Assessing the ecological effects of habitat change: moving beyond productive capacity[1]

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Abstract: Productive capacity can be defined as the "ecological effect" end of a habitat change → ecological effect cause–effect pathway. Determining whether and how a habitat manipulation, either inadvertently or deliberately, will affect productive capacity is the key analytical step of habitat management. We describe a process to ensure that this step is conducted in a manner that is rigorous and relevant. The process has four components: (1) determination of management objectives, (2) identification of indicators, (3) analysis of cause–effect pathways linking habitat changes to ecological effects, and (4) determination of strategies to effect desirable habitat change. The core of the process is the third step, in which we propose the use of hypotheses-of-effect, a network of cause–effect linkages leading from habitat change to ecological effects, to ensure rigorous assessment of possible effects. We illustrate the process using examples of timber management effects on migratory brook trout (*Salvelinus fontinalis*) and urbanization effects on littoral warmwater communities. We argue that this process, in addition to providing a rigorous means of assessing the evidence relevant to a particular issue, also provides an effective tool for examining uncertainty. We advocate the adoption of this process by management agencies as a method for adaptive habitat management.

Résumé : La capacité de production peut être définie comme l'«effet écologique» final résultant d'une modification de l'habitat, c'est-à-dire le résultat d'un processus de cause à effet. La principale étape d'une analyse de la gestion de l'habitat consiste à déterminer si et dans quelle mesure une modification de l'habitat, délibérée ou non, aura un effet sur la capacité de production. Nous décrivons une méthode permettant d'assurer que cette étape est menée de façon rigoureuse et pertinente. La méthode comporte quatre éléments : (1) la détermination des objectifs de gestion, (2) la détermination des indicateurs, (3) l'analyse des mécanismes de cause à effet qui s'exercent entre les modifications apportées à un habitat et les effets écologiques, et (4) la détermination des stratégies permettant d'apporter des modifications souhaitables à l'habitat. C'est le troisième élément de cette méthode qui est le plus important; nous proposons une série d'effets hypothétiques, c'est-à-dire un ensemble de causes liées à certains effets qui permettent de prédire les effets écologiques qu'entraîneront certaines modifications apportées à l'habitat, dans le but d'analyser de façon rigoureuse tous les effets possibles. Nous illustrons cette méthode à l'aide d'exemples: les effets de la gestion forestière sur les populations migratrices d'omble de fontaine et les effets de l'urbanisation sur les communautés vivant dans les eaux tempérées près du rivage. Nous sommes d'avis que cette méthode, outre le fait qu'elle constitue une façon rigoureuse d'évaluer les données dans un cas particulier, offre également un outil efficace pour évaluer l'incertitude. Nous proposons aux organismes de gestion d'adopter cette méthode pour une gestion adaptative de l'habitat.
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Introduction

In 1986, the Canadian federal government released a policy for the protection of fish habitat (DFO 1986) whose purpose was to ensure the net gain of fish habitats in Canada. One of the key tenets of this policy is that the fundamental attribute of fish habitat to be protected (restored or enhanced in the case of compensation) is its productive capacity. Productive capacity is defined in the policy as "the maximum natural capability of habitats to produce healthy fish, safe for human consumption,

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or to support or produce aquatic organisms upon which fish depend." As with many integrative ecological concepts, the term productive capacity is ambiguous. This ambiguity is beneficial, as it allows the concept to be applied to the broad array of circumstances wherein habitat modifications may be affecting valued components of aquatic ecosystems. The price to be paid for this generality, however, is the challenge, for any specific situation, of determining how to quantify changes to productive capacity. The productive capacity concept and its enshrinement in policy begs two important questions: (1) how should productive capacity be measured and (2) how well do we understand the relationship between productive capacity and human-induced habitat change. These two questions are the subject of this synthesis.

Although the above definition of productive capacity derives from a Canadian policy document, its relevance to the science of habitat management transcends political jurisdictions. Many of the formative ideas underlying the development of the productive capacity concept stem from seminal works in fisheries science (e.g., Ivlev 1966; Ricker 1975). In a contemporary context, the concept seeks to provide a practically useful measure of habitat suitability, such that changes in its value can be ascribed to ecologically significant habitat change. Defining meaningful, measurable metrics of habitat loss (or gain) is a need basic to all agencies whose mandate includes the conservation and restoration of aquatic habitats.

The need for a process for measuring productive capacity

The term productive capacity suggests a relationship to two common concepts in ecology: (1) production or productivity and (2) carrying capacity. Both concepts have been defined in the ecological literature, but neither definition is adequate to capture the intended breadth of definition of the productive capacity concept. While a loss of ecological production is often the most important metric of the effect of habitat loss, especially for exploited fish populations, there are many instances in which production is not the attribute of interest. For example, a habitat manipulation may result in no change to overall production but a pronounced shift in species composition or diversity. Depending on the human values associated with the species inhabiting the affected system, the implications of change can range from inconsequential to important (i.e., loss of an endangered species). Even where stock productivity is of primary interest, production in exploited populations can be affected by the level of harvesting, irrespective of changes in habitat, implying that production itself may not be a sensitive, diagnostic, indicator of important changes to habitat. We interpret the spirit of the productive capacity concept to mean something more than production, something whose definition is issue dependent and something that constitutes the "effect endpoint" of the cause–effect pathway linking habitat changes to ecological effects.

While a broad definition of productive capacity may be necessary to embrace the breadth of concerns about habitat manipulations, it is certainly not sufficient to allow scientifically rigorous habitat management. In practice, this broad definition must be translated into a set of specific, measurable ecosystem attributes that can form the basis of both predictions about, and monitoring of, effects. Human activities alter fish habitats in innumerable ways, leading to a host of different effects on the fish populations utilizing those habitats. The changes can be to physical, chemical, biological (e.g., vegetation removal) aspects of a fish species' or community's habitat; can be direct (e.g., substrate removal) or indirect (e.g., land-use changes affecting hydrology); and can occur at a variety of different spatial and temporal scales. The effects of such changes could range from altered contaminant levels (edibility) in individual fish to shifts in species diversity. With such a diverse array of potential interactions all being part of the habitat change → ecological effect linkage, it is important to define a process to focus the investigation of a particular issue. This is a significant challenge, but we argue that it is essential to utilize such a process to ensure comprehensiveness, objectivity, and analytical rigour. In this paper we propose such a process and illustrate it using two examples relevant to the Great Lakes basin.

The overall process

Habitat management issues can be broadly divided into two groups. The first (type A) consists of issues where management objectives have been specified, and the question is whether habitat manipulations can be used to achieve the stated objectives. Great Lakes Remedial Action Plans (RAPs) contain good examples of type A issues, wherein habitat manipulations are considered as means to restore impaired uses (Koonce et al. 1996). The second (type B) includes cases where a particular habitat manipulation or set of manipulations is proposed, and the question is what the effects of the manipulations might be. Type B issues are frequently part of environmental assessments, where the manipulations are proposed to meet economic objectives (e.g., dam construction, urban development), and concerns have been raised about ecological effects. These two groups of issues are quite different, but they have (or should have) in common four primary components: objectives, indicators of ecological effects, the habitat changes themselves, and tools or strategies to achieve the habitat changes. Our process comprises the systematic evaluation of each of these components and the linkages among them.

The analysis of all habitat management issues should begin with a careful articulation of ecological objectives or targets. For type A issues this requirement is obvious. However, even in cases (type B) where the challenge is to judge whether the effects of an already proposed manipulation are desirable, or at least not deleterious, it is essential to determine objectives at the outset. Consider a simple, but realistic case in which a dam removal is proposed that will enhance access for migratory salmonine species to the headwaters of a river system (Giesy et al. 1994). The migratory species are not native and contain elevated body burdens of organochlorine contaminants. The headwater areas are presently occupied by a native, nonmigratory salmonine species and by mammalian and avian predators that feed on salmonines and presently have low organochlorine body burdens. Before one can judge the suitability of this manipulation, it is necessary to know the ecological management objectives for the area (e.g., enhancing migratory salmonine fisheries; conserving native species; eliminating man-made barriers to fish movements; minimizing the exposure of wild populations to toxic substances; minimizing access of other migratory species such as the sea lamprey

(*Petromyzon marinus*) to new habitats). Regardless of the type of issue, the first step should be the specification of objectives or targets.

A clearly stated set of objectives is a prerequisite for the next step in the process: the determination of relevant indicators of ecological effects. The indicators are those aspects of the population, community, or ecosystem that provide a measurable reflection of whether objectives or targets are being met. The crux of habitat management is allowing or prescribing habitat changes that have desirable ecological effects and preventing or mitigating those changes that have undesirable effects. In our process, indicators provide the measures of productive capacity according to our earlier definition; they represent the endpoints of a chain of cause and effect that begins with habitat change. Beanlands and Duinker (1983) coined the expression "valued ecosystem component" to fulfil a similar purpose in environmental impact assessment. The essential attributes of the indicators are that they are measurable and that their measured state can be used to determine the extent to which the previously stated objectives are being met. Once these indicators have been determined, an important part of any habitat management study is to design and implement a procedure for assessing the current status of the indicators, a benchmark against which future change can be contrasted.

The third component of the process is the list of habitat changes to be considered. For type A issues one needs to consider what habitat change might influence the indicators. For type B issues the habitat changes have already been specified, as in our dam example above. The rigorous, analytical component of the process centres around systematically evaluating the evidence for linkages between the habitat changes under consideration and the indicators of ecological effects; we describe the steps in detail below. As the analysis proceeds, the appropriate scale for assessing these influences needs to be specified (Lewis et al. 1996). Modifications to habitat fundamentally have two components: the magnitude of change per unit area and the overall areal extent of the change (Minns 1995). To a large degree, the scale issue is one of emphasizing the importance of quantifying the second component (areal extent) when evaluating the overall effects of a habitat modification. Minns (1995) developed a quantitative methodology for integrating these components. As well, the relative influence of other factors on the indicators needs to be examined, including both habitat features that are not being considered for manipulation and processes other than habitat that affect the indicators (e.g., biotic interactions, exploitation). Failure to consider the contribution of these other factors to the dynamics of the indicators can easily lead to naive expectations for the effects of a particular manipulation when in fact some other ecosystem component is limiting. Finally, once the potential influence of the manipulation(s) has been evaluated in the proper spatial, temporal, and ecosystemic context, a strategy can be selected to achieve the objectives.

This process is not novel, nor does it embody any insights beyond what might be considered common sense. Similar approaches have been advocated for environmental impact assessment in Canada (Beanlands and Duinker 1983) and for environmental monitoring in the United States (EMAP 1994). Yet, despite its seemingly obvious nature, more often than not habitat management issues have been confronted without using a framework such as this. As a result, measures to protect or restore habitats have not adequately considered issues of scale, with the result that large-scale processes (e.g., watershed land-use changes) override the desired effects of small-scale manipulations (e.g., spawning site rehabilitation). Similarly, habitat manipulations may not have the desired effects because other processes (e.g., predation or a limiting habitat at another life stage) exert a greater control over the dynamics of the target species or community. Finally, the effects of the habitat alteration, even if they do occur, may not be observed because either inappropriate indicators were chosen, or inadequate commitment was made to monitoring the effects of the manipulation.

Components of the process

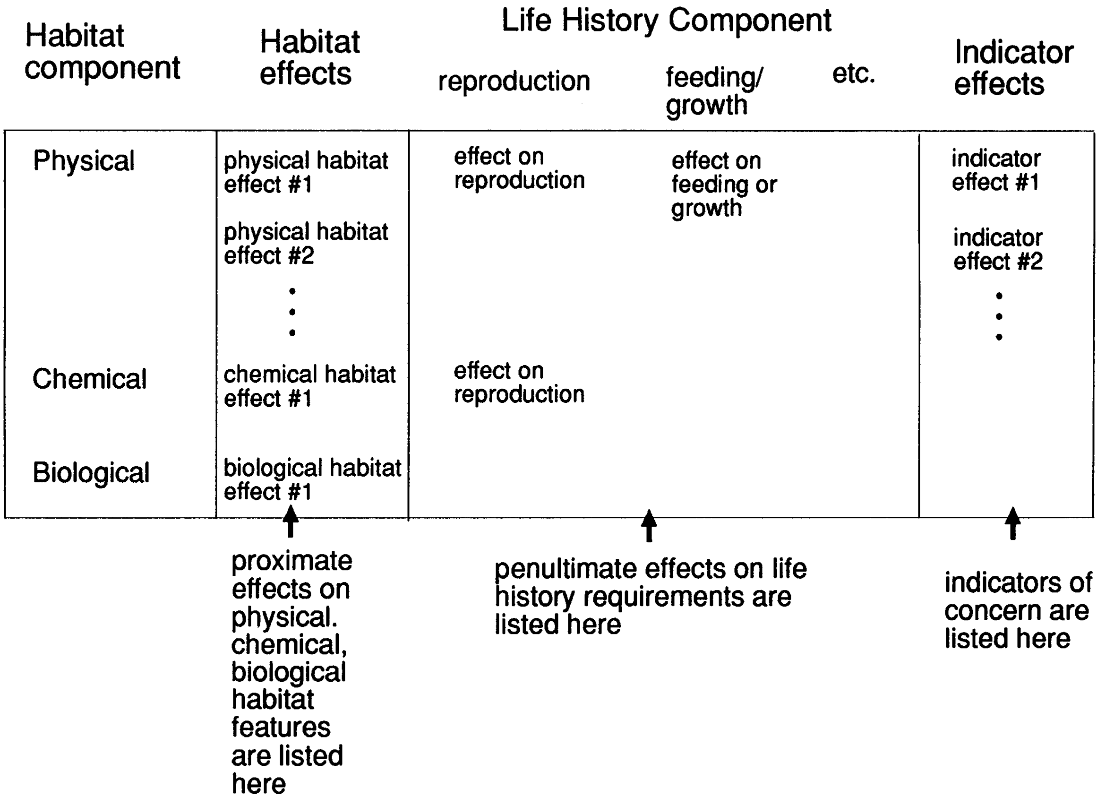
Objectives and indicators for habitat management

Each habitat management issue will have its own set of specific objectives. Most specific objectives, however, derive from one of four general goals for ecosystem management: (1) to maintain or increase (optimize) the harvest or yield of fish from an ecosystem; (2) to protect or conserve healthy ecosystems from the effects of human activities; (3) to preserve pristine or undisturbed natural systems; and (4) to restore degraded ecosystems to a healthier state.

The first of these goals reflects the traditional goal of fisheries management, namely the maintenance of productive fisheries in the face of pressures for alternative uses of the habitats upon which the fisheries depend for sustainable production. It is this goal that is most easily reflected in the concept of productive capacity as defined by DFO (1986), although the federal policy certainly recognizes the importance of the other goals. The remaining three goals reflect a more contemporary view of ecosystems as having value beyond simply their utilitarian purpose (e.g., Norton 1987; Callicott 1991; Olver et al. 1995). The second and third goals will generally apply to situations where a regulatory agency is evaluating potential effects of a proposed habitat manipulation, while the fourth is more concerned with determining the most suitable manipulations to achieve a particular restoration objective (type A issues). Sometimes, however, the distinction between these categories can break down, as is the case for the example presented above. If the dam is viewed as a man-made structure that has "degraded" access to the headwaters for migratory fishes the goals and objectives will be different than if the headwater areas are viewed as relatively healthy ecosystems at risk of invasion by non-native migratory species.

The most suitable set of indicators for a particular issue will depend upon the nature of the issue and the management objectives. Traditionally, the most commonly used indicators have been population-level measures of either supply (standing stock, production) or use (yield, catch rates). When the objectives include community-level concerns, measures of community status such as species diversity, species richness, and genetic diversity may provide more suitable indicators. Issues involving sub-lethal effects may call for other indicators such as contaminant levels, physiological changes, or behavioral changes. Finally, there are often practical impediments to the use of population- or community-level indicators. Sometimes, these indicators are simply too costly to accurately measure; alternatively, they may not be sufficiently diagnostic

Fig. 1. A general matrix to summarize the possible linkages between habitat modifications and ecological indicators. The matrix details the hypothesized changes to physical, chemical, and biological components of habitat and their potential effects on species life-history requirements and, ultimately, on population- or community-level indicators.



of the habitat changes that are being evaluated. In such cases, surrogate, nonbiological indicators (e.g., physical or chemical changes) may be proposed, although the utility of these measures as indicators depends crucially on a previously demonstrated linkage between the surrogate indicator and the ecological effect it is intended to reflect. The process described below provides an objective approach for determining whether the use of a surrogate indicator is defensible.

Cause–effect pathways

The first steps of the process define the scope of the problem, setting the context for the analysis that follows. The type of issue (A or B) is determined together with the set of habitat manipulations under consideration. The issue is placed in the context of management goals and more specific objectives for the system(s) that stand to be affected, and indicators are identified that will provide measures of whether objectives are being met. Now a systematic process must be followed to evaluate the range of effects that the manipulations might be expected to have on the chosen set of indicators. While it is relatively easy to speculate on the range of possible effects of a particular manipulation, determining which of these possible effects are likely to occur in the specific instance under investigation is more challenging and calls for a rigorous, comprehensive approach that not only identifies likely effects but also exposes critical uncertainties.

Virtually without exception, the linkages between habitat changes and ecological effects involve a complex network of cause and effect. Rarely is only a single pathway involved, so the relative importance of different pathways must be assessed, not to mention possible interactions. Each cause–effect pathway typically involves several steps. Removing a dam can involve alterations to hydrology, sediment dynamics, thermal regimes, and species composition above and below the former dam site. Each of these proximate effects may translate into a variety of further effects such as patterns of seasonal floodplain inundation, bank erosion, changes to stream channel morphology, and contaminant exposure for top predators. These changes in turn can affect the ability of species to fulfil their life-history requirements. Finally, these penultimate effects on life history may translate into changes to the chosen indicators of ecological effect.

We propose a two-stage approach to describing and evaluating this potentially complex network of habitat change → ecological effect linkages. The first stage is to divide the proximate effects of habitat changes into physical, chemical, and biological components; to divide the possible penultimate effects on the indicator organisms into broad life-history categories; and to summarize this information in a matrix (Fig. 1). The second stage involves recasting the cause–effect linkages implied by the matrix into a series of multistage hypotheses that can be systematically evaluated for evidence to support (or refute) the hypothesized cause–effect pathway. The process is designed to allow the practitioner to judge the likelihood of desirable effects and, equally important, the uncertainty associated with this judgement. A similar approach has been used

Table 1. Habitat change → ecological effect matrices for a migratory brook trout population.

		Life-history component				
Habitat component	Habitat effects	Reproduction	Feeding/growth	Cover/survival	Migration	Indicator effect
				Access road construction		
Physical	Creation of physical barriers to movement				↓Access to spawning and rearing areas	↓Production
	Acute exposure to sediment inputs	↑Egg mortality	↓Food consumption	↓Juvenile survival		↓Abundance
	Direct destruction of spawning and nursery habitat	↑Egg mortality		↓Juvenile survival		↓Genetic diversity
				Logging		
Physical	Changes to watershed hydrology	↓Incubation success		↓Overwinter survival		↓Production
	↑Sediment inputs	↑Egg mortality	↓Food availability			↓Abundance
	↓Streamside shading		↑Food availability	↓Survival during temperature extremes		↓Genetic diversity
Chemical	↑Nutrient inputs		↑Food availability			

successfully in an environmental assessment context (Bernard et al. 1993).

The best way to explain and demonstrate the generality of this process is to illustrate it using realistic and contrasting examples. We will use four habitat alteration examples, two for a migratory salmonid species and the other two for a littoral centrarchid community. These examples are not intended to be comprehensive treatments. Rather the examples are provided to illustrate the process we propose and to expose some of the challenges associated with its use.

The habitat change → ecological effect matrix

Example 1. Timber management and migratory brook trout (Salvelinus fontinalis) populations

Historical accounts suggest that large, migratory brook trout populations, locally known as “coasters,” were once an important part of the Lake Superior fishery (Roosevelt 1865; Shiras 1927). The coasters utilized Lake Superior tributaries for spawning and early rearing, and then moved to the lake where they grew to adult sizes in excess of 2–3 kg. As a result of exploitation and, perhaps, habitat loss, today only remnant populations remain in localized, relatively remote areas (e.g., Isle Royale, Nipigon River). Protection of these remnant stocks and restoration of stocks into streams where they historically occurred have become management priorities for fisheries management agencies around Lake Superior. An important component of this effort is to ensure that aquatic habitats in areas where coasters presently exist or in areas where restoration is targeted remain in a state that allow coasters to complete their riverine life-history requirements. The management objective in this case is to protect habitats in areas currently or potentially utilized by coaster brook trout from the effects of human activities. For streams currently utilized by coasters, an appropriate indicator might be the maintenance of juvenile (presmolt, age 1 and older) brook trout summer densities within the range of one to five fish per 100 m^2 of available habitat.

Much of the Lake Superior watershed is forested and is the object of an economically important timber industry. Both access road construction and clear cutting can have effects on aquatic habitats. The former results in a relatively localized, direct habitat alteration, while the effects of the latter are thought to occur on a larger scale and include indirect influences. Both activities, combined with the objective stated above, constitute examples of type B issues, in which the purpose is to evaluate the potential effect of a human activity on aquatic habitat.

Access road construction could affect coaster brook trout habitat in several ways (Table 1). If stream crossings result in excavation or burial of substrate typical of quality brook trout spawning habitat, localized, but permanent habitat loss may occur. During construction of both roads and crossings, the opportunity for large increases in sediment loads to streams arises. Such inputs of sediments will likely increase stream turbidity and alter substrate composition. Increased suspended sediment concentrations in streams can also affect instream erosion by altering flow characteristics and frictional forces within the channel (Parker et al. 1982; Gordon et al. 1992). These effects are likely to be distributed over a wider area of aquatic habitat but are also likely to be transient in nature. Depending on the design and construction of the crossings, access of brook trout to upstream spawning areas (or overwintering habitats) may be restricted. This is an example of a local alteration having a potentially wide ranging effect. Together these examples illustrate how consideration of spatial and temporal scales is a critical component of the evaluation of habitat effects.

Clear-cutting can also affect coaster brook trout habitats through a variety of pathways (Table 1). Removal of a large fraction of the forest cover from a catchment may have significant effects on the basin’s hydrology, including groundwater

Table 2. Habitat change → ecological effect matrices for a nearshore centrarchid community.

Habitat component	Habitat effects	Reproduction	Feeding/growth	Cover/survival	Migration	Indicator effect
		Macrophyte addition				
Physical	↑Macrophyte density	↑Spawning success		↓Predation risk		↑Community production
	↓Fetch					
	↓Erosion and siltation	↓Egg mortality				↑Species diversity
Chemical	↓Turbidity		↑Food availability	↑Predation risk		
Biological	↑Detritus		↑Food production			
		Urbanization				
Physical	↑Sediment loads to nearshore	↓Spawning success	↓Food availability	↓Predation risk		↓Community production
	↑Temperature	↓Egg mortality				↓Species diversity
Chemical	↑Nutrient inputs		↑Food availability			
	↓Oxygen levels	↑Egg mortality		↑Juvenile mortality		
	↑Contaminant loadings	↓Reproductive success				↑Body burdens

dynamics and overall basin water yield. Nutrient budgets may also be affected. During both the tree removal operations and the early period of subsequent regeneration, sediment dynamics can be greatly altered, especially if cutting is permitted in the riparian zone. Finally, removal of riparian vegetation may also expose stream reaches to increased solar radiation and thus increased water temperatures.

The habitat alterations described above could have a variety of effects on coaster brook trout populations. Removal or burial of spawning habitat, accumulation of fine material in spawning gravel, or reduced access to spawning areas will all affect spawning success. Reduced groundwater discharge may also render traditional spawning habitats less suitable. High sediment loads may affect juvenile feeding success. Increased nutrient loads together with increased temperatures and solar radiation due to reduced shading could lead to increased growth and survival, provided levels do not become excessive. As well, changes to groundwater inputs and reduced shading will interact to affect temperature extremes in summer and winter and through this, juvenile brook trout growth and survival.

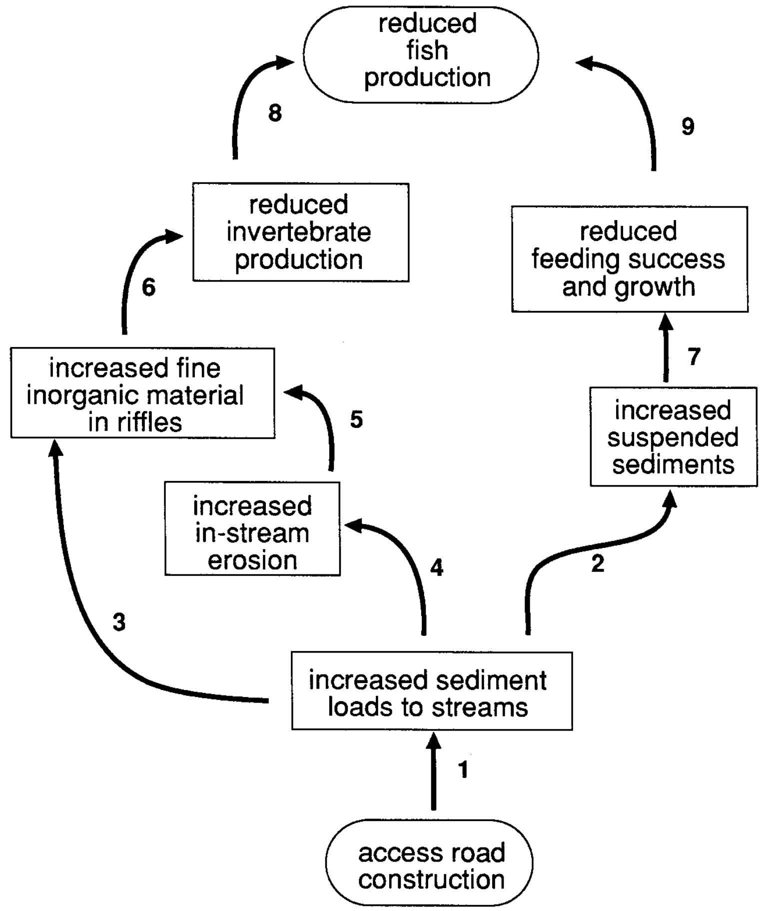
Example 2. Littoral centrarchid communities in Great Lakes coastal wetlands

Often, interest in the effects of habitat change is directed towards the community, rather than the population level. One example would be the complex of warmwater species, often dominated by centrarchids, found in nearshore embayments and wetlands around the Great Lakes. The vast majority of shoreline wetland areas around the Great Lakes have been lost during the past 100 yr as a consequence of the settlement and industrialization of the basin. Accordingly, much recent concern has been expressed about the protection and restoration of the few remaining areas. Two relevant but contrasting habitat management issues for Great Lakes littoral centrarchid communities are (1) will creation (addition) of areas of macrophytes benefit this fish community; and (2) will urbanization of lands adjacent to and draining into nearshore habitats degrade this community. The first of these is a type A issue, and is frequently found as a proposed strategy in RAPs. The second is a type B issue. The two issues also differ with respect to scale, the former operating primarily at the local, within-wetland scale while the latter embraces a larger, watershed scale that includes the littoral zone and the (urbanizing) upland areas that drain to the wetland. For both issues, the (ecological) management objective could be stated as to restore (issue 1) or maintain (issue 2) the health and productive capacity of the warmwater fish community in the affected nearshore areas. Indicators of the achievement of this objective would include (1) restoring or maintaining the abundance and production of species at levels within the natural bounds of variation found at healthy sites; (2) maintaining or increasing species diversity; and (3) maintaining levels of contaminants in fish low enough to allow safe human consumption.

The habitat change → ecological effect matrices for these examples have the same structure as for the migratory brook trout example (Table 2). Habitat changes caused by the addition of macrophytes would include the obvious consequence of increased macrophyte density (at the site level), but also indirect effects such as increased detritus production, and potentially reduced fetch, erosion, and turbidity. Habitat changes resulting from watershed urbanization are more difficult to predict and measure; in general effects on fish habitat in nearshore areas will result from changes in the quantitative and qualitative characteristics of streams draining from the urbanized area into the nearshore habitats. Urbanization tends to increase the imperviousness of watersheds, leading to changes in discharge patterns. Streams experience higher peak flows and lower base flows (Klein 1979). The hydrological changes and the increased erosion that tends to follow can result in greater sediment and nutrient inputs into nearshore areas. Reductions in oxygen concentrations can result if nutrient inputs are excessive. Water temperatures and contaminant levels may also be elevated.

These changes could lead to several effects on centrarchid communities utilizing these nearshore habitats. Increased macrophyte cover (Table 2) may provide cover and spawning habitat for fish and may increase food production resulting

Fig. 2. An example hypothesis-of-effect from the coaster brook trout – forestry access road case. The habitat manipulation is listed at the bottom and the various intermediate effects are depicted as boxes connecting the habitat change to the indicator listed at the top. The numbered arrows connecting each box represent the individual steps (sub-hypotheses) in the cause–effect pathway(s) leading from the habitat manipulation to the indicator.



from elevated primary production and especially detritus. Reductions in fetch, erosion, and turbidity may enhance feeding success or survival of incubating eggs but may also increase vulnerability to visual predators. As well, reduced turbidity may further enhance primary production, thereby allowing additional expansion of macrophyte cover in the affected areas.

Habitat changes potentially resulting from watershed urbanization can affect reproduction, feeding, and cover for fish (Table 2). Sediment loading may have a negative effect, specifically on the quality of spawning habitat for fishes, and on the habitat of the biota in general. Loadings of fine sediments will also increase turbidity, thereby reducing visibility for visual predators, as well as light penetration and, consequently, macrophyte growth. Increases in nutrients may increase both primary and secondary production, but changes in species composition may also occur. If nutrient inputs are excessive, lower oxygen levels may result because of decomposition and excessive biological oxygen demand. Another potential impact of watershed development is an increase in anthropogenic contaminants (e.g., lead and cadmium from automobiles, organochlorines from various sources). Contaminants may affect the edibility of fish and may also have short- or long-term effects on life-history processes such as reproduction or survival rates.

Hypotheses-of-effect: evaluating knowledge and uncertainty

The matrices presented in Tables 1 and 2 provide summaries of the possible effects of concern for a particular issue. Each matrix is a conceptual model of the connections between a habitat manipulation and the potentially affected ecosystem. Once a matrix has been developed, a systematic process of evaluating relevant knowledge can begin. The elements of the matrix imply a network of cause–effect linkages that connect the habitat changes to ecological effect indicators. Individual cause–effect pathways can be extracted from the matrix that form a multiple-step hypothesis that connects the initial habitat manipulation to the ultimate effect. We refer to these pathways as “hypotheses-of-effect.”

Each step or linkage in an overall hypothesis-of-effect should be described as a statement that constitutes, in effect, a potentially testable (sub-)hypothesis. For example, the first linkage in an hypothesis-of-effect connecting access road construction to coaster brook trout production via sediment loading impacts (Fig. 2) could read, "Forestry access road construction will lead to increased sediment loads to streams." Similar statements would be developed for each of the other linkages (2–9) depicted in Fig. 2.

The process of evaluating evidence then involves addressing a series of specific questions concerning each of the linkages in the overall hypothesis-of-effect: (1) How strong is the evidence supporting this linkage? (2) At what scale is it appropriate to evaluate or measure this linkage? (3) Are there other factors that, depending on their state, may affect the significance of this linkage? (4) What critical uncertainties exist that make it difficult to reach a firm conclusion on the likelihood of this linkage being true? (5) Assuming there is evidence for an overall effect on the indicator, can the effect be mitigated at the stage represented by this linkage?

Again, using the example of linkage 1 in the hypothesis-of-effect depicted in Fig. 2, the analysis might proceed as follows.

There is little doubt that, in the absence of any mitigative measures, the construction of forestry access roads will lead to increases in the loadings of suspended inorganic matter to streams, especially in the vicinity of stream crossings (Anderson 1971; Plamondon et al. 1982, cited in McNamee et al. 1988). The effect is likely to be greatest immediately downstream of crossings, diminishing as the suspended material is either diluted by mixing with water from other tributaries or deposited in low energy habitats such as pools. Forestry operations typically call for several crossings, sometimes of the same stream, however, so cumulative, larger scale effects cannot be ignored. The magnitude of this effect will depend on the topography and physiography of the areas, with the greatest concerns arising in areas with highly erodible soils and high relief.

In the rugged terrain north of Lake Superior where coaster brook trout are or were present, it is likely that significant sediment inputs would occur in the absence of mitigative measures. There are numerous techniques to mitigate increased sedimentation, however, such as silt curtains, coffer dams, and retention ponds (OMNR 1990; Kerr 1995). Provided these measures are satisfactorily applied, the increased inputs of sediments during and after construction can be minimized to the point where inputs are modest and the effects, if any, are very localized.

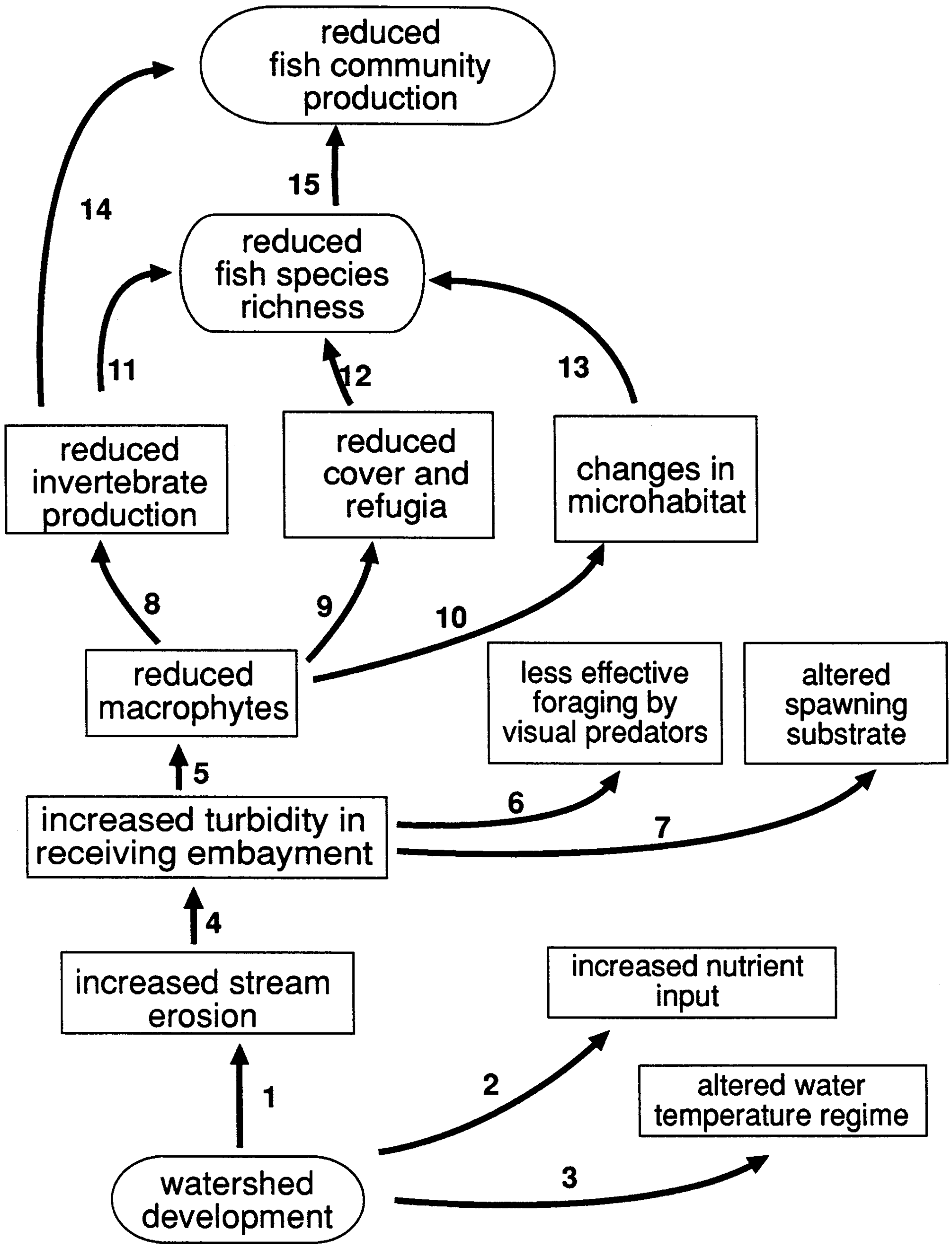
In this example, the linkage is relatively well understood as are the opportunities for mitigation. A fully developed analysis of this linkage should provide more detail (or a summary of useful references) on the circumstances wherein concerns are likely to be the greatest (e.g., types of road or crossing construction, critical soil characteristics) and on prescriptions for mitigative measures. In other cases, the evidence for the linkage being true may be much less clear. For example, linkage 8 in the brook trout hypothesis (Fig. 2) might read, "Reductions in invertebrate production from riffles will lead to reductions in juvenile brook trout production." Although it is well known that stream-dwelling juvenile salmonids depend on drifting invertebrates as their primary food source, defining quantitative relationships between secondary production and fish production has proven difficult (Hynes 1970; Richardson 1993; Waters 1993). Thus, while it is virtually certain that drastic reductions in invertebrate production will affect trout production, it is more difficult to predict the consequences of subtle changes (e.g., a 20% reduction persisting for one growing season). Evaluation of linkages such as this should include an attempt to bound the magnitude of effect that is likely to be detectable.

When the issue involves habitat modification effects on entire communities, particularly indirect effects such as urbanization effects on aquatic communities, the uncertainty surrounding individual linkages can become critical. One of the hypotheses-of-effect in the littoral centrarchid community example concerns effects of urbanization on centrarchid fishes as mediated through a sedimentation – loss of macrophyte production pathway. The series of pathways and linkages leading from urban development in a watershed to effects at the fish community level in nearshore habitats are numerous (Fig. 3). Some of the linkages are supported by strong evidence, but others are not. Confounding factors often apply at a specific effect level, and a particular cause–effect linkage is sometimes difficult to test. For example, linkage 4 in Fig. 3 could be defined as, "Increased instream erosion causes increased turbidity in receiving embayments." At Cootes Paradise in Lake Ontario, and Rondeau Bay in Lake Erie, high turbidity was linked at least in part to input of suspended solids from receiving tributaries (Hanna Associates Inc. 1984; Painter et al. 1989, 1991). However, turbidity was also attributed to the effect of wind, and in the case of Cootes Paradise, to increased algal primary production caused by elevated nutrient inputs and to the activity of carp (*Cyprinus carpio*). For this linkage, many cofactors would have to be investigated before links between the stream water quality and water turbidity of the receiving embayment could be isolated.

The spatial and temporal scales which apply also complicate this linkage. Cause and effect are spatially separated (upstream urban construction – downstream wetland turbidity), leaving room for proximate confounding factors to influence turbidity (wind, carp) as well as the distal factor of immediate concern (urbanization, suspended solids in the stream). Resuspension of materials in the embayment by wind-generated currents, contributing to turbidity, will increase with time as more material moves downstream and accumulates. Appropriate mitigation to reduce existing turbidity or to prevent future problems must address all significant contributing factors. Mitigation that focuses on preventing soil erosion and the resulting increases in inorganic suspended solids in stream effluent may help reduce turbidity, but increased nutrient loads and concurrent increases in stream temperature from urban development could override these mitigations. Ultimately, effective mitigation will require that the extent of urban development that is allowed in any one watershed be limited (Klein 1979), and that the mitigation actions be broad and multifaceted (e.g., Marshall Macklin Monaghan Ltd. 1994).

Higher in the pathway leading to community fish production (Fig. 3), other uncertainties become apparent. In the centrarchid example, species richness is assumed to be the fish community indicator of interest and is the accepted measure of productive capacity. Several investigators have demonstrated a positive link between macrophyte abundance and fish species richness in inland lakes (Keast et al. 1978; Bryan and Scarnecchia 1992), lower reaches of rivers (Killgore et al. 1993), and in the Great Lakes (Randall et al. 1995). Macrophyte reduction, resulting from increased turbidity, would thus be of concern. However, several factors associated with

Fig. 3. An example hypothesis-of-effect from the littoral centrarchid – urbanization case. The cause–effect pathway, which begins with "increased instream erosion," is one of several possible hypotheses-of-effect relevant to this case. The first step in two other pathways (nutrient loadings, temperature changes) are also presented. Each pathway would require a separate analysis, including consideration of interactions among pathways where appropriate.



macrophytes may account for the increase in species richness. Macrophyte beds are used by fishes for several functions: phytophilic species (Balon 1975) use macrophytes as spawning substrate or as refugia for reproduction; macrophyte beds provide a rich feeding environment (Killgore et al. 1993); and macrophytes provide cover and refugia from predators (Rozas and Odum 1988). To understand cause and effect between macrophyte abundance and a fish community indicator like species richness, at least three linkages must be considered (Fig. 3, linkages 11, 12, and 13). Similarly, mitigation must consider all factors associated with macrophytes (primary and secondary production, refugia and structure, and unique microhabitats); focusing on only one aspect (say using artificial habitat structure to replace the lost cover) would not result in compensation.

Uncertainties about species interactions and species-specific reactions to changes in habitat may further complicate these considerations. Because of unpredictable predator–prey interactions, and the role of cover, the response of individual species to macrophyte removal may not be fully understood. For the centrarchid largemouth bass (*Micropterus salmoides*), Durocher et al. (1984) reported a linear positive relationship between macrophyte cover and recruitment to harvestable size. In contrast, Bettoli et al. (1992) found that the elimination of vegetation had a positive effect on bass populations, because the lack of cover allowed the bass to become piscivores at a smaller size and thus significantly increase their growth rate during their first year. The structure of the forage fish community shifted, but ample fish prey existed for the largemouth bass before and after vegetation removal. The linkages between habitat and fish, when considered at the community level, will sometimes be poorly understood or unpredictable, even for well-studied species.

Enough evidence exists to indicate that macrophyte reduction, caused by increases in turbidity, will result in a decrease in fish species diversity. The pathways leading to this change are diverse and sometimes poorly understood, however. The matrix approach and a consideration of the hypotheses-of-effect linkages illustrate the complexity of the effects of habitat alteration at the community level and the number of issues that managers must face when trying to mitigate for the potential loss of habitat quality.

The final step in the process is to reach an overall conclusion regarding the hypothesis-of-effect. This conclusion should state whether an undesirable effect is likely to result from this cause–effect pathway. It should summarize the circumstances under which such an effect might be expected and should recommend ways to mitigate the effects if necessary. Often there will emerge a range of options for mitigation of the effects, ranging from costly interventions with a high likelihood of preventing the negative ecological effects to less expensive actions with greater uncertainty as to their effectiveness. These options should be summarized as part of the conclusions, together with an assessment of the risks and benefits associated with each.

In the majority of instances, the uncertainties will be sufficient to warrant research and monitoring recommendations as well. These recommendations should include details on what should be measured, as well as the spatial and temporal scales of observation. Monitoring provides opportunities for reducing uncertainties for the future; these opportunities should be considered when developing a recommendation.

Conclusions and recommendations

The matrix approach combined with the hypothesis evaluation method provides a systematic procedure for evaluating the effects of habitat change on ecological indicators of interest to resource and environmental managers. The method makes explicit the cause–effect linkages that must be considered if one is to rigorously evaluate the potential impacts of a habitat manipulation. Further, it provides an mechanism for considering related issues, such as that of scale and of the confounding effects of other forces on the linkage between habitat changes and ecological effects.

The specification of the matrix and evaluation of the evidence using the hypotheses-of-effect for a particular habitat management issue constitutes a substantial task. Reviewing the literature alone (much of which is not found in primary, peer-reviewed sources) will require a significant effort. It is unrealistic to expect that this level of effort can be directed at each issue confronted by the biologist asked to determine the appropriate action (i.e., do not allow habitat modification, compensate, more research or information required, etc.). On the other hand, there is redundancy in the habitat management issues faced by biologists throughout North America. To be useful, the framework we describe above should be applied to classes of habitat manipulations (e.g., road crossings, macrophyte plantings) and the matrices and hypotheses developed so as to be applicable over a broad geographic range. To achieve this generality the analysis of linkages within the hypotheses of effect will have to include consideration of how such contextual elements as physiography, topography, and climate affect the significance and magnitude of the linkage. If the analysis is done in this way, the results can then be applied to any specific issue that falls within that class, without redevelopment of the entire framework. We would challenge regulatory agencies to take the initiative to apply this framework, ideally in collaboration with proponents responsible for the relevant manipulations (e.g., forest industry for access roads).

For any habitat manipulation to which this framework might be applied, one of the inevitable outcomes will be the exposure of the uncertainty concerning some, if not all, of the linkages in the hypotheses-of-effect. This must not be viewed as a weakness of the framework. On the contrary habitat management processes that do not probe the cause–effect linkages to the extent done by this framework will tend to overlook some of the uncertainties, with (at least) two negative consequences. First, manipulations may be allowed for which the “best guess” would suggest there is no likely detrimental effect on the indicator of interest, but for which there is a substantial hidden risk. Conversely, conservative decisions may be made regarding a manipulation because the highly uncertain best guess suggests a detrimental impact. Second, ignoring key uncertainties squanders opportunities to learn and thereby reduce uncertainties for future decisions concerning the same issue. Identification of uncertainties exposes opportunities for adaptive management (Holling 1978; Walters 1986). Habitat management issues frequently offer opportunities for application of adaptive management principles, because similar manipulations are repeated in space and time, thereby affording the opportunity for experimental design and replication of adaptive experiments.

Another use of this framework for habitat management lies in the determination of suitable surrogate indicators of ecological effects. Generally, the ecosystem components or attributes that constitute the endpoints of our cause–effect pathways linkage tend to be population- or community-level attributes that can be costly and difficult to measure. To justify using a surrogate measure (e.g., water-quality parameters, fish growth) as the indicator, it is important to demonstrate an unequivocal linkage between the surrogate and the indicator of interest. Evaluation of the linkages in the hypotheses-of-effect that connect habitat or life-history attributes with population or community indicators should include whether the former provide reliable surrogates for the latter. Because effects monitoring should be a key component of habitat management (especially adaptive habitat management), and because monitoring fish population and community status can be both costly and burdened with measurement problems, the development of reliable surrogate measurements is a priority.

The future success of habitat management demands that we have mechanisms for examining and making the best possible use of what we know about linkages between habitat manipulations and ecological effects. Not only should we be making the best possible decisions regarding habitat manipulations, but we should also exploit opportunities for increasing our knowledge in areas where uncertainty makes it difficult to predict effects. The concept of productive capacity and the Canadian habitat policy that utilizes this expression have forced us to look more carefully at our knowledge of linkages between habitat change and ecological effects. The framework described in this paper offers a systematic methodology for organizing this knowledge. Whether this methodology is adopted or not, our most important recommendation is that, if we are to advance beyond the piecemeal one issue at a time approach to habitat management that is the current norm, an approach such as the one described herein will have to lead the way.

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