE METRICS, AND THEIR RELATIONSHIP WITH WITHDRAWAL INDEX (WI) AT IMPOUNDMENT SITES (■), INTAKE SITES (●), AND REFERENCE SITES (Δ). WI VALUES WERE CALCULATED FROM THE MAXIMUM DAILY PERMITTED WITHDRAWAL DIVIDED BY THE ESTIMATED 7Q10 AND LOG X + 0.1 TRASNFORMED TO ACCOUNT FOR NO WATER WITHDRAWALS AT REFERENCE SITES. REPRODUCED FROM KANNO, Y. & J.C. VOKOUN. 2010. FISHERIES MANAGEMENT AND ECOLOGY 17: 272-283 WITH PERMISSION GRANTED BY COPYRIGHT CLEARANCE CENTER INC ON JOHN WILEY AND SONS' BEHALF.

MANAGEMENT QUESTION 2: Which aspects of flow regimes have the most/least influence on stream species and ecosystems? How do alterations in flow affect species and ecosystems? Can the specific mechanisms responsible for flow alterations be determined and described?

At a basic hydrologic level, the quantity and timing of stream flow are critical aspects that shape aquatic ecosystem structure and function. Natural flow regimes vary along temporal gradients determined by landscape characteristics (e.g., basin size, climate, geology, and topography) and are described by patterns in their hydrography (Poff et al. 1997). In addition to other factors, stream biota are strongly influenced by components of the natural flow regime (Poff & Ward 1989) that include the magnitude, frequency, duration, timing, and rate of change (Knight et al. 2008, Konrad et al. 2008). Flow regimes interact with ecosystems at multiple spatial and temporal scales, which ultimately links flow variability to the habitat and biotic assemblages present in streams (DiMaoi & Corkum 1995, Poff & Allan 1995, Biggs et al. 2005, Monk et al. 2006).

The alteration of flow regimes, conversion of flowing water to impounded habitat, fragmentation of streams in watersheds, and reductions in baseflows has significantly affected the ecological integrity of streams and aquatic species (Poff et al. 1997, Graf 2006, Poff 2009, Carlisle et al. 2011). Multiple studies have indicated greater detriment to components of stream fish communities, specifically fluvial specialists, in comparison to habitat generalists in flow altered streams (Kinsolving & Bain 1993, Travnichek et al. 1995, Herbert & Gelwick 2003). These findings have been expanded upon by examining the relative influence water withdrawal magnitudes contribute to fluvial species richness in comparison to natural and anthropogenic factors (e.g., land cover, habitat, stream size) (Armstrong et al. 2010, Kanno & Vokoun 2010). In each study, species that specialized for or were dependent upon flowing water declined in response to increasing water withdrawal rate. Estimated richness was also lower than observed richness in Georgia streams with simple surface water intakes and those below reservoirs compared to reference streams (Freeman & Marcinek 2006). Likewise, several studies associated declines in native fish richness and increases in non-native species to flow alteration and water withdrawal (Marchetti & Moyle 2001, Gido et al. 2010, Meador & Carlisle 2011). Juvenile fishes and their associated nursery habitat were highly susceptible to impacts from altered flow regimes, which consequently structured the size of adult fish populations (Scheidegger & Bain 1995, Freeman et al. 2001).

Many authors (e.g., Lloyd et al. 2003, Matthews & Marsh-Matthews 2003, Dewson et al. 2007, Monk et al. 2007, Bradford & Heinonen 2008, Murchie et al. 2008, Poff & Zimmerman 2010, McManamay et al. 2011) reviewed comparative and descriptive studies that generally indicated stream fish and invertebrate populations were negatively affected by both natural and anthropogenic-induced irregularities in both low and high flows. Recent studies in the northeastern US found metrics of a modified flow regime explained a significant portion of benthic macroinvertebrate composition (Kennen et al. 2010). Reduced variability of streamflow was also related to a loss in native fish species and riffle-specialists (Meador & Carlisle 2011) (Figure 3). These flow-ecology hypotheses have been further corroborated in other regions (Poff & Allan 1995, Clausen & Biggs 1997, Monk et al. 2006, Konrad et al. 2008). Bunn and Arthington (2002) highlight four important principles linking hydrology to stream ecosystems that illustrate the potential ecological consequences of flow regime alteration and importance of maintaining natural disturbances versus high regulated flows (Table 3).

TABLE 3. PHILOSOPHIES AND CONSEQUENCES OF STREAMFLOW ALTERATION.

1. Streamflow is a major determinant of physical habitat in streams, which in turn is a major determinant of ecosystem structure.

2. Aquatic species have evolved morphological, physiological, and behavioral strategies in direct response to natural flow regimes.

3. Maintenance of natural patterns of stream connectivity (longitudinal and lateral) is essential to the viability of many stream species.

4. The invasion of exotic and non-native species is facilitated by flow regime alteration.

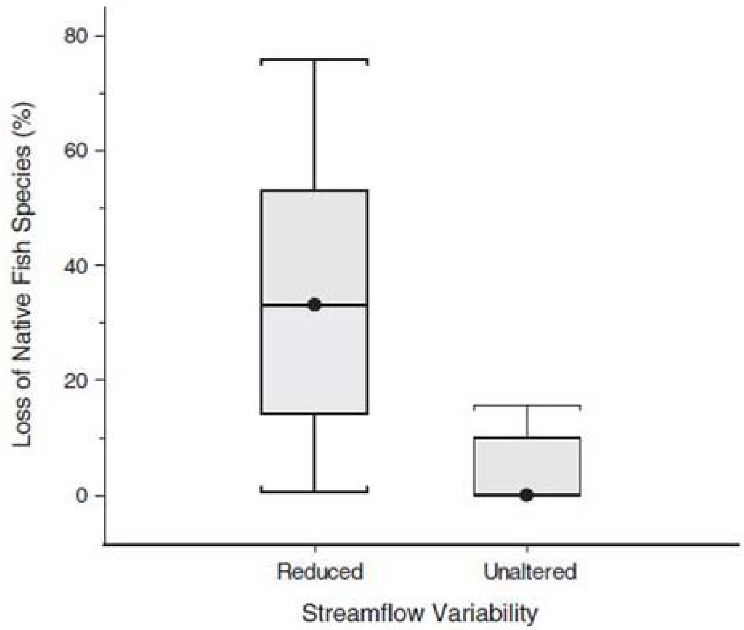

FIGURE 3. PLOT OF LOSS OF EXPECTED NATIVE FISH SPECIES RICHNESS FOR SITES IN THE EASTERN UNITED STATES CLASSIFIED AS HAVING REDUCED AND UNALTERED STREAMFLOW VARIABILITY. BOXES SHOW MEDIANS AND QUARTILES, WHISKERS INDICATE 10TH AND 90TH PERCENTILES. REPRODUCED FROM MEADOR, M.R. & D.M. CARLISLE. 2011. WITH PERMISSION GRANTED BY COPYRIGHT CLEARANCE CENTER INC ON JOHN WILEY AND SONS' BEHALF (HTTP://WWW.WILEY.COM/WILEY-BLACKWELL).

The recovery of aquatic ecosystems and species to flow alteration is highly variable, often dependent upon the magnitude, frequency, and duration of flow regime alteration, but also characteristics of organisms and communities (Lake 2003). For example, Wood & Armitage (2004) found that the benthic macroinvertebrate community in groundwater dominated streams recovered from supra-seasonal drought events after baseflow recovered with recharge of the aquifer. Recovery in aquatic communities downstream of hydroelectric dams has also been observed after the implementation of more natural flow regimes (Morgan et al. 1991, Weisberg & Burton 1993, Travnichek et al. 1995, Benarek & Hart 2005, Layzer & Scott 2006). The recovery process was more rapid in benthic macroinvertebrates, while fish and freshwater mussels took one or more years before improvement was observed. In contrast to anthropogenic mechanisms of flow alteration, recovery from natural mechanisms like drought appeared to happen more readily, as species have evolved to the frequency and magnitude of such events (Bunn & Arthington 2002, Matthews & Marsh-Matthews 2003, Dewson et al. 2007).

Groundwater interacts with surface water and is responsible for a variety of vital hydrologic and biotic processes. It generates a substantial portion of flow in headwater streams, is responsible for nutrient and mineral exchange, and stimulates stream productivity (Sophocleous 2000, Winter 2007). Power et al. (1999) reviewed the importance of groundwater to stream hydrology, habitat, and fish populations. In particular, he noted the profound influence of groundwater, including its contribution to baseflow, water temperature, and water quality, which have been highlighted in other studies. For example, Zorn et al. (2002) related brook trout distribution in Michigan to the amount of groundwater a stream received, which maintained stream flows and thermal regimes required by the aquatic community. Building on that relationship, Waco and Taylor (2010) modeled the influence of groundwater withdrawal and land use alteration on the availability of critical thermal habitat. They found that increased groundwater pumping raised water temperature, which ultimately exceeded the thermal maxima for brook trout survival. Jacobson et al. (2008) also used a habitat modeling approach to determine how populations of brown trout, fallfish, and tessellated darter in the Connecticut River would respond to alternative groundwater withdrawal scenarios. Their process illustrated how habitat availability, assuming a direct relationship to fish populations, was impacted by streamflow reductions due to groundwater pumping and alternative water management strategies that would minimize habitat flow depletion events. Finally, Gido et al. (2010) examined how decades of groundwater withdrawal in the High Plains aquifer of the Ogalla formation caused major shifts in fish assemblages. Falke et al. (2011) predicted how continued withdrawal would further fragment streams and reduce available habitat unless major reductions in pumping rates from this region were instituted. Groundwater recharge rates in this area are quite different than in Maryland, where consumptive water resource uses like irrigation are also not as common.

Benthic invertebrate taxa have been widely used to examine the effects of flow alteration on stream health because of well recognized tolerances to environmental disturbance (Claussen & Biggs 1997, Wood & Armitage 2004, Konrad et al. 2008). For example, Kennen et al. (2008) and DeGasperi et al. (2009) found that macroinvertebrate communities were impaired by high flow metrics associated with land use change. Chessman et al. (2011) observed minor, yet significant differences in communities between reference streams and streams with groundwater withdrawals of 1-20% mean annual flow. However, they concluded that the groundwater allocation did not cause site-specific biological impairment. Large, experimental flow diversions (50-90% of baseflow) caused a significant decline in the density of macroinvertebrate taxa (Wills et al. 2006) (Figure 4). These studies primarily used community and taxonomically-based metrics of stream integrity as explanatory variables, which have limited ability to distinguish mechanisms of impacts and the relative importance of multiple sources of stress. Unfortunately, trait-based inquiries into the response of benthic invertebrates to flow alteration were lacking (but see Poff et al. 2006, Wooster et al. 2011).

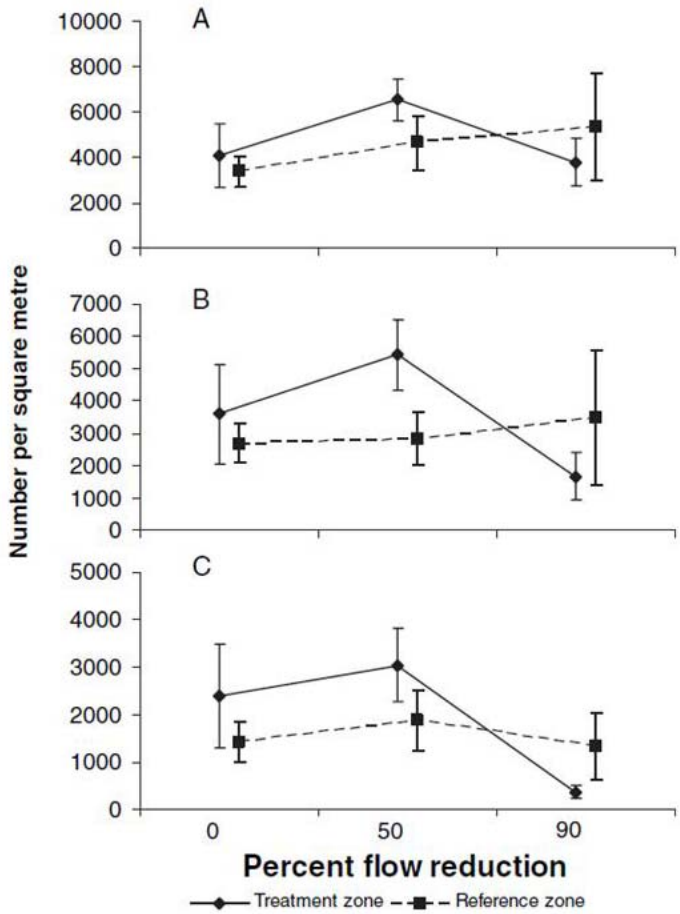

FIGURE 4. MEAN NUMBER OF INVERTEBRATES (A), INSECTS (B), AND EPT (EPHEMEROPTERA, PLECOPTERA, AND TRICOPTERA) TAXA (C) PER SQUARE METER (± 2 STANDARD ERROR) IN A DEWATERED TREATMENT ZONE AND REFERENCE ZONE. DISCHARGE IN THE REFERENCE ZONE WAS NOT ALTERED. REPRODUCED FROM WILLS, T.C., E.A. BAKER, A.J. NUHFER, & T.G. ZORN. 2006. RIVER RESEARCH AND APPLICATIONS 22: 819-836 WITH PERMISSION GRANTED BY COPYRIGHT CLEARANCE CENTER INC ON JOHN WILEY AND SONS' BEHALF (HTTP://WWW.WILEY.COM/WILEY-BLACKWELL).

The mechanisms of flow regime alteration associated with large dams are well known (Richter et al. 1996, Poff & Hart 2002, Graf 2006). In general, they reduce annual discharge, the range of daily discharge, and modify the timing of high and low flows and water temperature. The extent to which dams alter flow regimes, stream habitat, and biotic communities is highly variable and dependent upon operational factors including their size, storage capacity, water release mechanism, and primary use (e.g., hydro-power, water supply, flood control). In addition to flow alteration, they cause significant changes to geomorphologic and biological processes of rivers (Figure 5). Although the primary use of impoundments was not always clear, the presence of an impoundment appeared more influential than its operation when the primary use was for water withdrawal (i.e., public water supply).

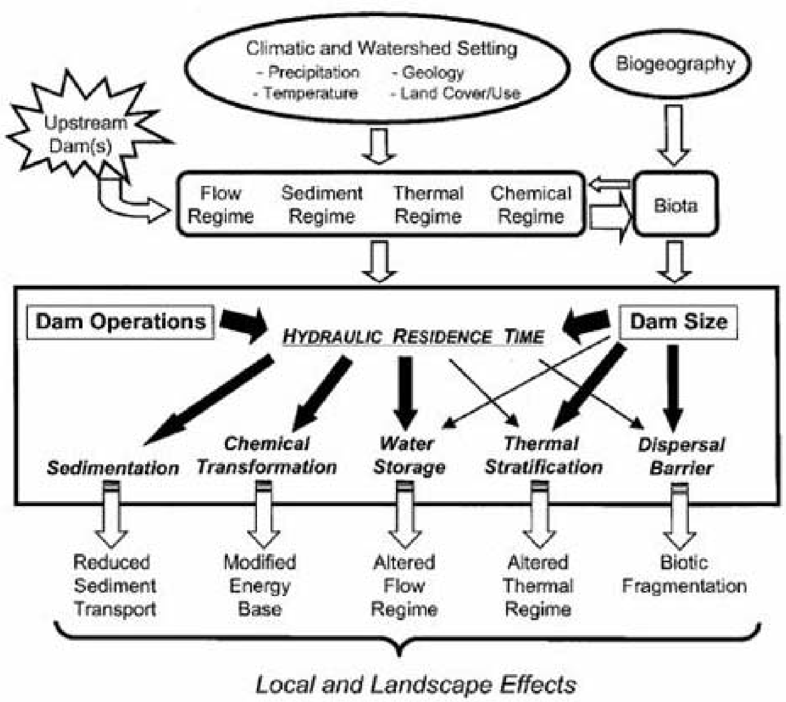

FIGURE 5. FLOW CHART ILLUSTRATING HOW ATTRIBUTES OF DAMS MODIFY RIVERINE BIOPHYSICAL PROCESSES TO CAUSE ALTERATIONS WITH LOCAL AND LANDSCAPE ENVIRONMENTAL EFFECTS. REPRODUCED FROM POFF, N.L. & D.D. HART. 2002. HOW DAMS VARY AND WHY IT MATTER FOR THE EMERGING SCIENCE OF DAM REMOVAL. BIOSCIENCE 52: 659-658. © 2002 BY THE AMERICAN INSTITUTE OF BIOLOGICAL SCIENCES. PUBLISHED BY THE UNIVERSITY OF CALIFORNIA PRESS.

Mechanisms of streamflow alteration associated with groundwater withdrawal are complex, because the contribution to surface water varies depending upon the hydrogeological and climatic setting. (Winter 2007). In order to understand groundwater influence on streams in relation to climate, landscape, and biotic factors, a sound hydrogeological framework is necessary (Power et al. 1999, Sophocleous 2002). In general, declining groundwater levels near surface water bodies can eventually capture groundwater that would have otherwise contributed to stream baseflow. As the surface-groundwater interaction becomes increasingly disconnected, streams ultimately cease to flow. Several authors have quantitatively described how streamflow was affected by groundwater removal (Wen & Chen 2006, Rugel et al. 2012). In a few studies, techniques that model surface-groundwater relationships and simulate altered flows (e.g., MODFLOW) were incorporated with biological assessment data to examine the response of stream biota and habitat to altered hydrology (Kennen et al. 2008, Jacobson et al. 2008, Waco & Taylor 2010, Falke et al. 2011). This complex, interdisciplinary process likely accounts for the rarity of such studies in hydroecological literature.

Land use change was also documented to be a major driver of flow regime alteration. Increasing impervious cover alters soil permeability, which reduces infiltration and increases runoff into surface waters (Sophocleous 2002). Changes in flow regime, stream temperature, and physiochemical characteristics were driven by the amount of impervious surfaces upstream of Piedmont streams in Maryland (Stranko et al. 2008, Utz et al. 2011). The biological integrity of streams was strongly (and negatively) related to the amount of upstream urban land (Wang et al. 1997). Morgan & Cushman (2005) also reported fish community health was negatively related to the amount of watershed urbanization in Maryland (Figure 6). Roy et al. (2005) observed a similar relationship in Piedmont streams in Georgia. They proposed urbanization and the resulting hydrologic alteration as the mechanism for shifts in fish assemblage composition away from species with specific habitat requirements and towards habitat generalist and pollution tolerant species. Furthermore, Armstrong et al. (2010) described significant relationships among imperviousness, stream flow reduction, and fish community health. Multiple studies have also documented that land use driven high flows also impaired benthic macroinvertebrate communities (Kennen et al. 2008, DeGasperi et al. 2009, Kennen et al. 2010, Steuer et al. 2010). In general, sensitive and habitat specialist invertebrate taxa were absent from urbanized streams.

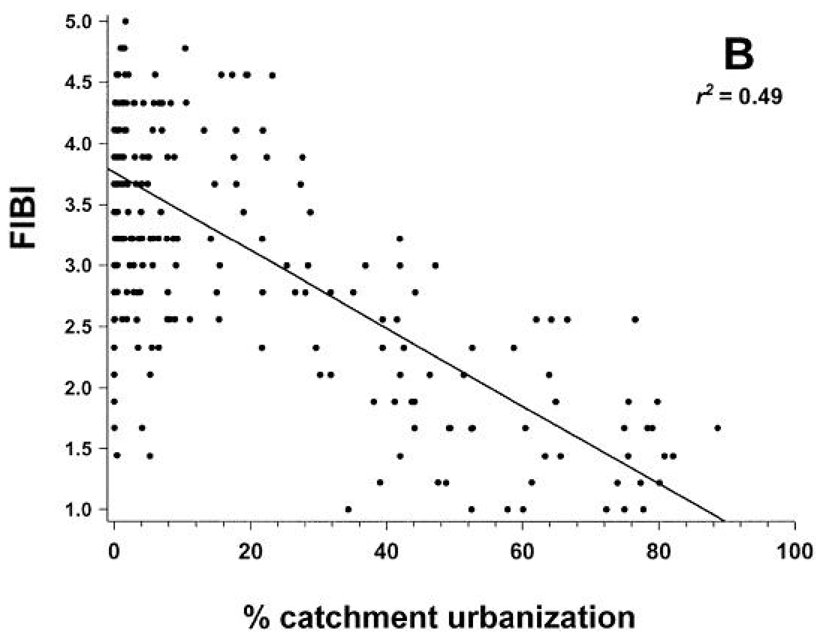

FIGURE 6. RELATIONSHIP BETWEEN % OF CATCHMENT URBANIZATION AND FISH INDEX OF BIOTIC INTEGRITY (FIBI) FOR 1ST-3RD ORDER PIEDMONT STREAMS, MARYLAND. REPRODUCED FROM MORGAN, R.P. & S.H. CUSHMAN. 2005. URBANIZATION EFFECTS ON STREAM FISH ASSEMBLAGES IN MARYLAND, USA. JOURNAL OF THE NORTH AMERICAN BENTHOLOGICAL SOCIETY 24: 643-655 WITH PERMISSION BY THE NORTH AMERICAN BENTHOLOGICAL SOCIETY.

Experimental and retrospective studies have primarily focused on ecological response associated with habitat loss (e.g., Gido et al. 2010). While these studies have consistently observed declines in biological condition resulting from flow reductions, the relationship between habitat quality/quantity and biology was not always clear. For example, Walters and Post (2011) observed shifts in stream habitat to be a major driver of biological response to flow reductions. Conversely, Wills et al. (2006) reported habitat change could only explain a portion of the response to flow reduction. Jacobson et al. (2008) illustrated consistent patterns in the habitat availability for indicator fish species as it varied in response to groundwater pumping scenarios.

MANAGEMENT QUESTION 3: Which components of flow-ecology relationships are most/least affected by surface (intake and impoundment) and groundwater withdrawals?

Summer baseflow and its various hydrologic components (e.g., magnitude, duration, and variability) are most sensitive to water withdrawal because extraction rates are coincidentally highest when flow is natural low. For example, low flows were reduced and their duration extended by extensive groundwater fed irrigation systems in the southeastern US and Great Plains (Wen & Chen 2006, Falke et al. 2010, Rugel et al. 2012). This processes typically results in decreased water velocity, water depth, and wetted channel width, increased sedimentation, and changes to water chemistry (Bradford & Heinonen 2007, Dewson et al. 2007) (Figure 7). Consequently, stream organisms and communities dependent upon flowing and shallow water habitats (i.e., fluvial specialists) appeared to be the most affected by water withdrawals. In contrast, resource generalists, species tolerant to ecological degradation, or invasive species were the least sensitive to water withdrawals and hydrologic alteration as a whole.

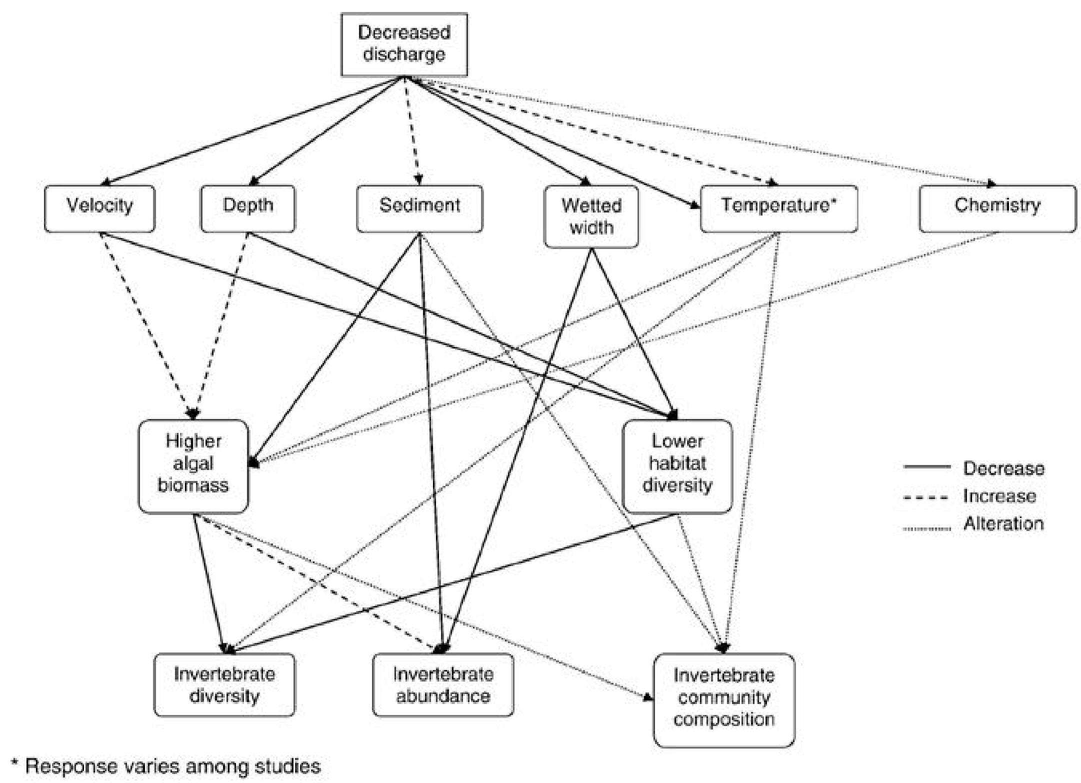

FIGURE 7. SUMMARY OF THE EFFECTS OF DECREASED STREAMFLOW ON HABITAT AND INVERTEBRATE COMMUNITY CONDITIONS. REPRODUCED FROM DEWSON, Z.S., JAMES, A.B.W. & R.G. DEATH. 2007. A REVIEW OF THE CONSEQUENCES OF DECREASED FLOW FOR INSTREAM HABITAT AND BENTHIC MACROINVERTEBRATES. JOURNAL OF THE NORTH AMERICAN BENTHOLOGICAL SOCIETY 26: 401-415 WITH PERMISSION OF THE NORTH AMERICAN BENTHOLOGICAL SOCIETY.

In general, stream fish respond adversely to the alteration associated with most water withdrawal practices. As baseflow was reduced in the Great Plains by groundwater withdrawal, habitat became fragmented and fish communities shifted towards lentic and invasive species from lotic species (Gido et al. 2010). Similar responses in flow-ecology relationships were observed between fish communities in streams with natural flow regimes and those impounded (Marchetti & Moyle 2001, Kanno & Vokoun 2010). When types of surface water withdrawal were compared, impoundments had a greater effect on fluvial fish species richness than simple intakes and richness was lower at intake sites than reference sites (Freeman & Marcinek 2006) (Figure 8). Reservoir storage capacity (i.e., impoundment size) was an important predictor of reduced stream flow variability in the northeastern United States (Meador & Carlisle 2011). Consequently, reduced streamflow was related to native fish and habitat specialist species loss (Figure 3). Dependent upon their size and storage capacity, reservoirs affect the magnitude and timing of high and low flow events, alter annual discharge, and reduce summer baseflow (Graf 2006). These various hydrologic changes resulting from dam presence and very operation have a variety of habitat and biological implications. In comparison to other types of water withdrawal (i.e., groundwater and impoundment), there was little information on the influence of surface intakes on flow-ecology relationships.

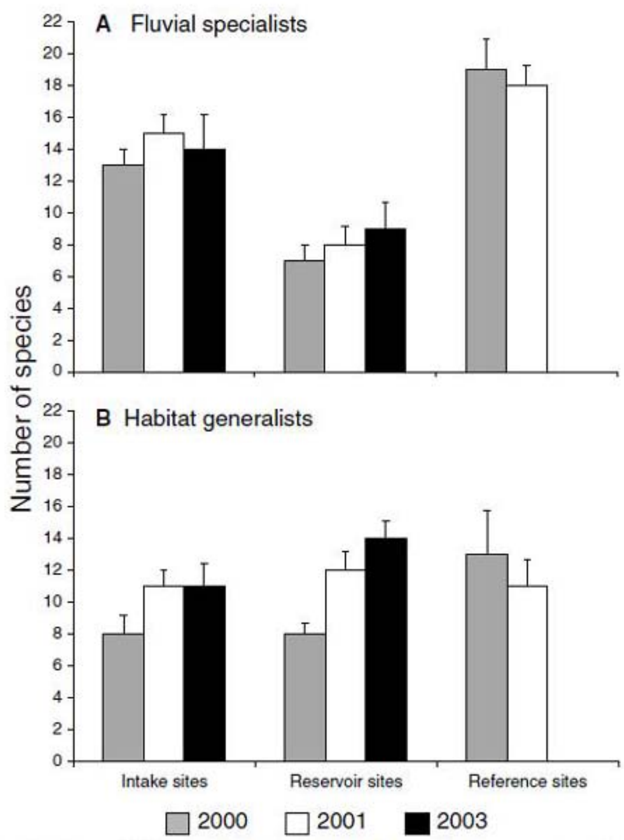

FIGURE 8. MEAN ESTIMATED SPECIES RICHNESS FOR FLUVIAL SPECIALIST (A) AND HABITAT GENERALIST (B) FISHES AT INTAKE, RESERVOIR, AND REFERENCE SITES IN PIEDMONT STREAMS, GEORGIA. ERROR BARS INDICATE ONE UNIT OF STANDARD ERROR. REPRODUCED FROM FREEMAN, M.C. & P.A. MARCINEK. 2006. FISH ASSEMBALGE RESPONSES TO WATER WITHDRAWALS AND WATER SUPPLY RESERVOIRS IN PIEDMONT STREAMS. ENVIRONMENTAL MANAGEMENT 38: 435-450 WITH KIND PERMISSION FROM SPRINGER SCIENCE+BUSINESS MEDIA B.V.

The potential effects of water withdrawal on flow-ecology relationships as they related to benthic macroinvertebrates were not as clear as they were on stream fish. Wills et al. (2006) documented sensitive taxa were significantly fewer when baseflow was reduced by 90%, but not when reduced by 50% (Figure 4). They also found little correlation between wetted usable habitat and invertebrate density. In contrast, Walters & Post (2011) reported the amount of wetted habitat was related to invertebrate community response under similar baseflow reductions. Multiple studies (Armitage & Petts 1992, Bickerington et al. 1993, Wood et al. 2000, Dewson et al. 2007) also noted positive, negative, or neutral responses in macroinvertebrate communities to various reductions in baseflow from groundwater withdrawals. Morgan et al. (1991) observed increased density and abundance of most invertebrate taxa after a reduction in the magnitude of low and high flows downstream of Brighton Dam (Figure 1). Although no change was made to reduce fluctuations associated with hydropeaking operations, increasing the minimum flow improved the benthic macroinvertebrate community below Conowingo Dam (Weisberg et al. 1990). An improvement in invertebrate community health was also reported after initiation of a minimum flow standard from impoundments in the Tennessee River basin of varying size and water release mechanism (Bednarek & Hart 2005).

In addition to flow modifications, impoundments and groundwater withdrawals can also modify the thermal regime of streams. The response of organisms with specific thermal requirements is variable and dependent upon the type of withdrawal. The direction and magnitude to which a dam alters downstream water temperatures depends largely upon their operation, height and water release mechanism (Poff & Hart 2002). Thermal regime alteration from impoundments affects nearly every aspect of aquatic communities, including assemblage composition, growth, productivity, and recruitment (Olden & Naiman 2010). For example, small impoundments with surface water (epilimentic) releases raised temperatures downstream, which coincided with lower densities of brook trout and sculpin along with reduced fish species richness (Lessard & Hayes 2003). Hypolimnetic releases resulted in a variety of biological impacts (Layzer et al. 1993, Travnichek et al. 1995, Bednarek & Hart 2005, Moles & Layzer 2008). The disturbance gradient produced by the hydrologic and thermal alteration can manifest for long distances downstream before habitat and biological communities recover (Kinsolving & Bain 1993, Lessard & Hayes 2003, Layzer & Scott 2006). A loss of groundwater input increased stream temperature and reduced the available thermal refuge habitat for cold water dependent species (Zorn et al. 2002, Waco & Taylor 2010).

MANAGEMENT QUESTION 4: What relationship between surface and groundwater withdrawals and stream ecological integrity can be established?

General flow alteration-ecological response relationships, such as loss of sensitive and habitat specialist species after a reduction in streamflow, were reflected in studies that also assessed water withdrawal and ecological integrity (Figures 2, 4, and 8). In addition, Freeman and Marcinek (2006) found a higher probability of biological impairment (as indicated by a failing index of biotic integrity score) in Piedmont streams of Georgia as the rate of surface water withdrawal increased. They also observed differences among the fish assemblages present at reference sites and those having reservoir or intake associated withdrawals. Several studies also indirectly established relationships between water withdrawal and biological integrity by assessing the ecological response to diminished flows. In a national biological assessment, the integrity of fish and macroinvertebrate communities was best primarily predicted by severity of diminished flows. Furthermore, the probability of biological impairment doubled with increasing severity of diminished streamflow (Carlisle et al. 2011) (Figure 9). Additionally, altered streamflow variability resulted in a higher probability of fish assemblage impairment (Meador & Carlisle 2011). Gido et al. (2010) noted a steady decrease in native, fluvial fishes with a coincident increase in invasive and tolerant species. They inferred that biological degradation in Great Plains streams was a result of reduced streamflow due to extensive groundwater withdrawal for irrigation and habitat fragmentation due to impoundment.

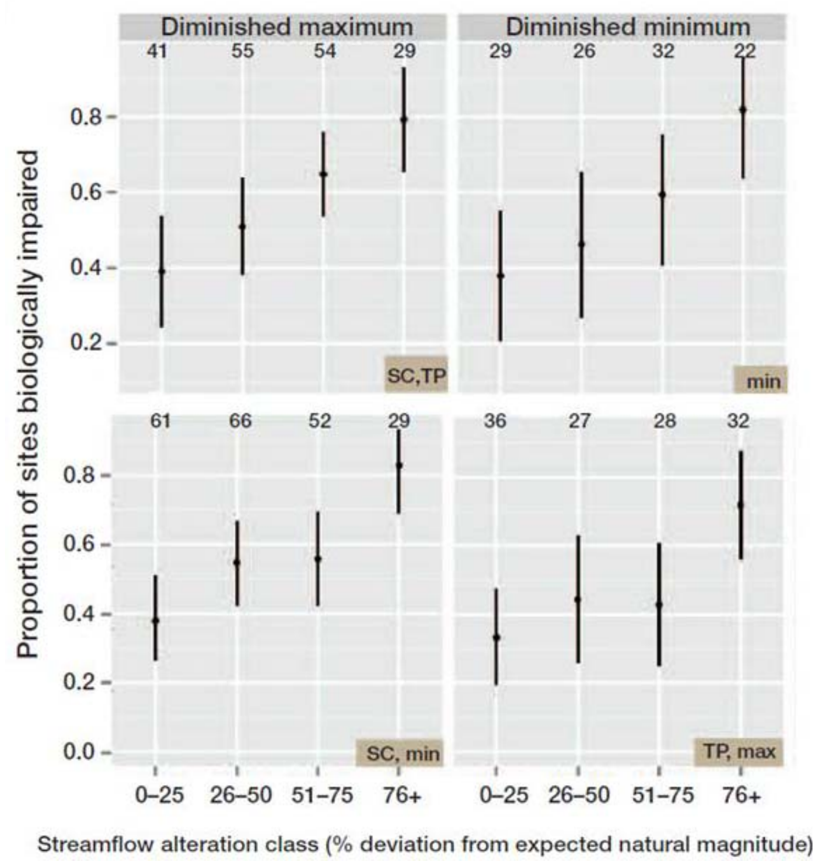

FIGURE 9. PROPORTION OF BIOLOGICAL MONITORING SITES WITH IMPAIRED FISH (A) AND MACROINVERTEBRATE (B) COMMUNITIES WITHIN CLASSESS OF STREAMFLOW ALTERATION FOR THE UNITED STATES. VERTICAL BLACK LINES REPRESENT 95% CONFIDENCE INTERVALS AND VALUES ABOVE LINES INDICATE THE SAMPLE SIZE WITHIN EACH CLASS. INSET BOXES DISPLAY COVARIATES THAT DIFFERED SIGNIFICANTLY ($P < 0.05$) AMONG SEVERITY CLASSES, WHERE SC = SPECIFIC CONDUCTANCE, TP = TOTAL PHOSPHORUS, MAX = MAXIMUM FLOW OBSERVED/EXPECTED, AND MIN = MINIMUM FLOW OBSERVED/EXPECTED. REPRODUCED FROM CARLISLE, D.M., WOLOCK, D.M. & M.R. MEADOR. 2011. ALTERATION OF STREAMFLOW MAGNITUDES AND POTENTIAL ECOLOGICAL CONSEQUENCES: A MULTIREGIONAL ASSESSMENT. FRONTIERS IN ECOLOGY AND THE ENVIRONMENT 9: 264-270 WITH PERMISSION FROM THE ECOLOGICAL SOCIETY OF AMERICA.

Studies assessing the relationship between water withdrawals and benthic macroinvertebrate community health were primarily conducted outside of the United States (Dewson et al. 2007) and relatively few empirical studies have assessed the influence of reduced flows on the ecology of stream ecosystems (but see Wills et al. 2006, Walters & Post 2011). Armitage and Petts (1992) studied the potential impacts of various types of water extraction on macroinvertebrates within 22 chalk rivers in the United Kingdom. Their main conclusion was that benthic communities did not suffer adverse effects as a consequence of water withdrawal. Where ecological degradation was apparent, it was not attributable to withdrawal, as major regional differences in water quality likely masked localized impacts. Finally, they recommended against using biotic scores with RIVPACS set ecologically based minimum flows because they could not distinguish the response in community-based metrics from other anthropogenic factors. This recommendation was in part because community-based metrics appeared unresponsive to flow alteration, but also because other potentially confounding anthropogenic influences were not measured. Bickerton et al. (1993) further examined the ecological effects of groundwater withdrawal in a subset of streams studied by Armitage and Petts (1992). They attributed the differences in macroinvertebrate community index scores to groundwater abstractions, but the affects of withdrawal were difficult to separate from between-site variations in habitat, which were also affected by water withdrawal to some extent. In a hydroecological integrity assessment of New Jersey streams, Kennen et al. (2008) related invertebrate community impairment to flow regime modifications that primarily resulted from changes in watershed land use.

MANAGEMENT QUESTION 5: For past and future water-uses, how have/might surface and groundwater withdrawals impact individual species and ecosystems (include scenarios such as: flooding, drought, increasing population, cumulative impacts, climate change, confounding factors, etc.)?

The past impacts of moderate to large dams on aquatic species have been widespread, numerous, and well documented (Vaughn & Taylor 1999, Poff & Hart 2002, Graf 2006, Murchie et al. 2008). In addition to direct impacts on species and communities (Bain et al. 1988, Kinsolving & Bain 1993, Lazyer et al. 1993, Morgan et al. 2001), habitat downstream of impoundments is changed by fluctuations associated with dam operation (Scheidegger & Bain 1995, Freeman et al. 2001), upstream habitat is fragmented (Herbert & Gelwick 2003), and thermal regimes are altered (Clarkson & Childs 2000). Although generally less studied, smaller dams also have negative effects on aquatic species and communities (Figure 10), which often differ from the effects of with larger dams (Watters 1996, Lessard & Hayes 2003, Tiemann et al. 2004). Ecological consequences associated with the potential construction of new impoundments for water supplies should be considered no different, although advances in operational techniques can minimize the extent of impacts to stream biota (Travnichek et al. 1995, Bednarek et al. 2005, Layzer & Scott 2006, Moles & Layzer 2008).

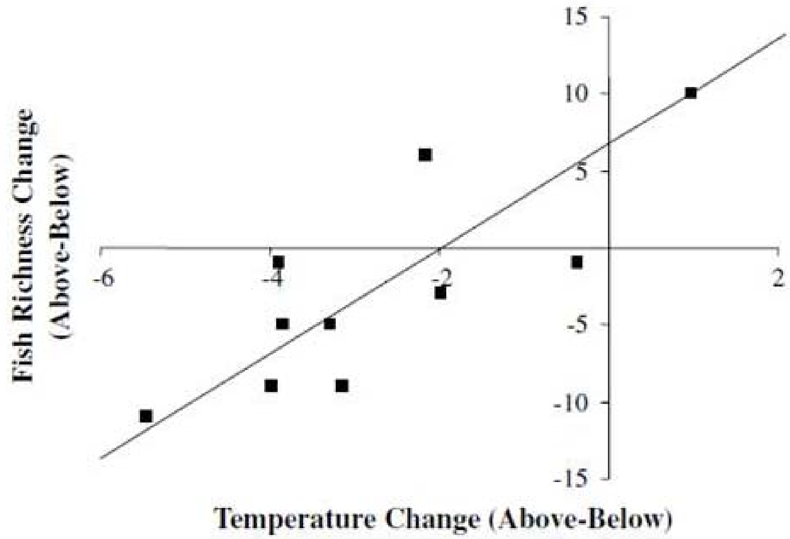

FIGURE 10. REGRESSION OF DIFFERENCES IN FISH SPECIES RICHNESS ON DIFFERENCES IN MEAN SUMMER TEMPERATURE BETWEEN ABOVE AND BELOW DAM REACHES ($R^2 = 0.79$). REPRODUCED FROM LESSARD, J.L. & D.B. HAYES. 2003. EFFECTS OF ELEVATED WATER TEMPERATURE ON FISH AND MACROINVERTEBRATE COMMUNITIES BELOW SMALL DAMS. RIVER RESEARCH AND APPLICATIONS 19: 721-732 WITH PERMISSION GRANTED BY JOHN WILEY AND SONS (HTTP://WWW.WILEY.COM/WILEY-BLACKWELL).

Based on the results of multiple studies (Jacobson et al. 2008, Gido et al. 2010, Falke et al. 2011, Kanno & Vokoun 2010, Waco & Taylor 2010) scenarios of increasing water withdrawals (e.g., cumulative impacts) are likely to reduce habitat, fragment streams, and cause declines in native and flow-specialist species. This ultimately results in biological impairment as these components of aquatic communities are lost. We would expect the biological response to flow alteration to be magnified if the water withdrawal was associated with an impoundment due to additional spatial and temporal modification in the hydrologic and thermal regimes (Herbert & Gelwick 2003, Lessard & Hayes 2003, Freeman & Marcinek 2006, Galbraith et al. 2011, Meador & Carlisle 2011). Limestone streams and their unique biological communities may have further potential to become impaired by increasing amounts of groundwater withdrawal. This is in part due to the physiochemical processes that result from surface-groundwater interactions aquatic communities depend upon (Bickerton et al. 1993, Power et al. 1999, Pragel et al. 2006), which would be lost when these interactions are broken.

Biological integrity in the Mid-Atlantic has already been impaired by hydrologic alteration associated with land use change (Morgan & Cushman 2005, Kennen et al. 2008, Kennen et al. 2010). Increasing imperviousness from expanding human population centers increases flashiness and the duration of summer low-flows in Piedmont streams while disrupting physiochemical processes (Utz et al. 2011). In turn, this process reduces sensitive and flow specialist species and facilitates tolerant and invasive species (Roy et al. 2005). In light of the relationships found by Stranko et al. (2008) and others (Zorn et al. 2002, Armstrong et al. 2010, Waco & Taylor 2010), future water supply demands in the Fractured-Rock area of Maryland have the potential to affect the viability of brook trout populations through the synergistic effects of increasing groundwater withdrawal and impervious surfaces, which reduce baseflow and raise water temperature. While the effects of land use change often manifest as changes in water chemistry, flow or habitat, there are several appropriate analytical techniques to account for potentially confounding and correlated variables while determining their relative influence upon stream biota and condition (e.g., Field et al. 1982, Clarke 1993, Anderson et al. 1999, Cade & Noon 2003).

Lake (2003) thoroughly reviewed drought related impacts to stream ecosystems (Table 3). Drought conditions disturb streams by reducing water inflow, discharge, and availability to extremely low levels for long durations. Ultimately, these changes disrupts hydrological processes and connectivity that cause both direct (e.g., loss of habitat) and indirect (e.g., changes in interspecific relationships, water quality) effects to stream ecosystems. Of particular concern to ecosystem health is the potential for droughts to exacerbate impacts during periods of naturally low flow, which coincide with the period of high water demand (i.e., summer) (Bradford & Heinonen 2008). Biological response to seasonal drought by aquatic species, populations, and communities has been well documented (Matthews & Marsh-Matthews 2003, Dewson et al. 2007). However, there was seemingly little information about the potential ecological effects of supra-seasonal drought, which generally requires long-term data. The potential effects to stream biota from drought are numerous, complex, and in general poorly understood (Table 4).

TABLE 4. PHENOMENA RELATED TO FISHES REPORTED OR PREDICTED TO BE AFFECTED BY DROUGHT. REPRODUCED FROM MATTHEWS, W.J. & E. MARSH-MATTHEWS. 2003. EFFECTS OF DROUGHT ON FISH ACROSS AXES OF SPACE, TIME AND ECOLOGICAL COMPLEXITY. FRESHWATER BIOLOGY 48: 1232-1253 WITH PERMISSION GRANTED BY JOHN WILEY AND SONS (HTTP://WWW.WILEY.COM/WILEY-BLACKWELL).

Individuals
Survivorship and mortality as a result of desiccation, physiological tolerances
Reduced growth, reproduction, and recruitment
Local movements and emigration
Microhabitat changes, with food resource or predator pressure
Local populations
Local extinction
Intraspecific competition and density effects
Change in population size, biomass, or connectivity
Year-class failure
Local assemblages
Change in assemblage composition including diversity, richness, evenness, and biomass
Increased interspecific competition, predation
Effects of fish in ecosystems
Altered primary productivity and structure of algal communities
Changes in invertebrate assemblages or biomass
Changes in fish-mediated processing or transport of nutrients
Altered rates of ecosystem processes

The overall response of aquatic organisms and communities is in part a function of the magnitude, duration, and frequency of disturbance. Additionally, the presence of drought refugia, hydrologic connectivity, and a species' dispersal ability influence its survival and ecosystem recovery. For example, short-lived benthic macroinvertebrates have the ability to seek refuge in the hyporheic zone or leave aquatic environments entirely until conditions are suitable for recolonization (Clausen & Biggs 1997, Wood & Armitage 2004). Recovery in fish communities to reduced minimum flows can be rapid, as they are highly mobile (Carlisle et al. 2010). In contrast, long-lived freshwater mussels are easily stranded in isolated pools or out of the wetted channel because they are relatively sessile. As a result, their mortality can be high and capacity for recovery low (Gagnon et al. 2004, Haag & Warren 2008, Galbraith et al. 2010) (Figure 11).

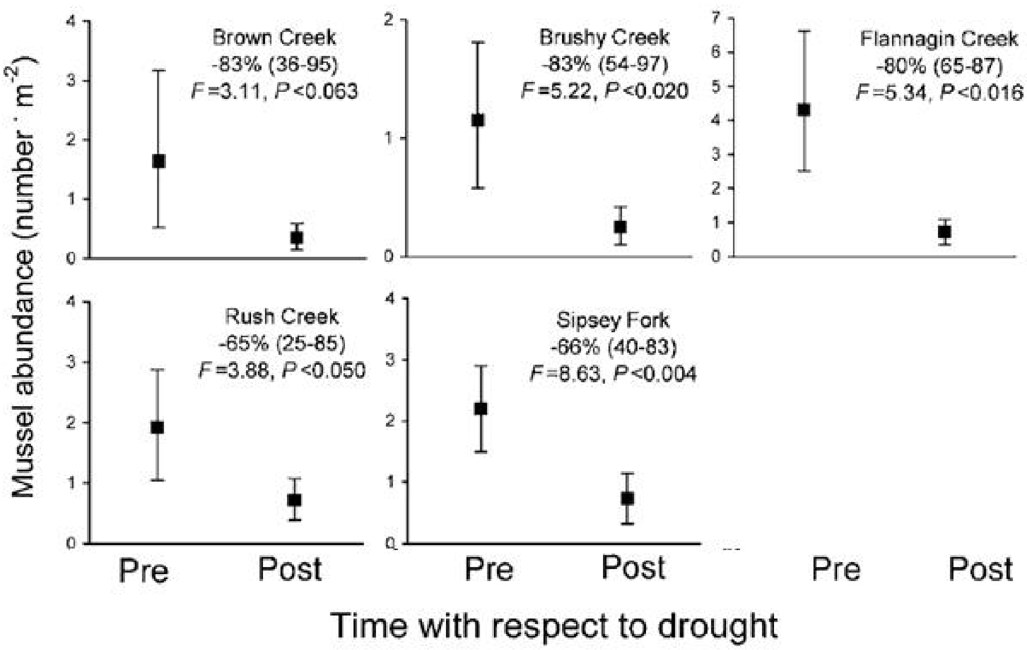

FIGURE 11. MEAN PRE- AND POST-DROUGHT ABUNDANCE OF FRESHWATER MUSSELS AT FIVE SMALL-STREAM SITES (1993 AND 2002); THIN VERTICAL LINES REPRESENT 95% CONFIDENCE INTERVALS OF THE MEANS. THE PERCENTAGE DECLINES (95% CI IN PARENTHESES) AND RESULTS OF SIGNIFICANCE TESTS ARE GIVEN. REPRODUCED FROM HAAG, W.R. & M.L. WARREN. 2008. EFFECTS OF SEVERE DROUGHT ON FRESHWATER MUSSEL ASSEMBLAGES. TRANSACTIONS OF THE AMERICAN FISHERIES SOCIETY 137: 1165-1178 WITH PERMISSION FROM COPYRIGHT CLEARANCE CENTER INC (CCC) ON TAYLOR & FRANCIS'S BEHALF (HTTP://WWW.TANDF.CO.UK/JOURNALS).

Falke et al. (2011) noted that past and current groundwater levels in aquifers of the Great Plains coupled with droughts could drastically reduce habitat for stream fish without unrealistic reductions in groundwater pumping. While less extreme, Jacobsen et al. (2008) noted alternative (reduced) groundwater pumping rates that must be implemented during seasonal periods of low flow to alleviate impact to aquatic species and habitat. Recent hydrologic studies (Wen & Chen 2006, Rugel et al. 2006) also expressed concern about the current rates of groundwater withdrawal for irrigation on surface water resources given climate change and population growth scenarios. The transferability of these studies and their findings to Maryland is tenuous at best, because the hydrogeological characteristics of the areas studied and magnitude of consumptive water use are quite different. Recent and continued growth in population and urban centers in Maryland is well known as are the subsequent effects of impervious surfaces to stream hydrology and biotic integrity are well established (Morgan & Cushman 2005, Stranko et al. 2008, Utz et al. 2011). Additional climate related impacts (e.g., rising temperatures and increasing drought frequency) to streams, coupled with projected water demand, may lead to substantial loss of aquatic biodiversity and ecosystem health (Xenopolous & Lodge 2006, Chu et al. 2008, Spooner et al. 2011), particularly in headwater streams (Freeman et al. 2007, Winter 2007). While future projections for stream biota appear bleak, analogous patterns of species loss, community shifts, and habitat degradation have already been observed in locations of intensive water management (e.g., Layzer et al. 1993, Gido et al. 2010, Galbraith et al. 2010).

> **MANAGEMENT QUESTION 6:** What spatial and seasonal aspects of flow need to be maintained for specific streams, including under drought conditions to ensure the protection of stream species and ecosystems?

Although a relatively recent concept for managing riverine ecosystems, streamflow variability is increasingly noted as an important component of flow regimes and factor that structures stream ecosystems (Richter et al. 1996, Poff et al. 1997). Natural variation includes a wide array of flows that occur at various frequencies, durations, and magnitudes during both high and low-flow disturbance events (Poff 2009). All of this takes place at multiple spatial and temporal scales and is relative to the measure being used (Lytle & Poff 2004, Biggs et al. 2005). The level of influence flow variability exerts upon abiotic processes and the attributes of biotic communities primarily relates to its magnitude (Poff & Ward 1989, Poff & Allan 1995). Streamflow variability also provides a useful template to classify streams that span environmental gradients in order to assess its importance to ecological condition (Poff 1996, Snelder et al. 2005, McManamay et al. 2011b) (Figure 12). The aforementioned topics were extensively reviewed by Monk et al. (2007).

Since aquatic biota evolved to the hydrologic variability of rivers and streams, it often explains the distributional patterns and composition of fish (Poff & Ward 1989, Poff & Allan 1995, Knight et al. 2008), macroinvertebrate (Clausen & Biggs 1997, Monk et al. 2006, Konrad et al. 2008), and mussel communities (DiMaoi & Corkum 1995). Consequently, the alteration of streamflow variability has been credited with the degradation of biological integrity (Kennen et al. 2008, Carlisle et al. 2010, Meador & Carlisle 2011). Dams, especially large ones, are the most common anthropogenic mechanism that alters flow regimes and their variability (Graf 2006). Their ecological and physical impacts persist well downstream (Kinsolving & Bain 1993, Marchetti & Moyle 2001); however, modification of dam operation to mimic more natural flow regimes has improved aquatic communities (Weisberg et al. 1990, Morgan et al. 1991, Travnichek et al. 1995, Cooke & Leach 2003, Bednarek & Hart 2005, Layzer & Scott 2006). Watershed urbanization is also a major cause of increased hydrologic variability (Steuer et al. 2010, Utz et al. 2011) and is frequently implicated in the decline of biological integrity (Morgan & Cushman 2005, Roy et al. 2005, DeGasperi et al 2009).

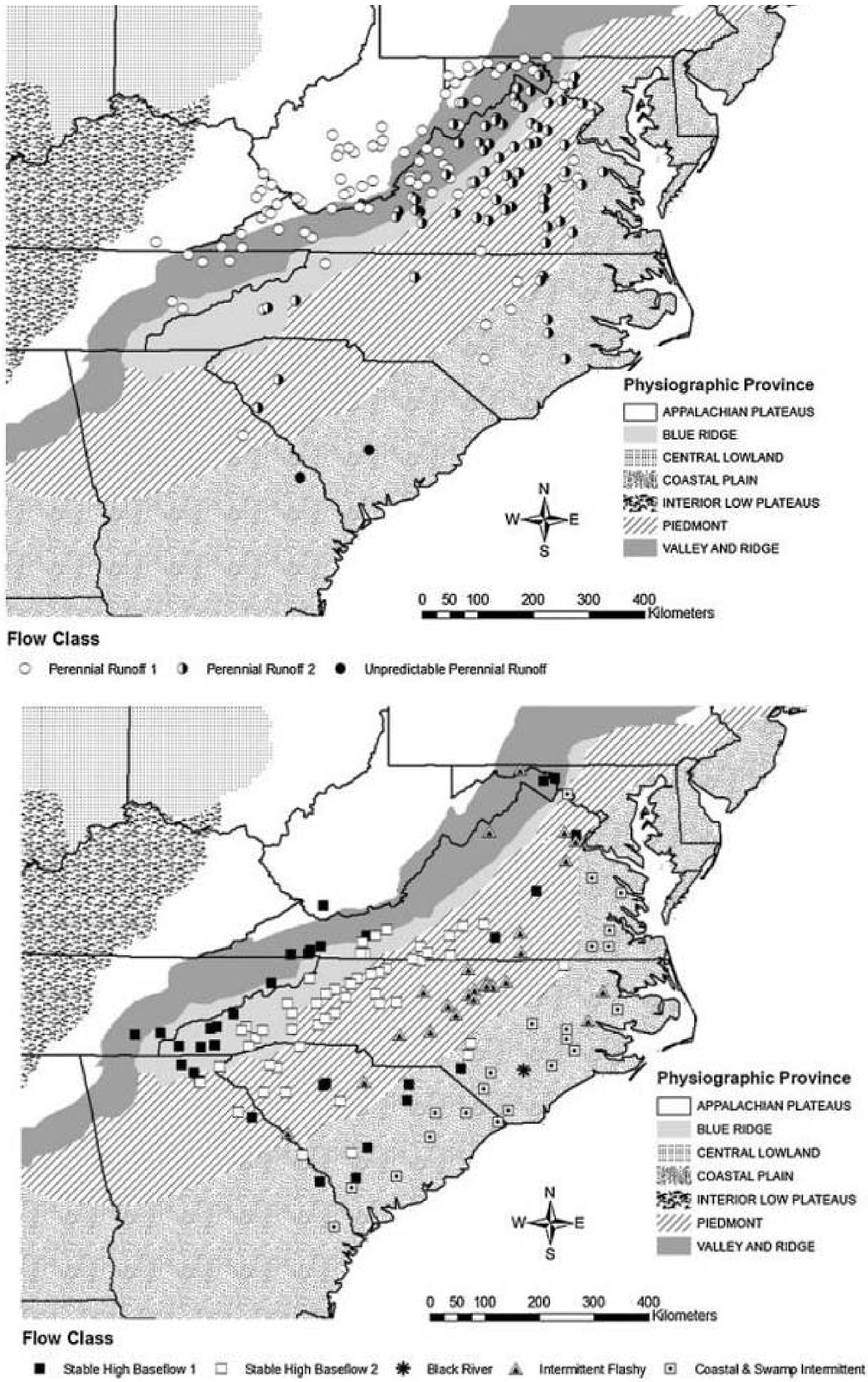

Figure 12. Geographic distribution of eight flow classess across physiographic provinces across the southeastern United States. Reproduced from McManamay, R.A., Orth, D.J. Dollof, C.A. & E.A. Frimpong. 2011b. Regional frameworks applied to hydrology: can landscape-based frameworks capture the hydrologic variability? River Research and Applications 28: 1325-1339 with permission granted by John Wiley and Sons (http://www.wiley.com/wiley-blackwell).

Connectivity is an important spatial aspect of stream hydrology, both within surface water systems and between surface and groundwater. Disruption of hydrologic connectivity within surface water systems is most noticeably caused by dams. The physical separation of the stream continuum a dam creates and the altered flow regime that results from their operation influences biological communities. These effects are evident when comparing communities above and below impoundments (Herbert & Gelwick 1993, Lessard & Hayes 2003) or in regulated and unregulated streams (Bain et al. 1998, Freeman et al. 2001, Freeman & Marcinek 2006). Groundwater plays an important role in providing and sustaining streamflow within the headwaters of watersheds that maintains hydrologic connectivity, water quality, and biological integrity (Power et al. 1999, Zorn et al. 2002, Freeman et al. 2007). Its connection to surface waters also supplies important biogeochemical processes (Sophocleous 2002). Interruption of the connectivity between surface and groundwater can influence streamflow and aquatic communities in a variety of ways. When surface-groundwater connectivity is broken streamflow generally decreases (Winter 2007). Additionally, thermal regimes and refugia of streams may become altered (Chu et al. 2008, Waco & Taylor 2010). Multiple studies (e.g., Wen & Chen 2006, Jacobsen et al. 2008, Rugel et al. 2012) also found that excessive groundwater withdrawal can exacerbate the disconnection and cause surface water to reduce to the point it ceases to flow (Figure 13).

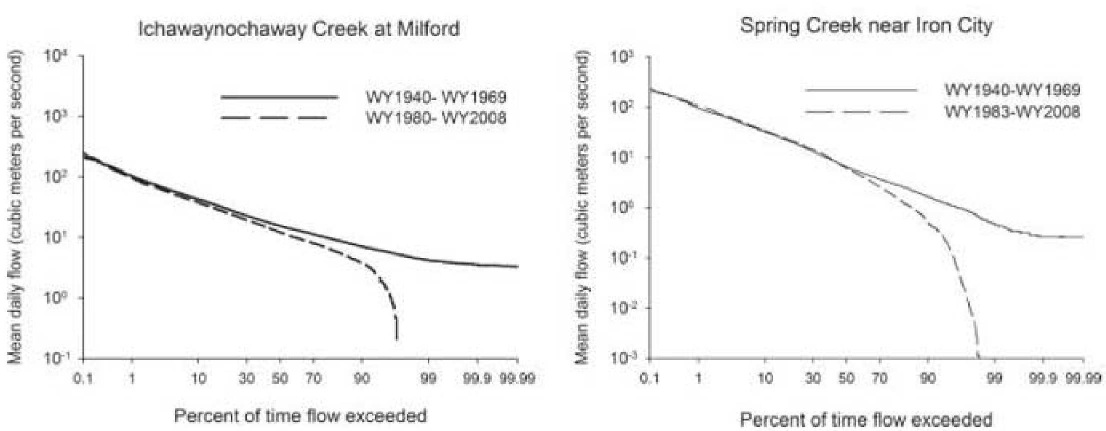

FIGURE 13. FLOW DURATION CURVES FOR PRE- AND POST-PUMPING PERIODS FOR IRRIGATION. ADAPTED FROM RUGEL, K., JACKSON, C.R., ROMEIS, J.J., GOLLODAY, S.W., HICKS, D.W. & J.F. DOWD. 2012. EFFECTS OF IRRIGATION WITHDRAWALS ON STREAMFLOWS IN A KARST ENVIRONMENT: LOWER FLINT RIVER BASINS, GEORGIA, USA. HYDROLOGICAL PROCESSES 26: 523-534 WITH PERMISSION GRANTED BY JOHN WILEY AND SONS (HTTP://WWW.WILEY.COM/WILEY-BLACKWELL).

Fragmented stream networks affect aquatic biota in a number of ways across multiple scales. These impacts often arise from drought conditions (Lake 2003, Matthews & Marsh-Matthews 2003, Dewson et al. 2007); however, the magnitude of impact can vary by type and duration of drought (e.g., seasonal or supra-seasonal). Species and populations become stressed and may ultimately become locally extirpated as isolated habitat becomes reduced, degraded, or desiccated. At the same time, the abundance of tolerant, non-native, and invasive species generally increases, further stressing native and intolerant organisms (Wood & Armitage 2004, Bradford & Heinonen 2008). In arid regions, current water management practices coupled with drought conditions have severely fragmented streams and impacted stream biota (Galbraith et al. 2010, Gido et al. 2010). While the conclusiveness of studies of groundwater withdrawal, streamflow, and ecological integrity is mixed (Armitage & Petts 1992, Bickerington et al. 1993, Chessman et al. 2011), there is clearly important hydroecological interactions that must be further studied protect stream species and ecosystems from the compounding effects of habitat loss related to drought and water withdrawal.

Seasonal flows that are critical to maintain stream ecological integrity often relate to life history cues of species (e.g., spawning, migration), population level controls (e.g., resource competition, predation, recruitment), and physiochemical processes (e.g., habitat reduction or desiccation, adequate dissolved oxygen) (Freeman et al. 2001, Jessop 2003, Wills et al. 2006, Dewson et al. 2007, Bradford & Heinonen 2008). It is recognized that during periods of naturally low flow, some minimum amount of flow is necessary to provide sufficient and suitable habitat to aquatic species (Bain et al. 1998). These habitat based techniques are useful for specific ecological and flow objectives (e.g., Weisberg & Burton 1993, Travnichek et al. 1995), but are not easily applied on a wide spatial scale and to unregulated streams due to inherent the spatial and temporal variability in stream hydrology and ecology that is not accounted for by site-specific relationships (Tharme 2003, Acerman & Dunbar 2004). With the advancement of hydrologic data analysis techniques, many studies have critically examined traditional minimum flow standard approaches to determine appropriate ecologically based flow standards to protect species, communities, habitat, and ecosystems and proposed several alternatives (Richter et al. 1996, Jowett 1997, Richter et al. 1997, Henriksen et al. 2006, Mathews & Richter 2007, Gao et al. 2009, Bartholow 2010, Poff & Zimmerman 2010).

The reduction of warm season low flows often coincides with the greatest period of surface and groundwater demand. Not surprisingly, anthropogenic mechanisms (i.e., urbanization and withdrawal) that further reduce low flows impair aquatic species, communities, and degrade their habitat (Roy et al. 2005, Freeman & Marcinek 2006, Wills et al. 2006). These effects are intensified by the added stress of drought (Wood & Armitage 2004, Gido et al. 2010); freshwater mussels are acutely sensitive to drought-induced stress (Haag & Warren 2008 Galbraith et al. 2010). Fish and macroinvertebrate communities are generally less sensitive and appear to recover relatively quickly from drought conditions, but their recovery is highly variable dependent upon species mobility and tolerance to stress (Matthews & Marsh-Matthews 2003, Dewson et al. 2007). Finally, climate change projections indicate potential reductions or even extirpations of species and loss of ecosystem function is probably without careful conservation of water resources (Power et al. 1999, Lake 2003, Chu et al. 2008, Waco & Taylor 2010, Falke et al. 2011, Spooner et al. 2011).

MANAGEMENT QUESTION 7: Is additional research/monitoring needed?

Although the field of hydroecology and its body of knowledge has substantially grown, multiple challenges remain that hamper water management decisions. Chiefly among these is the paucity of long-term datasets, although authors (Monk et al. 2006, Souchon et al. 2008, Poff & Zimmerman 2010) have suggested that the examination of existing biomonitoring data could lead to significant progress. Several proposed analyses in Stranko et al. (2011) would take advantage of such existing data to examine relationships between the annual variability in species and flow and biotic integrity and flow alteration along with potential applications of studies previously discussed. Secondly, there is a need for sampling efforts and analyses along a gradient of least disturbed to highly altered to infer ecological response, test flow-ecology hypotheses, and address uncertainty in response to a given hydrologic change (Bradford & Heinonen 2008, Kennard et al. 2010, Poff & Zimmerman 2010). Likewise, opportunities to establish foundational flow-ecology relationships have often been missed because monitoring of sites that have experienced flow alteration has typically not been conducted (Souchon et al. 2008). Conversely, targeted sampling designs in environmental flow studies have been criticized for their inherent bias when applying data collected from one location to an entire stream (Williams 2010). Finally, there are few studies on the biological effects of water supply reservoirs (but see Freeman & Marcinek 2006, Kanno & Vokoun 2010), which are typically smaller than the more often studied flood control and hydroelectric impoundments. This may be in part because studies are often ambiguous as to the primary use of an impoundment (e.g., Lessard & Hayes 2003, Tiemann et al. 2004), but is an important distinction because reservoir storage capacity is an important factor in determining the magnitude of flow regime alteration (Graf 2006, Meador & Carlisle 2011).

While often impractical and rarely done (but see Travnichek et al. 1995, Wills et al. 2006, Walters & Post 2011), experimental studies provide a valuable opportunity to validate the efficacy of water management decisions to protect instream biota versus alternative scenarios and establish empirical relationships between flow alteration and biological integrity. Such research could be carried out within an adaptive management framework structured to balance natural resource and water supply sustainability while informing future management decisions (Poff et al. 2003). Finally, several authors (Murchie et al. 2008, Souchon et al. 2008, Poff & Zimmerman 2010) have noted that understanding the mechanisms behind ecological response-flow alteration relationships could be improved with the collection of data from more rigorous statistical designs and analyses, such as a before-after-control-impact designs or information theoretic analyses (e.g., Underwood 1994, Anderson et al. 2000, Cade & Noon 2003).

Aside from issues of data quantity and sampling design quality, basic information on flow-ecology relationships that integrate multiple spatial and temporal scales, describe flow alteration mechanisms, and bridge the hydrological-ecological interface was generally lacking in the literature. Foremost was a paucity of studies that directly linked groundwater withdrawals to biological condition (but see Jacobson et al. 2008, Waco & Taylor 2010, Falke et al. 2011), even though various methods to develop relationships between streamflow and groundwater have been established. Only a few studies compared the potential effects of groundwater extraction qualitatively (e.g., Armitage & Petts 1992, Bickerton et al. 1993, Gido et al. 2010, Chessman et al. 2011). Furthermore, just a handful of studies incorporated both surface and groundwater withdrawals and included details on their interaction (e.g., Armitage & Petts 1992, Kennen et al. 2008, Armstrong et al. 2010). Studies taking into account the differential effects due to type of surface water withdrawal (intake versus impoundment) were also scarce (but see Freeman & Marcinek 2006); instead, flow alteration due to water withdrawal or other mechanisms were generalized into flow alteration statistics or indexes (e.g., Armstrong et al. 2010, Meador & Carlisle 2011). A thorough understanding of groundwater-surface water interactions and how they influence hydroecological processes relative to human-induced changes may be the greatest challenge to quantifying the affects on habitat and biology in response to water resource decisions (Sophocleous 2002). Much of the evidence for impacts on aquatic resources due to groundwater withdrawals in this review was based on the research of Falke et al. (2010), Gido et al. (2010), Wen and Chen (2006) and Rugel et al. (2010). Given differences in climate, hydrology, geology, and water consumption, these examples may not be applicable to groundwater resources in the portion of Maryland underlain by fractured bedrock.

Empirical relationships that incorporate the flow variability, in lieu of static flow-by requirements, are also needed to develop water management policies that can help sustain stream ecosystem health (Postel 2000, Lytle & Poff 2004, Arthington et al. 2006, Richter et al. 2011). An explicit recognition of the hierarchical nature of streams and their ecosystems (e.g., Poff & Allan 1995) must also be made and incorporated into hydroecological assessments that span multiple regions (McManamay et al. 2011a, b). Finally, many authors of various disciplines (Sophocleous 2002, Dewson et al. 2007, Monk et al. 2007, Bradford & Heinonen 2008, Murchie et al. 2008, Bartholow 2010, Poff and Zimmerman 2010, and others) have proposed several research directions yet to be fully addressed including, 1) a focus on non-salmonid fishes, 2) the need for more interdisciplinary studies that integrate hydraulic data and models with ecological data, 3) an examination of physiochemical covariates of flow, 4) studies that propose and test flow alteration-ecological response hypotheses in various hydrogeological regions and stream classes, 5) methods that extrapolate relationships from streams reaches to watersheds and basins, 6) and a better accounting of hydrologic and ecological uncertainty. These complex and interdisciplinary issues should all be considered when designing specific monitoring plans and data analyses to perform under the Maryland Hydroecological Integrity Assessment (Stranko et al. 2011) to better inform water and natural resource management policy (Wolman 2008).

CONCLUSION

The findings of numerous literature reviews indicate that many types of natural and human-induced flow alterations result in a variety of ecological responses, which were overwhelmingly detrimental (Lloyd et al. 2003, Matthews & Marsh-Matthews 2003, Dewson et al. 2007, Monk et al. 2007, Bradford & Heinonen 2008, Murchie et al. 2008). The studies evaluated in this review further highlight the relationship among streamflow and aquatic species, communities, and ecosystems. Many of these studies examined the influence of large, regulated rivers on fish, benthic invertebrates, and their habitat or compared them to unregulated rivers. However, an increasing number of assessments investigated how stream biota responded to changes in components of flow regimes (i.e., magnitude, timing, frequency, and duration) through anthropogenic influence, such as withdrawal of surface or groundwater. Although the exact mechanisms or magnitude of flow regime alterations were not always clear, the findings of these and other studies indicated that flow alteration was overwhelmingly detrimental to stream ecosystems in a variety of ways and at multiple scales. This consensus view from individual research papers was corroborated by multiple reviews of hydroecology and flow alteration as previously noted and most recently by Poff & Zimmerman (2010) and McManamay et al. (2011c).

Most of the studies that evaluated the potential impacts of water withdrawals or flow reductions on stream biology used benthic macroinvertebrates as response organisms. Their findings were mixed and occasionally inconclusive. However, this was more likely because flow-ecology relationships for macroinvertebrates appeared to be heavily influenced by high flows. There were fewer sources that related fish community health to quantitative measures of flow alteration from water withdrawal. This could be in part because only recently have 1) many states developed or began developing methods to assess the integrity of fish communities, 2) various tools to quantify large data sets of flow statistics become available, 3) more rigorous analysis and design techniques been used in hydroecological studies, and 4) resource conflicts spread from sparsely populated arid regions to more densely populated temperate regions. The often reactive nature of flow-alteration studies can likely be credited with the lack of information from Maryland and the Chesapeake Bay, as the issue is relatively new (Wolmann 2008).

The information reviewed and discussed in this review should provide valuable insight into potential ecological outcomes posed by management questions in Stranko et al. (2011). For example, the findings from other studies on the effects of dams and their operation (e.g., Bednarek & Hart 2005) could be incorporated into a project's design to avoid potentially costly mitigation and often contentious user conflicts to restore biological integrity. More qualitative relationships, such as the importance of groundwater contribution to streams that harbor cold-water obligate species (e.g., brook trout), could be used to integrate water allocation policy with anti-degradation or stream use-class policy. In addition, this review should help interpret the often confounded and correlated patterns that could be observed in future evaluations of flow-ecology and biological response to flow alteration in Maryland. Although there were few directly transferable relationships for some management questions, many tools and flow-ecology hypotheses from other areas were available (e.g., Armstrong et al. 2010, Kennen et al. 2010). In this case, our summary should be used to guide the development of objective oriented field studies and data analyses that evaluate current and alternative flow-by practices and apply, refine, or develop flow-ecology hypotheses to better inform land, water, and natural resource management policy in Maryland.

A myriad of methods are available to define environmental and minimum flow requirements for stream ecosystems fueled by recognition of the widespread hydrologic alteration of rivers and streams (Tharme 2003, Acerman & Dunbar 2004). These methods have been greatly improved by advances in the analyses of hydrologic data (Richter et al. 1996, Henriksen et al. 2006, Carlisle et al. 2010, Poff et al. 2010) and refined through hydrogeographic classifications based on statistical and ecological relevance (Poff 1996, Claussen & Biggs 2000, Snelder et al. 2005, Matthews & Richter 2007, Brenden et al. 2008, Gao et al. 2009, McManamay et al. 2011a, b). Whatever methods are used to determine environmental flow requirements, as costs and applicability often widely vary, assessments of hydroecological integrity must be carried out within a well defined framework that incorporates rigorous design and analytical techniques to addresses specific management questions (e.g., Cottingham et al. 2005, Souchon et al. 2008). Some of these steps have already been taken with the development of plans to assess regional water resources and their hydroecological integrity in Maryland (Stranko et al. 2011, Fleming et al. 2012). To accomplish the goals of these plans, it is clear that an active, multidisciplinary collaboration will be needed to integrate large, complex data sets and quantify associations across multiple spatial and temporal scales to help resource managers move away from hydraulic or habitat based methodologies towards more holistic approaches that consider water requirements for ecosystems and human populations.

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APPENDIX II. Number of hydroecological studies reviewed by subject and the primary aspect of hydrology examined. Literature reviews generally considered all subjects and aspects of flow regimes, although some were focused on particular topics or response variables. Superscripts correspond to literature in Appendix I.

		Aspect of flow regime studied				
Subject	*N*	Classification	Indices	Minimum / Low	Regime	Variability
Literature review	8	---	---	---	---	---
Hydrology	27	8[14, 52, 74, 75, 86, 90, 105]	6[24, 41, 57, 72, 84, 109]	2[31, 125]	9[17, 37, 43, 45, 100, 103, 116, 128]	2[12, 88]
Fish	34	0	0	10[6, 13, 24, 33, 36, 55, 73, 114, 123, 132]	20[8, 18, 20, 25, 35, 42, 50, 51, 61, 62, 71, 82, 83, 96, 102, 104, 108, 113, 118, 131]	4[49, 53, 77, 89]
Benthic invertebrates	16	0	0	8[5, 10, 29, 81, 122, 127, 129]	7[19, 23, 28, 58, 59, 64, 119]	1[79]
Freshwater mussels	12	0	0	5[38, 39, 44, 46, 67]	5[40, 66, 78, 117, 120]	2[30, 47]
Thermal regimes	5	0	0	0	5[22, 56, 68, 85, 111]	0
Environmental flow	13	---	---	---	---	---
Analysis and design	17	---	---	---	---	---

APPENDIX III. Common biological or hydrological response reported in studies of flow-ecology alteration from a review of scientific literature in relation to the Maryland Hydroecological Integrity Assessment management questions.

Management Question	Response variable	Common response
1. Which stream species (including rare, threatened, endangered, game, invasive, and migratory species) and ecosystems are most/least sensitive to flow alterations? Are there specific biological indicators of water withdrawal?	Hydrology	Change in components of physical habitat including wetted area, bar/island formation, presence of riffle and pool habitat, availability of woody debris, and substrate composition. Disruption of instream and floodplain connectivity.
	Biological	Sensitive, cold-water, and flow specialist species sensitive to alteration and often used as indicators. Tolerant and non-native species respond positively to increased alteration. Native, specialist, and sensitive species responded negatively.
2. Which aspects of flow regimes have the most/least influence on stream species and ecosystems? How do alterations in flow affect species and ecosystems? Can the specific mechanisms responsible for flow alterations be determined and described?	Hydrology	Availability and quality of shallow water habitat affected by baseflow reductions due to withdrawals, impoundments, and land use change. Change in magnitude and frequency of flow effects habitat complexity. Natural flow regime important for biogeochemical processes and structure.
	Biological	Magnitude, frequency, timing, and variability of flow regimes influence species richness, diversity, abundance, and assemblage composition. Reductions in invertebrate taxa richness and density. Habitat fragments, specialist species decline and generalists increase
3. Which components of flow-ecology relationships are most/least affected by surface (intake and impoundment) and groundwater withdrawals?	Hydrology	Reduced base-flow and variability coincides with high withdrawal demand. Impoundments alter magnitude, flood and low-flow frequency, and duration of high and low flows. Thermal regimes altered by epilimnetic and hypolimnetic releases of dams.
	Biological	Species richness and relative abundance affected by withdrawals. Community shifts from specialist and intolerant species towards generalist, tolerant, and invasive species. Habitat connectivity, thermal refugia, recruitment, and survival decrease.

APPENDIX III. CONTINUED

Management Question	Response variable	Common relationships
4. What relationships between surface and groundwater withdrawals and stream ecological integrity can be established?	Hydrology	Decreased magnitude of base-flow, duration of floodplain connectivity. Increased intermittency of flow and habitat fragmentation. Alteration of flow and thermal regime from excessive groundwater withdrawal or impoundment.
	Biological	Increased surface water withdrawals reduced flow specialist and sensitive species, flow regime reflected dam operation. Diminished flow magnitude increased chance of biological impairment. Reductions in groundwater input affect cold- and headwater species.
5. For past and future water-uses, how have/might surface and groundwater withdrawals impact individual species and ecosystems (including scenarios such as: flooding, drought, increasing population, cumulative impacts, climate change, confounding factors, etc.)?	Hydrology	Reduction in annual discharge due to withdrawals and climate change. Impervious area decreased groundwater recharge, increased low flow frequency and duration, and reduced annual base-flow. Groundwater withdrawals decreased baseflow and stream connectivity
	Biological	Decline in native species richness from increase in withdrawal. Loss of biodiversity and ecosystem function. Cold water species vulnerable to climate and land use change where groundwater input is low or excessively withdrawn.
6. What spatial and seasonal aspects of flow need to be maintained for specific streams, including under drought conditions, to ensure the protection of stream species and ecosystems?	Hydrology	Inter- and intra-annual variability should be sufficient to maintain hydrogeomophic processes. Minimum flows should reflect natural range and be sufficient to flush fine sediments and provide adequate water and habitat quality.
	Biological	Minimum flows must protect critical habitats and thermal refuges of species. Variability in regime should maintain abiotic and biotic processes, such as sediment flushing, flood plain connectivity, discourage invasive species, etc. Seasonal high and low flows necessary for reproduction and recruitment.
7. Is additional research and monitoring needed?	Hydrology	Examination of physiochemical variables that co-vary with flow. Need for more rigorous statistical analysis, study designs, and interdisciplinary studies of hydrology and ecology. Better relationship between groundwater and streamflow.
	Biological	Studies on flow-ecology relationships in low range of alteration. Better understanding of relationships between flow alteration and biological response along alteration gradient. Studies at multiple spatial, temporal, ecological, and life-history scales.

APPENDIX IV. Primary and secondary mechanisms of flow alteration responsible for hydrological or ecological response from studies reviewed subjects of biological organisms, stream hydrology, and thermal regimes. The total numbers of studies by primary flow alteration mechanism are in addition to studies that also considered a secondary alteration mechanism. Superscripts correspond to literature in Appendix I.

Flow alteration mechanism	Number of studies
Impoundment	31[8, 10, 22, 25, 40, 43, 45, 47, 49, 50, 61, 62, 66-68, 71, 78, 81, 83, 90, 104, 114, 117, 120, 122, 123]
Withdrawal	16[5, 6, 11, 13, 19, 29, 31, 33, 35, 51, 103, 119, 125, 127]
Land use	8[28, 58, 59, 82, 102, 109, 111, 116]
Climate	6[20, 38, 44, 46, 73, 129]
Impoundment + Withdrawal	3[36, 55, 113]
Impoundment + Climate	1[39]
Withdrawal + Climate	2[108, 131]
Withdrawal + Land use	2[42, 118]