

THE BIOLOGICAL CONDITION GRADIENT: A DESCRIPTIVE MODEL FOR INTERPRETING CHANGE IN AQUATIC ECOSYSTEMS

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Abstract. The United States Clean Water Act (CWA; 1972, and as amended, U.S. Code title 33, sections 1251–1387) provides the long-term, national objective to “restore and maintain the ... biological integrity of the Nation’s waters” (section 1251). However, the Act does not define the ecological components, or attributes, that constitute biological integrity nor does it recommend scientific methods to measure the condition of aquatic biota. One way to define biological integrity was described over 25 years ago as a balanced, integrated, adaptive system. Since then a variety of different methods and indices have been designed and applied by each state to quantify the biological condition of their waters. Because states in the United States use different methods to determine biological condition, it is currently difficult to determine if conditions vary across states or to combine state assessments to develop regional or national assessments. A nationally applicable model that allows biological condition to be interpreted independently of assessment methods will greatly assist the efforts of environmental practitioners in the United States to (1) assess aquatic resources more uniformly and directly and (2) communicate more clearly to the public both the current status of aquatic resources and their potential for restoration.

To address this need, we propose a descriptive model, the Biological Condition Gradient (BCG) that describes how 10 ecological attributes change in response to increasing levels of stressors. We divide this gradient of biological condition into six tiers useful to water quality scientists and managers. The model was tested by determining how consistently a regionally diverse group of biologists assigned samples of macroinvertebrates or fish to the six tiers. Thirty-three macroinvertebrate biologists concurred in 81% of their 54 assignments. Eleven fish biologists concurred in 74% of their 58 assignments. These results support our contention that the BCG represents aspects of biological condition common to existing assessment methods. We believe the model is consistent with ecological theory and will provide a means to make more consistent, ecologically relevant interpretations of the response of aquatic biota to stressors and to better communicate this information to the public.

Key words: aquatic ecosystems; Biological Condition Gradient; biological integrity; biological monitoring; Clean Water Act; disturbance gradient; generalized stressor gradient; quantitative measures in biological assessment; stressors; tiered aquatic-life uses.

INTRODUCTION

Legislative context: the Clean Water Act

Environmental goals expressed in laws and policies articulate the political will of societies to preserve and restore valued aquatic resources. Two examples are the objective of the United States Federal Water Pollution Control Act or “Clean Water Act” (CWA) (United States Code title 33, sections 1251–1387) to “restore and maintain the chemical, physical and biological integrity

of the Nation’s waters” and the objective of the European Commission Water Framework Directive (WFD; European Parliament 2000) to “restore and maintain healthy aquatic ecosystems.” Scientists provide the technical foundation for implementing environmental laws and policies. They develop operational definitions and methods that allow us to measure aquatic resource condition directly, and hence, to attain legislative, policy, and management goals. For example, in both the United States and the European Union, scientists are collaborating with resource managers to strengthen the link between current scientific advances and ecologically sound resource management. Such collaboration enables us to better organize management actions around ecological boundaries rather than

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political jurisdictions and to communicate with the public about environmental conditions in a more meaningful and consistent fashion.

This paper focuses on efforts in the United States, guided by the CWA, to use biological assessments to evaluate aquatic resource condition more uniformly and directly, and to set protection and restoration goals for aquatic life. The CWA integrity objective provides the long-term ecological goal for U.S. water quality programs but does not define the ecological components, or attributes, that constitute biological integrity nor does it recommend scientific methods to measure the condition of aquatic biota. One way to define biological integrity was described over 25 years ago (Frey 1977) and has been refined to mean a balanced, integrated, adaptive system having a full range of ecosystem elements (genes, species, assemblages) and processes (mutation, demographics, biotic interactions, nutrient and energy dynamics, and metapopulation dynamics) expected in areas with no or minimal human influence (Karr and Dudley 1981, Karr and Chu 2000).

To help achieve the integrity objective, the CWA also established, among other things, an interim goal for the protection and propagation of fish, shellfish, and wildlife (U.S. Code title 33, section 1251 (a) (2)). The interim goal for aquatic life has been interpreted by the U.S. Environmental Protection Agency (EPA) to include the protection of the aquatic community, not just fish, residing in or migrating through a waterbody (USEPA 1994). Under the CWA, States have the primary authority for setting water quality goals to protect aquatic life for their waterbodies, i.e., designated aquatic-life uses (U.S. Code title 33, section 1251 (b), 1313). The type of designated aquatic-life use (ALU) assigned to a water body can vary. For example, salmon spawning and recreational fisheries are two types of ALUs. Additionally, with proper demonstration, states may establish ALUs that are limited by factors other than natural condition, e.g., water conveyances for waterbodies that have been significantly altered by concrete channelization.

Over the past 30 years states have independently developed technical approaches to assess condition and set ALUs specific to their own settings. This situation has fostered innovative technical approaches, but it has complicated the development of a nationally consistent approach to interpreting the condition of aquatic resources. A consistent approach to interpreting biological condition will allow scientists and the public to more effectively evaluate the current and potential conditions of specific waters and watersheds and use that information to set appropriate ALUs. Assessment results may be difficult to compare if quantitative outcomes (i.e., index or indicator values) represent different qualitative conditions. Additionally, without a common interpretative framework, the use of different methods can hinder collaboration among natural resource agencies that have complementary missions.

Growing frustration with the inability to communicate effectively about the ecological meaning and management relevance of different quantitative measures of condition spurred our attempt to articulate the conceptual underpinnings that are common to all assessment methods. To help address this issue, we propose a scientific model of biological response to increasing effects of stressors, the "biological condition gradient" (BCG). The BCG encompasses the complete range, or gradient, of aquatic resource conditions from natural, e.g., undisturbed or minimally disturbed conditions, to severely altered conditions. It describes changes in 10 ecological attributes along the gradient caused by increasing levels of stressors. We divide the gradient into six condition tiers, with tier 1 representing natural, or undisturbed conditions, and tier 6 representing severely altered conditions. The tiers describe the ecological condition of the aquatic resource in terms of how close a water body is to the natural state.

The ecological condition to support an ALU for a specific waterbody can be described in terms of the BCG tiers. For example, the ecological condition needed to support salmon spawning corresponds with an exceptional, high-quality, natural stream and will be either a tier 1 or 2 on the BCG. However, the ecological conditions that support adult fish that are desirable for a recreational fishery may span a broader range of conditions, e.g., tiers 1–4. The ecological attributes that characterize the BCG tiers can be measured with methods used by each state, and these condition assessments can be directly linked to a state's ALUs. The BCG provides a rational and consistent means for helping to determine appropriate ALUs in state water quality standards and for assessing whether the standards are attained.

At present, the model applies best to permanent, hard-bottom streams that are exposed to increases in temperature, nutrients, and fine sediments. However, we expect that with appropriate modifications, the model will be applicable to other aquatic ecosystems and stressors. By providing a common foundation for comparing biological conditions, it should be possible to communicate the ecological consequences of different management choices more clearly to scientists, managers, and the public, even when condition is measured by different methods.

Existing conceptual models of biological response to increasing stress

Conceptual models formalize the state of knowledge and guide research. Empirically-based generalizations have led to conceptual models that describe the behavior of biological systems under stress (Margalef 1963, 1981, Odum et al. 1979, Karr and Dudley 1981, Rapport 1985, Schindler 1987, Fausch et al. 1990, Brinkhurst 1993). For example, Brinkhurst (1993:449) observed that "Everyone knew (in 1929) that increases in numbers and species could be related to mild pollution, that

moderate pollution could produce changes in taxa so that diversity remained similar but species composition shifted, and that eventually species richness declined abruptly and numbers of some tolerant forms increased dramatically.” Such ecosystem responses to stress have been portrayed as a progression of stages that occur in a generally consistent pattern (Odum et al. 1979, Odum 1985, Rapport et al. 1985, Cairns and Pratt 1993). Establishing scientifically credible and quantifiable thresholds along that progression is a priority need for resource managers (Cairns 1981).

Conceptual models of ecosystem response to stress have been successfully used to develop resource management strategies that emphasize preservation of important ecological attributes. For example, Lubinski and Theiling (1999) proposed multiple narrative criteria for evaluating the ecosystem health of the Upper Mississippi River. Lorentz et al. (1997) proposed biotic and abiotic indicators of river condition based on theoretical concepts describing natural rivers. Conceptual models of biological response to stressors have been legally codified for management purposes in Maine and Ohio (Courtemanch et al. 1989, Yoder and Rankin 1995a). These states have incorporated multiple tiers of resource quality in their water quality standards (State of Maine 2003, 2004, State of Ohio 2003, Davies et al. 1995). The tiers describe both aquatic-life management goals, e.g. designated aquatic life uses, and attainment criteria for different types of water bodies.

For example, in Maine a water body is assigned to one of four management tiers by considering both its existing biological condition and its highest attainable condition as determined by a public and legislative process. These four tiers of biological quality in Maine’s Water Quality Standards (Table 1) are based on Odum’s subsidy stress gradient (Odum et al. 1979, Odum 1985). Attainment of standards is assessed by determining to which tier a sample of macroinvertebrates is most similar (Courtemanch et al. 1989). Data on taxonomic composition and other metrics are used in a discriminant model to identify the class of waterbody from which the sample was taken (Shelton and Blocksom 2004; S. P. Davies, F. Drummond, D. L. Courtemanch, and L. Tsomides, *unpublished manuscript*). Incorporating multiple tiers has been useful for water quality management in Maine in five significant ways: (1) identifying and preserving the highest quality resources, (2) more accurately depicting existing conditions, (3) setting realistic and attainable management goals, (4) preserving incremental improvements, and (5) triggering management action when conditions decline (Davies et al. 1999).

Our goal in developing the BCG was to extend the empirical work of earlier researchers and practitioners to create a nationally consistent conceptual model that could be used to better link biological goals for resource condition with the quantitative measures used in biological assessments. The BCG was designed to describe

TABLE 1. Maine’s narrative aquatic-life and habitat standards for rivers and streams (summarized from Maine Revised Statutes Annotated).

Class	Biological standard†
AA	Habitat shall be characterized as natural and free flowing. Aquatic life shall be as naturally occurs.
A	Habitat shall be characterized as natural. Aquatic life shall be as naturally occurs.
B	Habitat shall be characterized as unimpaired. Discharges shall not cause adverse impacts to aquatic life. Receiving water shall be of sufficient quality to support all aquatic species indigenous to the receiving water without detrimental changes in the resident biological community.
C	Habitat for fish and other aquatic life. Discharges may cause some changes to aquatic life, provided that the receiving waters shall be of sufficient quality to support all species of fish indigenous to the receiving water and maintain the structure and function of the resident biological community.
Impoundments	Support all species of fish indigenous to those waters and maintain the structure and function of the resident biological community.

Source: Maine Revised Statutes: title 38 [Waters and Navigation], chapter 3 [Protection and Impairment of Waters], Article 4-A [Water Classification Program], sections 464–465.

† The narrative aquatic life standard is the same for Class AA and Class A.

ecological response to stress in sufficient enough detail (i.e., 10 system attributes and six condition tiers) that sample data describing taxonomic composition or biological indicator values could be readily placed into a tier of the BCG continuum.

To build this model, we began with the empirical work of earlier researchers and the conceptual model of Cairns et al. (1993) (Fig. 1). The ideas in Cairns et al. (1993) provided the conceptual foundation for the BCG because they included the concept of “natural” conditions and showed how biological condition declines in relation to spatial and temporal disturbance gradients. Early drafts of the model were modified based on critiques by aquatic scientists from different biogeographic areas, each of whom had 15–30 years of experience in the field. Additionally, to ensure that the model would have maximum potential application, we developed the tiering of the BCG based on the practical experience that states have had in designing and implementing tiered aquatic-life uses. We specifically designed the BCG to meet the following four objectives:

- 1) it describes the complete scale of condition from natural to severely altered;
- 2) it is capable of synthesizing existing field observations and generally accepted interpretations of patterns of biological degradation within a common framework;

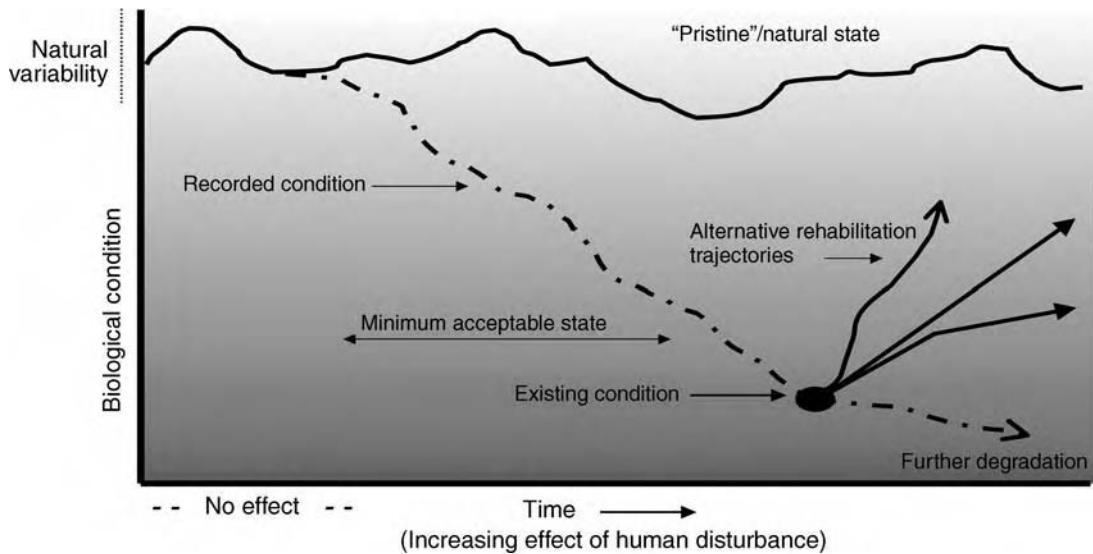


FIG. 1. Conceptual model relating changes in measurable ecosystem attributes to human disturbance over time (modified from Cairns et al. [1993: fig. 1], with permission of Springer Science and Business Media).

- 3) it is based on measurable, ecologically important attributes, or those likely to be measurable in the future, that aid in judging the degree that a system may have departed from natural condition; and
- 4) it is consistent with empirical evidence documenting the trajectories of ecological attributes across stressor gradients.

DEVELOPMENT OF THE BIOLOGICAL CONDITION GRADIENT (BCG) MODEL

The BCG model was developed and tested by a national working group comprised of scientists and managers from Federal, State, and Tribal water resource agencies and academia (Appendix A). Based on recommendations from the full work group, a steering committee created a matrix that summarized the current state of knowledge about how biological attributes change in response to increasing levels of stress in aquatic ecosystems (Table 2, Fig. 2, Appendices C and D). In developing the BCG, we believed it was important to ground the model in both theory and relevance of application to current bioassessment programs. The model had to have a theoretically sound context as well as meet the needs of practitioners around the country. We followed an iterative, inductive approach, similar to means-end analysis (Martinez 1998), in building the model.

We entered the process of model building by testing whether biologists from different parts of the country would draw similar conclusions regarding the condition of a waterbody from simple lists of organisms and their counts. Our approach was based on Maine's experience in which expert biologists independently assigned samples of macroinvertebrates to a priori defined classes of biological condition defined by differences in assemblage

attributes (Davies et al. 1995). In Maine, decision rules were provided to biologists in the form of a 4×31 matrix of expected trajectories of quantifiable aspects of the invertebrate assemblage that corresponded with biological expectations for different water-quality management classes (Table 1). The high level of agreement among experts in placing samples into different classes allowed Maine to develop a predictive statistical model that is now used to assess the biological condition of new sites (Courtemanch 1995, State of Maine 2003, Shelton and Blocksom 2004; S. P. Davies, F. Drummond, D. L. Courtemanch, and L. Tsomides, *unpublished manuscript*).

The BCG describes ecological condition in terms of 10 key attributes expressed at different spatial scales. In biological assessments, most information is collected at the spatial scale of a site or reach and the temporal scale of a single sampling event. Many of the attributes that contribute to the BCG are based on these scales. Site scale attributes include aspects of taxonomic composition and community structure (Attributes I–VI) and organism and system performance (Attributes VII and VIII). To address larger temporal and spatial scales, physical-biotic interactions are also included (Attributes IX and X) because of their importance in evaluating and prioritizing intervention actions and in determining potential for improvement. To provide a practical framework for practitioners, we describe how each of these attributes varies across six tiers of biological response to increasing levels of stressors (Table 2; Appendix C). Terms used in the BCG are defined in Appendix B. Appendix C provides additional narrative detail on transitions between tiers. We recognize that some monitoring programs may be unable to distinguish, or may not require, six tiers. However, the work-group members concluded that six tiers can be

quantitatively distinguished by well-designed and rigorous monitoring programs, and smaller increments of change are useful to show improvements or losses in biological condition.

Finally, the general model is described in terms of the biota of a specific region (Maine) to illustrate how specific ecological attributes vary across the BCG tiers (Appendix D). In the Maine example we describe how the relative densities of specific taxa of varying sensitivities to disturbance change across tiers. This example is based on 20 years of genus/species benthic macroinvertebrate data (400 samples from rivers and streams spanning conditions from near-natural to severely altered) (Davies et al. 1999).

Taxonomic composition and tolerance (Attributes I-V)

Taxa differ in their sensitivities to stressors. Changes in the numbers, kinds, and relative abundance of taxa across stressor gradients are important and useful indicators of adverse effects (Cairns 1977, Karr 1981). Sensitivity of taxa to stress can vary both among species and with stressor. Shifts in taxa as a function of differing sensitivities to aquatic and riparian disturbance are well documented (Table 3). For perennial streams in temperate zones, disturbance tends to select for short-lived, tolerant species and against longer-lived, less-tolerant species (Pianka 1970, Odum 1985, Rapport et al. 1985). In the highest-quality tiers of the gradient, locally endemic taxa that are long lived and ecologically specialized are well represented and the relative abundances of generalists and pollution-tolerant organisms are low. With increasing stress, assemblage composition shifts towards tolerant species or short-lived taxa that can rapidly colonize disturbed environments. Assemblages in the lower tiers are dominated by eurytopic taxa with generalist or facultative feeding strategies.

Nonnative taxa (Attribute VI)

Nonnative taxa represent both an expression of biological condition and a stressor in the form of biological pollution. Although some intentionally introduced species are valued by large segments of society (e.g., gamefish), these species may be just as disruptive to native species as undesirable opportunistic invaders (e.g., zebra mussels). Many rivers in the United States are now dominated by nonnative fishes and invertebrates (Moyle 1986), and introductions of alien species are the second most important factor contributing to fish extinctions in North America (Miller et al. 1989). The BCG identifies maintenance of native taxa as an essential characteristic of tier 1 and 2 conditions. The model allows for the occurrence of nonnative taxa in these tiers if those taxa do not displace native taxa or have a detrimental effect on native structure and function. Tiers 3 and 4 depict increasing occurrence of nonnative taxa. Extensive replacement of native taxa by tolerant or invasive, nonnative taxa occurs in tiers 5 and 6.

Organism condition (Attribute VII)

Organism condition includes direct and indirect indicators such as fecundity, morbidity, mortality, growth rates, and anomalies such as lesions, tumors, and deformities, and for the purposes of the BCG, primarily applies to fish and amphibians. Some of these indicators are readily observed in the field and laboratory, whereas the assessment of others requires specialized expertise and much greater effort. The most common approach for state and tribal programs is to forego complex and demanding direct measures of organism condition (e.g., fecundity, morbidity, mortality, growth rates) in favor of indirect or surrogate measures (e.g., percentage of organisms with anomalies, age or size class distributions) (Simon 2003). Organism anomalies in the BCG vary from naturally occurring incidence in tiers 1 and 2 to higher-than-expected incidence in tiers 3 and 4. In tiers 5 and 6, biomass is reduced, the age structure of populations indicates premature mortality or unsuccessful reproduction, and the incidence of serious anomalies is high.

Ecosystem function (Attribute VIII)

Ecosystem function refers to the aggregate performance of dynamic interactions among an ecosystem's biological parts (Cairns 1977). In this paper, we use the term "ecosystem function" to include measures of both the interactions among taxa (food-web dynamics) and energy and nutrient processing rates (energy and nutrient dynamics). These attributes are included in the BCG because ecologists universally recognize their fundamental importance. At present the level of effort required to assess properties of ecosystem function directly is beyond the means of most state and tribal monitoring programs. Instead, most programs rely on taxonomic and structural indicators to make inferences about functional status (Karr et al. 1986). For example, shifts in the primary source of food may cause changes in trophic-guild indices or indicator species. Although direct measures of ecosystem function are not commonly measured by state or tribal bioassessment programs, they may become practical in the future (Gessner and Chauvet 2002).

Attribute VIII includes aspects of individual, population, and community condition. Altered interactions between individual organisms and their abiotic and biotic environments may result in changes in growth rates, reproductive success, movement, or mortality. These altered interactions are ultimately expressed at ecosystem levels of organization (e.g., shifts from heterotrophy to autotrophy, onset of eutrophic conditions) and as changes in ecosystem process rates (e.g., photosynthesis, respiration, production, decomposition) (Table 4). To illustrate dynamic processes such as these the Maine case example (Appendix D) describes a progression of functional change. It presents a naturally oligotrophic and heterotrophic system with the photosynthesis-to-respiration ratio (P/R) <1 , in tiers 1 and 2.

TABLE 2. Narrative descriptions of the 10 attributes that distinguish the six tiers of the biological condition gradient (BCG).

BGC tier (1–6)	Description
Tier description	
1	Natural or native condition
2	Minimal changes in structure of biotic community; minimal changes in ecosystem function
3	Evident changes in structure of biotic community; minimal changes in ecosystem function
4	Moderate changes in structure of biotic community; minimal changes ecosystem function
5	Major changes in structure of biotic community; moderate changes in ecosystem function
6	Severe changes in structure of biotic community; major loss of ecosystem function
General description of biological condition	
1	Native structural, functional, and taxonomic integrity is preserved; ecosystem function is preserved within range of natural variability
2	Virtually all native taxa are maintained with some changes in biomass and/or abundance; ecosystem functions are fully maintained within range of natural variability
3	Some changes in structure due to loss of some rare native taxa; shifts in relative abundance of taxa but sensitive-ubiquitous taxa are common and abundant; ecosystem functions are fully maintained through redundant attributes of the system
4	Moderate changes in structure due to replacement of some sensitive-ubiquitous taxa by more tolerant taxa, but reproducing populations of some sensitive taxa are maintained; overall balanced distribution of all expected major groups; ecosystem functions largely maintained through redundant attributes
5	Sensitive taxa are markedly diminished; conspicuously unbalanced distribution of major groups from that expected; organism condition shows signs of physiological stress; system function shows reduced complexity and redundancy; increased buildup or export of unused materials
6	Extreme changes in structure; wholesale changes in taxonomic composition; extreme alterations from normal densities and distributions; organism conditioning is often poor; ecosystem functions are severely altered
Attribute I: Historically documented, sensitive, long-lived, or regionally endemic taxa	
1	As predicted for natural occurrence except for global extinctions
2	As predicted for natural occurrence except for global extinctions
3	Some may be absent due to global extinction or local extirpations
4	Some may be absent due to global, regional, or local extirpations
5	Usually absent
6	Absent
Attribute II: Sensitive-rare taxa	
1	As predicted for natural occurrence, with at most minor changes from natural densities
2	Virtually all are maintained with some changes in densities
3	Some loss, with replacement by functionally equivalent sensitive-ubiquitous taxa
4	May be markedly diminished
5	Absent
6	Absent
Attribute III: Sensitive-ubiquitous taxa	
1	As predicted for natural occurrence, with at most minor changes from natural densities
2	Present and may be increasingly abundant
3	Common and abundant; relative abundance greater than sensitive-rare taxa
4	Present with reproducing populations maintained; some replacement by functionally equivalent taxa of intermediate tolerance
5	Frequently absent or markedly diminished
6	Absent
Attribute IV: Taxa of intermediate tolerance	
1	As predicted for natural occurrence, with at most minor changes from natural densities
2	As naturally present with slight increases in abundance
3	Often evident increases in abundance
4	Common and often abundant; relative abundance may be greater than sensitive-ubiquitous taxa
5	Often exhibit excessive dominance
6	May occur in extremely high or extremely low densities; richness of all taxa is low
Attribute V: Tolerant taxa	
1	As predicted for natural occurrence, at most minor changes from natural densities
2	As naturally present with slight increases in abundance
3	May be increases in abundance or functionally diverse tolerant taxa
4	May be common but do not exhibit significant dominance
5	Often occur in high densities and may be dominant
6	Usually comprise the majority of the assemblage; often extreme departures from normal densities (high or low)
Attribute VI: Nonnative or intentionally introduced taxa	
1	Nonnative taxa, if present, do not displace native taxa or alter native structural or functional integrity
2	Nonnative taxa may be present, but occurrence has a non-detrimental effect on native taxa
3	Sensitive or intentionally introduced nonnative taxa may dominate some assemblages (e.g., fish or macrophytes)

TABLE 2. Continued.

BGC tier (1–6)	Description
4	Some replacement of sensitive nonnative taxa with functionally diverse assemblage of nonnative taxa of intermediate tolerance
5	Some assemblages (e.g., fish or macrophytes) are dominated by tolerant nonnative taxa
6	Often dominant; may be the only representative of some assemblages (e.g., plants, fish, bivalves)
Attribute VII: Organism condition (especially of long-lived organisms)	
1	Any anomalies are consistent with naturally occurring incidence and characteristics
2	Any anomalies are consistent with naturally occurring incidence and characteristics
3	Anomalies are infrequent
4	Incidence of anomalies may be slightly higher than expected
5	Biomass may be reduced; anomalies increasingly common
6	Long-lived taxa may be absent; biomass reduced; anomalies common and serious; minimal reproduction except for extremely tolerant groups
Attribute VIII: Ecosystem functions	
1	All are maintained within range of natural variability
2	All are maintained within range of natural variability
3	Virtually all are maintained through functionally redundant system attributes; minimal increase in export except at high storm flows
4	Virtually all are maintained through functionally redundant system attributes, although there is evidence of loss of efficiency (e.g., increased export or decreased import)
5	Apparent loss of some ecosystem functions manifested as increased export or decreased import of some resources, and changes in energy exchange rates (e.g., <i>P/R</i> , decomposition)
6	Most functions show extensive and persistent disruption
Attribute IX: Spatial and temporal extent of detrimental effects	
1	Not applicable; a natural-disturbance regime is maintained
2	Limited to small pockets and short duration
3	Limited to the reach scale and/or limited to within a season
4	Mild detrimental effects may be detectable beyond the reach scale and may include more than one season
5	Detrimental effects extend far beyond the reach scale leaving only a few islands of adequate conditions; effect extends across multiple seasons
6	Detrimental effects may eliminate all refugia and colonization sources within the catchment and affect multiple seasons
Attribute X: Ecosystem connectance	
1	System is slightly connected in space and time, at least annually
2	Ecosystem connectance is unimpaired
3	Slight loss of connectance but there are adequate local recolonization sources
4	Some loss of connectance but colonization sources and refugia exist within the catchment
5	Significant loss of ecosystem connectance is evident; recolonization sources do not exist for some taxa
6	Complete loss of ecosystem connectance in at least one dimension (i.e., longitudinal, lateral, vertical, or temporal) lowers reproductive success of most groups; frequent failures in reproduction and recruitment

Note: For fuller description of BGC tiers, see Appendix C.

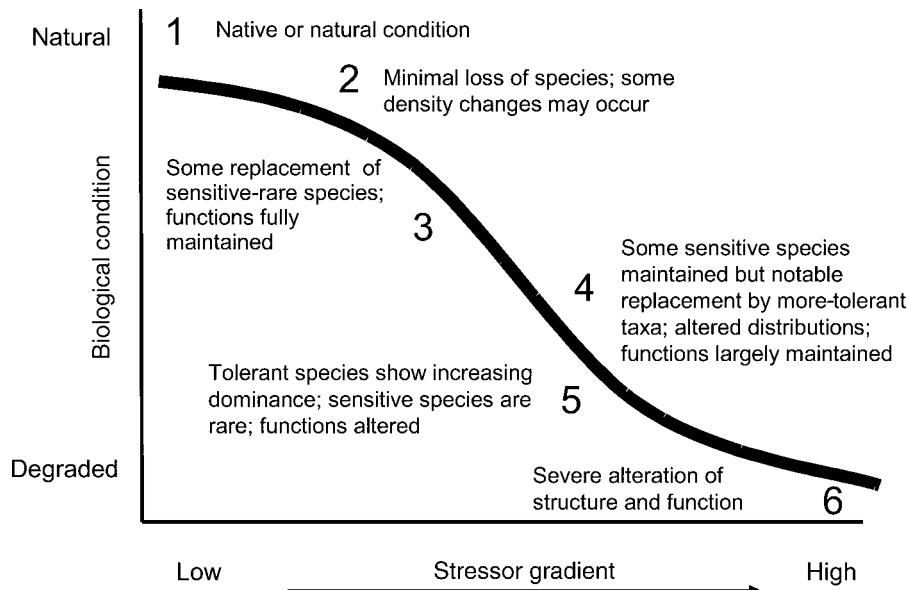


FIG. 2. Conceptual model depicting stages of change in biological conditions in response to an increasing stressor gradient.

TABLE 3. Observational evidence in support of the predicted responses of the ecological attributes in the biological condition gradient (BCG).

BCG response	Case-specific documentation and reference(s)
Attributes I–V	
Shifts in numbers and kinds of species present and number of individuals per species as function of varying tolerances to different kinds of aquatic and riparian disturbance	<p>Changes in lake diatom species composition in response to intentional fertilization (Zeeb et al. 1974, Yang et al. 1996)</p> <p>Loss of sculpins downstream of metal mines (Mebane et al. 2003)</p> <p>Changes in algal species across a nutrient gradient in the Florida Everglades (Stevenson et al. 2002)</p> <p>Changes in diatom assemblages with increased acidification and eutrophication of lakes (Dixit et al. 1999)</p> <p>Shifts in species composition along a gradient of pulp and paper mill effluent concentrations in a Maine river (Rabeni et al. 1988)</p> <p>Shifts in damselfly species from specialist species to generalist species along a gradient of organic pollution in an Italian river (Solimini et al. 1997)</p> <p>Variable sensitivities of benthic macroinvertebrate species to acidic conditions (Courtney and Clements 2000)</p> <p>Changes in fish species composition in an Oregon river with increased nutrients and temperature (Hughes and Gammon 1987)</p> <p>Changes in fish species composition in response to human disturbance (Hughes et al. 1998, Hughes and Oberdorff 1998)</p> <p>Differentially tolerant fish species in response to heavy-metal and dissolved-oxygen gradients in two Indian rivers (Ganasan and Hughes 1998)</p> <p>Variable responses of stream amphibians to severe siltation (Welsh and Ollivier 1998)</p>
Shifts from <i>K</i> -selected strategists to <i>r</i> -selected strategists following disturbance	<p>Shifts from fragmentation-sensitive to fragmentation-tolerant bird species in relation to disturbed riparian habitats (Croonquist and Brooks 1993, Allen and O'Connor 2000, Bryce et al. 2002, Bryce and Hughes 2003)</p> <p>Higher proportion of <i>r</i>-selected species in a flow-regulated river than a natural-flow-regime river (Nilsson et al. 1991)</p> <p>Shift to <i>r</i>-selected, generalist damselfly species along a gradient of increasing pollution (Solimini et al. 1997)</p> <p>Water-level fluctuation in a mesocosm resulted in increased proportion of <i>r</i>-strategist species (Troelstrup and Hengenrader 1990)</p> <p>High pollution stress correlated with increase in <i>r</i>-selected strategists in the same river 21 years apart (Richardson et al. 2000)</p>
Regional and national species-attribute lists and taxonomic-tolerance values	<p>Compendium of pollution tolerance, habitat preferences, feeding guilds for fish species of the Pacific Northwest (USA) (Zaroban et al. 1999)</p> <p>Organic pollution tolerance ranks for Wisconsin stream insect taxa (Hilsenhoff 1987)</p> <p>Compendium of pollution tolerance, habitat preferences, feeding guilds of North American fish and aquatic macroinvertebrate taxa (Barbour et al. 1999)</p> <p>Compendium of pollution tolerance, habitat preferences, feeding guilds for fish species of the northeastern United States (Halliwell et al. 1998)</p>
Attribute VI	
Detrimental effects of nonnative taxa	<p>Loss of 150–200 endemic species in Lake Victoria following intentional introduction of Nile perch (<i>Lates niloticus</i>) and Nile tilapia (<i>Oreochromis niloticus</i>; Witte et al. 1992); dominance of many lowland rivers in western United States by nonnative fishes and invertebrates (Miller et al. 1989, Moyle 1986)</p> <p>Food-web disruption and loss of native mussels from zebra mussel invasion (Whittier et al. 1995)</p> <p>Loss of small, soft-finned fish species from northeast U.S. lakes following predator introductions (Whittier and Kincaid 1999)</p> <p>Mid-20th-century collapse of native salmonid fisheries following colonization of Laurentian Great Lakes by sea lamprey (<i>Petromyzon marinus</i>) and alewife (<i>Alosa pseudoharengus</i>) (Smith 1972)</p>
Attribute VII	
Changes in organism condition or increase in anomalies in response to pollution gradients	<p>Increased fish anomalies in vicinity of toxic outfalls (Hughes and Gammon 1987, Yoder and Rankin 1995b)</p> <p>Altered blood chemistry and mortality in fish associated with wetlands that received oil-sands effluent (Bendellyoung et al. 2000)</p> <p>Changes in growth, organism condition, fecundity, and feeding strategies for creek chub (<i>Semotilus atromaculatus</i>) across a variety of disturbance gradients (urbanization, agriculture, temperature) (Fitzgerald et al. 1999)</p>

TABLE 3. Continued.

BCG response	Case-specific documentation and reference(s)
Attribute VIII	
Disruptions of function at the ecosystem level	Extinction and succession of littoral lake invertebrate species secondary to lake acidification; initially detected by temporal changes in taxonomic and density measures but followed by top-down and bottom-up effects at all trophic levels, caused by reduced nutrient cycling. A trophic cascade ultimately involved loss of fish and increased biomass of primary producers.
Attribute IX	
Influence of spatial and temporal scale of disturbance on biological response and recovery potential	Large-scale, multistate status and trends assessment of Pacific salmon influenced the listing of species under the Endangered Species Act (Nehlsen et al. 1991) Environmental factors operating at different spatial and temporal scales influence production and survivorship of juvenile Atlantic salmon (Poff and Hury 1998) Past land-use activity has long-term effects on aquatic biodiversity (Harding et al. 1998) Assessments of stream-fish and benthic-macroinvertebrate assemblages at state and regional scales reveal serious alterations in indicators of biological integrity (USEPA 2000)
Attribute X	
Ecosystems connectance	Extirpation of Pacific Northwest salmon following construction of impassable dams (Frissell 1993) Extirpation of Colorado River fishes following dam construction (Holden and Stalnaker 1975)

Tiers 3 and 4 show functional changes commonly associated with the effects of increased temperature and nutrient enrichment ($P/R > 1$, diurnal sags in dissolved oxygen, changes in taxonomic composition and relative abundance, increased algal biomass). Tier 5 describes an autotrophic system impaired by excessive algal biomass. Poor water quality described in tier 6 results in negligible algal production. The resulting low photosynthesis and high bacterial respiration causes a reversal back to heterotrophy and $P/R < 1$.

Scale-dependent factors (Attributes IX and X)

Attribute IX describes the spatial and temporal extent of cumulative adverse effects of stressors, and Attribute X describes changes in ecosystem connectance across a disturbance gradient. Both attributes are associated with alterations that occur within entire catchments or regions, or within seasonal and annual cycles. These attributes were included in the BCG because the extent of ecosystem alteration has important implications in terms of an individual water-body's risk of further

TABLE 4. Functional ecological attributes or process rates and their structural indicators (i.e., Attribute VIII: ecosystem function).

Biotic level and function or process	Structural indicator
Individual level	
Fecundity	Maximum individual size, number of eggs
Growth and metabolism	Length/mass (condition)
Morbidity	Percentage anomalies
Population level	
Growth and fecundity	Density
Mortality	Size- or age-class distribution
Production	Biomass, standing crop, catch per unit effort
Sustainability	Size- or age-class distribution
Migration, reproduction	Presence or absence, density
Community or assemblage level	
Production/respiration ratio, autotrophy vs. heterotrophy	Trophic guilds, indicator species
Primary production	Biomass, ash-free dry mass
Ecosystem level	
Connectivity	Degree of aquatic and riparian fragmentation longitudinally, vertically, and horizontally; presence or absence of diadromous and potadromous species

TABLE 5. Assemblage data sources, raters, and concurrence scores for a trial of the draft biological condition gradient (BCG).

Sampling-event type	State data sources	No. biologists; no. states†	Regional subgroups	Concurrence of assignments (%)
Benthic macro-invertebrate (54 samples evaluated)	Arizona ⁴ , Florida ² , Kansas ⁴ ,	33; 21	Northeast ¹	76
	Maine ¹ , New Jersey ¹ , North		South-Central ²	88
	Carolina ² , Ohio ² , Oregon ³ ,		Northwest ³	79
	Texas ⁴ , Vermont ¹		Southwest–Great Plains ⁴	85
Fish (58 samples evaluated)	California, Kansas, Maine, Maryland, Minnesota, Missouri, New Jersey, North Carolina, Ohio, Oregon, Pennsylvania, Texas, Vermont	11; 9	one group	74

Notes: The states are listed in alphabetical order. The superscript numbers in the “State data sources” column correspond to the superscript numbers in the “Regional subgroups” column.

† The number of biologists who reviewed the data and the number of states they represented.

alteration as well as potential for restoration. For example, ecosystem connectivity is fundamental to the successful recruitment and maintenance of organisms into any environment. A single impaired stream reach in an otherwise intact watershed has far more restoration potential than a similar site in a basin that has undergone extensive landscape alteration (Table 3). Tiers 1 and 2 depict a highly connected system in which a natural disturbance regime is maintained. The effects of increasing levels of stressors on the biota in tiers 3 and 4 are limited to the reach or seasonal scale. The two lowest tiers depict a system with stressor effects extending to the catchment scale and affecting multiple seasons. A few “islands” of suitable conditions serve as refugia in tier 5, but extensive loss of connectance and refugia occurs in tier 6.

EVALUATION OF THE BCG MODEL

To test the general applicability of the BCG model to sampling data, we evaluated how consistently individual aquatic ecologists classified typical state and tribal biological data, based on the BCG attributes. Scientists from 23 states and one tribe participated in the data evaluation exercise (Appendix A) and the data that were used represented the basic core elements common to nearly all biological monitoring programs. The full work group was divided into five breakout groups according to regional (Northeast; South-Central; Northwest; Southwest-Great Plains) or assemblage (fish; invertebrates) expertise (Table 5). We used invertebrate and fish data that had been collected by state-tribal programs, from similar-sized, hard-bottom, wadeable streams subjected to a similar stressor gradient (increases in temperature and nutrients from nonpoint and/or point sources). Samples were selected to span as many of the tiers described in the BCG as possible. The 54 invertebrate samples and 58 fish samples used in the tests were collected from six broad geographic regions within the United States and included information about sampling methods; taxonomic names; densities; in some cases, index values; and basic descriptors of stream physical characteristics (substrate, velocity,

width, depth, etc.) (Appendix E). Individuals were asked to place each sample into one of the six condition tiers but were cautioned not to apply a simple relative quality ranking, because all six tiers of degradation did not necessarily occur within the data sets. Biologists primarily relied upon differences in relative abundance and sensitivities of taxa (i.e., Attributes I–VI) to make tier assignments because information needed to evaluate the status of the other attributes was not available.

In the first stage of the data exercise, we evaluated between-biologist differences by asking individual work-group participants to rate a single data set of 6–8 samples from their region. Individuals then were asked to classify samples from larger and more variable data sets. In each case a matrix was produced to show how each biologist rated each site, and overall stream-specific concurrence was calculated (Table 6). Group discussion followed, to summarize the within and between regional consistency of biologists’ interpretations and to identify biological responses to stressors that were not captured by the BCG. Finally, the participants were asked to evaluate how the tiers corresponded to how they currently interpret biological integrity and the CWA interim goal for protection and propagation of aquatic life.

OUTCOME OF THE EVALUATION: LEVEL OF CONCURRENCE AND RECOMMENDED REVISIONS

To evaluate the level of agreement in tier assignments for each break-out group, perfect concurrence was set to equal the product of the number of raters by the number of streams. Any tier assignment that differed from the mode tier assigned by the break-out group members was considered to be nonconcurring (Table 6). Overall average concurrence was 82% for the 54 benthic macroinvertebrate samples (evaluated by four break-out groups) and 74% for the 58 fish samples (one breakout group). When tier assignments differed, they were usually within one tier’s distance in either direction.

Each of the break-out groups independently reported that the ecological characteristics conceptually described by tiers 1–4 corresponded to how they interpret the Clean Water Act (CWA)’s interim goal for protection

TABLE 6. Example results matrix of biological condition gradient (BCG) tier assignments from five reviewer biologists in the invertebrate break-out group for two states in the South-Central region.

Stream name†	BCG tier assignments							
	Reviewer					Summary		
	<i>A</i>	<i>B</i>	<i>C</i>	<i>D</i>	<i>E</i>	Mode	Mean	Consensus
Mill ¹	5	5	5	5	6	5	5.2	5
Stillwater ¹	3	3	3	3	4	3	3.2	3
Salt ¹	1	1	1	1	2	1	1.2	1
Hocking ¹	6	6	6	6	6	6	6	6
Loramie ¹	4	4	4	4	4	4	4	4
Deer ¹	2	2	2	3	2	2	2.2	2
Mud ²	5	4-5	5	4	5	5	4.7	5
Hazel ²	1	1-2	1-2	2	1	1	1.4	1
Alarka ²	2	1	1-2	1-2	2	2	1.6	2
Collasaja ²	4	3-4	4	3-4	4	4	3.8	4
Savannah ²	3	3	3	2-3	3	3	2.9	3
Little Buffalo ²	4	3-4	4	3-4	4	4	3.8	4

Notes: These assignments show 88% concurrence (53 concurring, stream-specific tier assignments out of maximum possible score of 60). Italic numbers indicate non-concurring assignments.

† Superscript numbers indicate states: 1, Ohio; 2, North Carolina.

and propagation of aquatic life, and identified the characteristics described by tiers 1 and 2 as indicative of biological integrity.

Work-group members reported that key concepts were important with respect to classifying samples into tiers and identifying boundaries between tiers. For tiers 1 and 2, biologists identified the maintenance of native species populations as essential to their understanding of biological integrity. Although many participants noted that criteria for distinguishing differences between tiers in Attribute VIII (ecosystem function) were poorly defined, and assessment experience was lacking, most nevertheless identified changes in ecosystem function (as indicated by marked changes in food-web structure and guilds) as critical in distinguishing between tiers 4 and 5.

Participants reported that they mostly use Attributes I–V (taxonomic composition and tolerance), Attribute VI (nonnative taxa, for tiers 2–6 only) and Attribute VII (organism condition, applied to fish) in their monitoring programs to evaluate biological conditions. In contrast, because Attributes VIII–X (ecosystem function and scale-dependent features) are rarely directly assessed by biologists, the evaluation of these attributes in the data exercise was accompanied by relatively high uncertainty. Even so, work-group members strongly advocated retaining these attributes in the BCG because of the practical need for this information in making decisions on restoration potential. Following full work-group recommendations, tiers were revised so that transitions were more distinct.

The presence of nonnative taxa in tier 1 was also the subject of considerable discussion. Knowledge of the extensive occurrence of some nonnative taxa in otherwise near-pristine systems conflicted with the desire by many to maintain a conceptually pure and natural tier. Further discussion resulted in agreement that the presence of nonnative taxa in tier 1 was permissible only if they cause no displacement of native taxa,

although the practical uncertainties of this provision were acknowledged. We also discussed the applicability of the BCG when evaluating the status of threatened or endangered species in a water body. Work-group members concluded that because Attributes I and II (e.g., historically documented and sensitive taxa) assess the status of native taxa, these attributes could be useful in helping to identify species listed as threatened or endangered when classifying a site or assessing its condition.

DISCUSSION

The biological condition gradient (BCG) was designed to facilitate more accurate communication about the existing and potential condition of aquatic resources. For example, the grounding of the BCG in natural conditions will help practitioners and the public recognize that current conditions do not necessarily represent natural conditions. In areas where natural, or near-natural conditions exist, people are generally familiar with what is natural and what has been altered by stressors. But, many of the work-group members with experience in extensively altered regions observed that practitioners and the public alike tend to accept the “best of what is left” as the optimal recovery potential for a system. In these places, it is difficult to visualize those natural conditions that were once present, which results in a truncated perspective on which to base decisions. An improved understanding of the changes that have occurred may result in a more rigorous evaluation of what remains and what could be restored. Use of the BCG facilitates recognition and protection of remaining high-quality waters.

Critical gaps in our knowledge were uncovered during the development of the BCG. For example, the work group identified the need for regional evaluations of species tolerance to stressors. Tolerance information presented in the current version of the BCG tends to be

based on generalized taxa responses to a generalized stressor gradient. At this time, tolerance information is not available for most taxa and for many common stressors (temperature, nutrients, and sediments). In some cases, tolerance values are based on data collected in other geographic regions or for other purposes (e.g., Von Damm's European diatom tolerances are used for North American taxa). Improved tolerance-value information is needed to both refine application of the BCG and evaluate probable causes of biological alteration when developing restoration or remediation strategies.

Additionally, taxa that are considered intolerant of, or sensitive to, changes in environmental condition in one region of the country may not be classified that way in another region. For example, in perennial streams in temperate regions, long-lived taxa have generally been characterized as sensitive to increasing levels of stressors and tend to be replaced by short-lived taxa. As such, the presence of long-lived taxa in a water body has been used to indicate high quality conditions, whereas the predominance of short-lived taxa indicates stress. However, in the arid western United States, extreme changes in hydrology define the natural regime for some systems, and an opposite trend has been observed: short-lived taxa can dominate the biological community in natural settings where the magnitude and frequency of flow is highly variable. In these systems, a shift to long-lived taxa may be an indicator of altered, less variable flow regimes.

The development of the BCG brought the role of science in management into sharper focus. One such issue was the presence of introduced, or nonnative, species in otherwise high-quality aquatic systems. As mentioned earlier, the work group unanimously agreed that maintenance of native species populations was the key determinant for membership in tiers 1 or 2, the biological-integrity categories. However, the role of introduced or nonnative species within these highest categories was vigorously debated. The resulting tier descriptions, allowing for nonnative species in the highest tiers as long as there is no detrimental effect on the native populations, has practical management implications. For example, introduced European brown trout (*Salmo trutta*) have replaced native brook trout (*Salvelinus fontinalis*) in many eastern U.S. streams. In some catchments, brook trout persist only in stream reaches above waterfalls that are barriers to brown trout. The downstream reaches are nearly pristine except for the presence of brown trout (D. Lenat, North Carolina Department of Natural Resources, *personal communication*). In these places, if introduced trout are removed and if stream habitat is preserved throughout the catchment, brook trout could potentially repopulate downstream reaches. In the use-designation process, recognizing that the entire catchment has the potential to attain tier 1 conditions will inform the public that a very-high-quality resource exists. This knowledge could result in management actions to preserve brook trout

where present and maintain potential for restoration where they are not.

Conclusions

The BCG is a descriptive model of biological response to increasing levels of stressors that synthesizes scientific knowledge with the practical experience and needs of resource managers and scientists. We developed the BCG model to serve as an underlying, heuristic framework that (1) synthesizes what we know into testable hypotheses and (2) identifies knowledge gaps in need of further research. By calibrating the model to individual regions, scientific knowledge can be reviewed and consolidated, and research needs can be expressed in a context relevant to management. The BCG data exercise revealed that biologists interpret raw taxonomic data with remarkable consistency. Because we chose to use data sets typical of those that are readily available from state biomonitoring programs, a test of all the attributes described in the BCG was not possible. The introduction of practical and accurate means to assess the status of Attributes VIII–X will extend the ability of resource managers to evaluate restoration potential. Although regional modifications will be needed (Table 7), biologists from across the United States agreed that a similar sequence of biological degradation occurs in streams in response to stressors. This agreement supports the feasibility of using the BCG as a common framework to better define biological goals for a water body.

Use of the BCG should help promote clearer communication of the status and potential of aquatic resources by applying a common accounting framework to diverse extant conditions. At the national level, it should allow us to translate different regional and state assessment measures and standards to a common yardstick. At the regional and state level, the BCG should facilitate organizing management actions along ecological rather than political boundaries, thereby facilitating sharing of data and information. Based on the experience of Maine and Ohio, this model should provide a means for regional and state resource managers to identify and protect outstanding resources, recognize incremental improvements in degraded locations, and appropriately allocate resources and management actions.

We believe future work should focus on developing a comparable model for tiering the generalized stressor gradient and quantifying the relationships between the BCG and both general and stressor-specific gradients (Allan et al. 1997, Yuan and Norton 2003; R. M. Hughes, *unpublished manuscript*). A generalized stressor-gradient model will assist us to better interpret the BCG by defining "reference" and determining how biology responds to different types of individual and cumulative stressors. These are especially important issues to address because (1) least-disturbed "reference" sites differ significantly across states and ecoregions in their degree of departure from historical or natural condi-

TABLE 7. Taxa designated as representative of Attribute I: Historically documented, sensitive, long-lived, regionally endemic taxa, for four different regions of the United States.

State and taxon	Taxa representative of Attribute I
Maine	
Mollusks	brook floater (<i>Alasmodonta varicosa</i>), triangle floater (<i>Alasmodonta undulata</i>), yellow lampmussel (<i>Lampsilis cariosa</i>),
Fishes	brook stickleback (<i>Culaea inconstans</i>), swamp darter (<i>Etheostoma fusiforme</i>)
Washington	
Fishes	steelhead (<i>Oncorhynchus mykiss</i>)
Amphibians	spotted frog (<i>Rana pretiosa</i>)
Arizona	
Mollusks	spring snails (<i>Pyrgulopsis</i> spp.)
Fishes	Gila trout, (<i>Oncorhynchus gilae</i>), Apache trout (<i>Oncorhynchus apache</i>), cutthroat trout (endemic strains) (<i>Oncorhynchus clarki</i>),
Amphibians	Chihuahua leopard frog (<i>Rana chiricahuensis</i>)
Kansas	
Mollusks†	hickorynut (<i>Obovaria olivaria</i>), black sandshell (<i>Ligumia recta</i>), ponderous campeloma (<i>Campeloma crassulum</i>)
Fishes	Arkansas River shiner (<i>Notropis girardi</i>), Topeka shiner (<i>Notropis topeka</i>), Arkansas darter (<i>Etheostoma cragini</i>), Neosho madtom (<i>Noturus placidus</i>), flathead chub (<i>Platygobio gracilisa</i>)
Other invertebrates	ringed crayfish (<i>Orconectes neglectus neglectus</i>), Plains sand-burrowing mayfly (<i>Homoeoneuria ammophila</i>)
Amphibians	Plains spadefoot toad (<i>Spea bombifrons</i>), Great Plains toad (<i>Bufo cognatus</i>), Great Plains narrowmouth toad (<i>Gastrophryne olivaceae</i>), Plains leopard frog (<i>Rana blairi</i>)

† Although not truly endemic to the central plains, these regionally extirpated mollusks were widely distributed in eastern Kansas prior to the onset of intensive agriculture.

tions, and (2) the expected biotic response to otherwise-similar generalized stressor gradients likely varies due to biogeographical differences across the country (Hughes et al. 1986, Hughes 1994, Bryce et al. 1999, Wallin et al. 2003, Stoddard et al. 2006). The integration of BCG and stressor gradients should ultimately provide us with a comprehensive approach to evaluate ecological condition (biological, physical, and chemical) and to more effectively prioritize management actions for either preservation or remediation.

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APPENDIX A

A list of the members of the Tiered Aquatic-Life Use Work Group (*Ecological Archives*: A016-042-A1).

APPENDIX B

Definitions of terms used in the biological condition gradient (*Ecological Archives*: A016-042-A2).

APPENDIX C

Description of the six biological condition gradient tiers (*Ecological Archives*: A016-042-A3).

APPENDIX D

Example of the biological condition gradient using State of Maine data from a cold-water stream catchment (*Ecological Archives*: A016-042-A4).

APPENDIX E

Example of the benthic macroinvertebrate site data used in a U.S. Environmental Protection Agency arid-west regional biological condition gradient data exercise (*Ecological Archives*: A016-042-A5).