Information needs for assessing critical habitat of freshwater fish

Jordan S. Rosenfeld and Todd Hatfield

Abstract: The core assumptions of critical habitat designation are a positive relationship between habitat and population size and that a minimum habitat area is required to meet a recovery target. Effects of habitat on population limitation scale from (i) effects on performance of individuals (growth, survival, fecundity) within a life history stage, to (ii) limitation of populations by habitats associated with specific life history stages, and (iii) larger-scale habitat structure required for metapopulation persistence. The minimum subset of habitats required to achieve a recovery target will depend on the extent, quality, and spatial configuration of habitats available to sequential life history stages. Although populations may be limited by available habitat for a single life history stage, altering habitat quality for subsequent stages will also affect individual survival and population size, providing multiple leverage points within a life history for habitat management to achieve recovery targets. When habitat-explicit demographic data are lacking, consequences of uncertainty in critical habitat assessment need to be explicit, and research should focus on identifying habitats most likely to be limiting based on species biology.

Introduction

Many developed nations, including Canada, have recently enacted legislation to prevent extinction of endangered species to fulfill domestic and international commitments (e.g., Rio Biodiversity Convention). Identification and protection of critical habitat is central to the management of species at risk. The rationale for protecting critical habitat is rooted in the observation that particular habitats are often disproportionately important to population limitation (Fausch et al. 2002), and therefore they represent priorities for habitat protection. The need to designate critical habitat is recognized by scientists, resource managers, and the general public, but operational definitions, approaches, and information requirements for identifying critical habitat remain poorly defined.

Credible designations of critical habitat are necessary for two reasons: first, designation of critical habitat based on inaccurate science may fail to ensure the long-term persistence of species at risk. Second, critical habitat designations that affect economic activity will be closely scrutinized by...
stakeholders who bear the lost opportunity costs of habitat protection and will be challenged if their scientific basis is questionable.

Defining critical habitat remains one of the most challenging problems of species management because it involves multiple aspects of population biology, ranging from local habitat effects on growth and survival of individuals to large-scale metapopulation and landscape issues. Despite its complexity, the core issue is the same for all species: to determine the role of habitat in population limitation and viability (by limitation we mean the influence of a factor on population size or carrying capacity, as opposed to regulation, which is a process whereby density-dependent effects maintain a population near the carrying capacity of a habitat). Because time and resources are rarely available to assess all aspects of the role that habitat plays in population limitation, biologists need to focus research efforts on habitats most likely to be limiting the species of interest. For species at risk, the challenge is to correctly identify and collect the minimum information required to credibly identify critical habitat in a short time frame and to refine these designations as future resources permit.

The primary objective of this review is to provide meaningful biological interpretations of critical habitat and a conceptual framework for prioritizing data collection in support of critical habitat designation. We first provide practical operational definitions of critical habitat. We then develop a conceptual framework for identifying the information needed for critical habitat assessment based on the roles habitat plays in population limitation. Finally, we illustrate application of the framework using selected case studies for species with divergent biology and distributions representing a broad spectrum of information needs.

**Legal and practical definitions of critical habitat**

The fundamental premise of critical habitat protection is that certain habitats are more important than others for species persistence, and this hierarchy of importance should guide the prioritization of habitat protection. The legal definition of critical habitat in the US Endangered Species Act is

...the specific areas within the geographical area occupied by the species...on which are found those physical or biological features essential to the conservation of the species. [Endangered Species Act of 1973]

The equivalent definition of critical habitat in the Canadian Species at Risk Act is

...the habitat that is necessary for the survival or recovery of a listed wildlife species and that is identified as the species' critical habitat in a recovery strategy or in an action plan for the species. [Species at Risk Act 2002, s. 2(1)]

Both of these definitions are clear in intent but can be interpreted so broadly that they provide limited practical guidance for identifying critical habitat. This wording is presumably deliberate; rather than constrain designation through a restrictive legal definition, the identification of critical habitat is deferred to experts involved with species recovery. The onus is therefore placed on the recovery scientists to justify critical habitat designation using the best information available. Criteria for identification of critical habitat under the US Endangered Species Act specifically require consideration of social-economic impacts (U.S. General Accounting Office 2003). Under Canadian law, it appears that the intent is for the identification of critical habitat in the Recovery Strategy to be based purely on the biology of the species, but recovery activities identified in the Recovery Planning process (including the identification of critical habitat) are directed to consider social-economic impacts, and the ultimate discretion for accepting the definition of critical habitat recommended by recovery team scientists remains with the federal Minister of Environment. The federal Minister of Environment may choose to protect only a subset of habitats recommended by the recovery team or may choose to not list a species at all if the socio-economic impacts of recovery (e.g., protection of critical habitat) are deemed unacceptable (Irvine et al. 2005).

The Species at Risk Act also includes a definition of habitat that has broad implications for critical habitat designation. Habitat for aquatic species is defined as

...spawning grounds and nursery, rearing, food supply, migration, and any other areas on which aquatic species depend directly or indirectly [our emphasis] in order to carry out their life processes, or areas where aquatic species formerly occurred and have the potential to be reintroduced... [Species at Risk Act 2002, s. 2(1)]

This definition provides for critical habitat to be defined both in terms of the abiotic (physical, chemical) and biotic (prey species, competitors, predators) features of the environment. It also explicitly permits the designation of presently unoccupied habitat, as well as habitat in which a species does not occur but whose loss or degradation will affect critical habitat directly used by a listed species. This latter circumstance is especially relevant to aquatic organisms, since aquatic habitats are subject to both indirect and cumulative impacts from diffuse (terrestrial) activities in a watershed (Slosser 1991).

To complement these legal definitions of critical habitat, we suggest several practical working definitions that provide more general guidance and can serve as primary screening criteria for evaluating potential candidate critical habitat areas: (i) habitat that is disproportionately important whose singular or cumulative loss will result in significant population-level effects (for a recovered population); (ii) the minimum subset of habitats required for a species or population to persist (or achieve a recovery target); and (iii) habitats that are necessary to maintain ecosystem integrity and function.

The first working definition emphasizes the prioritization of habitat protection based on the population consequences of habitat loss or gain (i.e., if a particular type of habitat can be lost without population-level effects, then it is unlikely to be critical). The second definition emphasizes that the default objective may not be to protect the entire range of a species, and that for some species, different configurations or subsets of habitat of varying quality may ensure species persistence (although in other cases protection of all available habitat may be necessary).
Fig. 1. Defining critical habitat is illustrated as a three step process. (1) A population recovery target is determined (N_target). (2) A relationship between habitat and abundance is developed. (3) The recovery target and the habitat–abundance relationship jointly define the quantity of habitat required to meet the recovery target (H_crit). H_crit will differ depending on the form of the habitat–abundance function. Habitat–abundance relationships will be linear if the number of recruits to a habitat increases proportionally with area (solid line). If the number of recruits is fixed, the relationship will asymptote and display nonlinearity because of density-dependent effects on survival (broken line). High-quality habitat will generally have higher survival rates, resulting in a steeper abundance–area relationship. Note that the horizontal axis can be any measure of habitat quantity (area, volume, stream discharge, etc.).

Fig. 2. For species with multiple life history stages, sufficient individuals need to recruit to each life history stage to meet the adult recovery target. When life history stages are dependent on different habitats, separate habitat–abundance relationships, stage-specific population targets, and critical habitat areas need to be defined to meet the adult population recovery target. Population targets for early life history stages will depend on stage-specific survival rates. Note that the habitat area required by different life stages will depend on species ecology, although this figure assumes that individual and cohort area requirements increase from eggs to juveniles to adults. Egg to juvenile and juvenile to adult survivals are set at 25% and 40%, respectively, for illustration purposes. N_target, a population recovery target; H_crit, the quantity of habitat required to meet the recovery target.

The third definition emphasizes that discrete habitat features will only persist if the processes that generate those features are maintained in a broader landscape context (e.g., river flooding, riparian inputs, etc.; Barinaga 1996; Imhof et al. 1996; Roni et al. 2002). This expands the suite of candidate habitats suitable for critical designation beyond those involved in population limitation to include habitats that are essential for maintaining critical habitat. For instance, removal of streamside forest may lead to excessive sedimentation and solar heating, degradation of water quality, and siltation of critical spawning habitat. We expand on the logic underlying these working definitions later in this review.

Finally, it is important to distinguish between general characteristics of critical habitat and the location of specific critical habitat areas (Canadian Wildlife Service 2005a). The definition of critical habitat under the Species at Risk Act, in contrast with US legislation, appears to permit the designation of both spatial areas with fixed coordinates as well as discrete habitat features that may shift through space or time. Identifying the general properties of critical habitat — for example, the characteristics of suitable spawning habitat (substrate size distribution, water temperature, etc.) — is also necessary to establish the range of conditions that need to be maintained within critical habitat for maintenance of function, and to provide benchmarks for restoration of degraded habitat (Lewis and Casselman 1996). The specific location of critical habitat (as opposed to its general characteristics) is also clearly essential from a management perspective (National Recovery Working Group 2004), as well as for modelling the effects of different habitat areas and configurations on population size and persistence.

The critical habitat concept

The core assumptions of critical habitat designation are a positive relationship between habitat and population size and that a minimum area is required to achieve a recovery target. For some species habitat may play a minor role in population limitation compared with other factors (e.g., predators, invasive species, disease). In this case, other limiting factors may modify the designation of critical habitat (e.g., refuges from predation may be limiting), or critical habitat identification may be irrelevant depending on the suite of threats facing a listed species, which must be thoroughly assessed in the early stages of recovery planning. For those species where habitat plays a key role in population limitation, the logical steps involved in identifying critical habitat are (1) identify a population recovery target; (2) define a quantitative relationship between habitat and population size; and (3) define sufficient habitat to meet the recovery target based on the habitat–population relationship (Fig. 1).

For species with multiple life history stages that use different habitats, this process will need to be repeated for each life stage (Fig. 2). This will require estimates of stage-specific survival (fraction of the population that successfully recruits to each life history stage) and separate relationships between habitat and abundance for each life stage (e.g., Minns et al.
mark, whether it be the current population size or a specific recovery target. This target may be either quantitative (e.g., 20,000 individuals) or qualitative relative to the present population (e.g., no decline). Quantitative targets can be either distributional (e.g., maintain the current or historic distribution of a species) and (or) population-based (e.g., a minimum adult population size of 8000 individuals).

While population recovery targets are required to determine the total amount of habitat needed for long-term persistence, they are not necessarily required for proactive designation of critical habitat for severely depleted populations. If a population is clearly below the minimum necessary for long-term survival (often a listing criteria), then all limiting habitat for that population can legitimately be designated as critical even in the absence of a recovery target. This habitat is the subset of critical habitat necessary to support the present population and is termed “survival” habitat (National Recovery Working Group 2004). Currently unoccupied habitat may have to be designated as critical to permit the population to increase to meet a recovery target; this additional habitat is designated “potential” habitat. Credible designation of full recovery habitat (survival and potential combined) requires both a population recovery target and sufficient understanding of habitat–abundance relationships to define the area of habitat necessary to meet the target.

Population recovery targets are usually set at a level that will ensure the long-term persistence of a species. This target may be arrived at in several ways. If sufficient data exist to parameterize a population model that incorporates temporal variability in demographic and environmental conditions, then a formal population viability analysis (PVA; Morris and Doak 2002) can be performed to establish a minimum recovery target. The validity of PVA has come under intense scrutiny as a method for assessing extinction risk (Coulson et al. 2001; Ellner et al. 2002; Reed et al. 2002), but it remains a useful quantitative tool for setting recovery targets and exploring how different management scenarios affect extinction risk (Brook et al. 2000; Haight et al. 2002), provided the results are interpreted with caution (Brook et al. 2002; Lindenmayer et al. 2003). However, sufficient information to perform a PVA is often lacking for listed species (Morris et al. 2002), usually because time and resources have not been available to obtain the necessary demographic parameters. In this case interim recovery targets need to be set based on available data until more accurate targets can be derived. One simple approach is to set recovery targets based on generic minimum viable population (MVP) sizes. Although early research in PVA suggested that MVPs should vary over a wide range depending on the biology of a species (Lande 1988; Simberloff 1988), recent evidence suggests that there is less variation in MVPs among different taxa than previously thought (e.g., Reed et al. 2003).

Thomas (1990) presents a general argument based on temporal population variability (probability of population decline below a threshold that could trigger extinction) that MVPs for species should be in the low to mid thousands, and suggested a mean recovery target of 5500 reproductively mature individuals. Reed et al. (2003) performed a more formal review of MVPs based on PVA of 102 vertebrate taxa (including one freshwater fish species) and observed a mean
A MVP of 7300 (+560 standard error) adults and a median of 5800. Reed et al. (2003) concluded that MVPs on the order of 5000–7000 adults could be used as an interim recovery target for listed vertebrate species pending derivation of specific data to parameterize a more formal PVA.

The use of generic recovery targets needs to be tempered by several considerations. First, any interim recovery target based on a generic value should be adjusted up or down based on the known biology of a species and associated threats. Some species, such as the passenger pigeon (Ectopistes migratorius) or marine fishes (Hutchings 2001) may have much larger MVPs (hundreds of thousands) if, for example, large aggregations are required for successful reproduction or recruitment (Carlton et al. 1999). Conversely, for naturally rare endemics with a limited distribution, the intrinsic capacity of a habitat (as determined by pre-impact population size) may provide a natural limit to a recovery target that is well below a generic value. Second, the species used to calculate MVPs using PVA in Reed et al. (2003) were experiencing good habitat conditions; species that were in decline (i.e., experiencing negative population growth) were explicitly excluded from their analysis. Listed species are often in decline, indicating that the quality of habitat they are experiencing is below its historic mean. In this case, MVPs may be substantially larger than those recommended by Reed et al. (2003) because population growth rate (the ability of a species to recovery following a stochastic population decline) will be lower in poor-quality (e.g., degraded) habitat, increasing the probability of extinction and therefore the minimum population required for species persistence. Third, the relevance of the MVP as a recovery target will depend on the status of a species and its population trajectory. For species that are already below an MVP threshold, the MVP is a useful and compelling recovery target. For species that are in the early stages of decline and far above an MVP threshold, the broader goal of recovery planning is to first arrest the population decline and then take steps to move the population towards a recovery target, rather than to simply permit a population collapse towards a relict MVP (Olver et al. 1995). In this case, an appropriate recovery target could be well in excess of the MVP.

To some degree, recovery targets, as established by the recovery team, are and should be context dependent (Elphick et al. 2001). The MVP represents a minimum recovery target that cannot be compromised unless a species is deemed unrecoverable for biological, logistic, or economic reasons. However, recovery targets in excess of an MVP can be established if it is required to move a species to a lower risk category (as defined by quantitative listing criteria) or if the recovery team decides that, for instance, the reestablishment of a species throughout its former range is a legitimate long-term goal. In principle, recovery planning is intended to ensure emergency protection and management until species have recovered to a point where they can be delisted and routine management legislation and procedures can take over (e.g., Johnston et al. 2002). This may never occur for species that are endangered because of extreme natural endemism (Caughley 1994; Doremus and Pagel 2001), but is in principle possible for historically abundant taxa where the ultimate goal of recovery is to move a species to a lower level of endangerment (e.g., from endangered to threatened or not at risk).

Habitat–abundance relationships

Designation of critical habitat requires quantitative relationships between habitat and abundance, because these relationships are needed to establish the amount of habitat required to achieve a population recovery target. Biologists regularly develop relationships between habitat and organism abundance for management purposes or during basic ecological research. These are often fairly simple relationships between habitat area and population size (e.g., lake area vs. sockeye salmon (Oncorhynchus nerka) abundance (Burgner 1991) or total stream length vs. coho salmon (Oncorhynchus kisutch) smolt production (Bradford et al. 1997)). These examples represent very general relationships between population size and total habitat area that may be appropriate for identifying critical habitat in ecosystems with little spatial variation in habitat quality, or for endemics with very small ranges (see Appendix A).

When organisms are patchily distributed across a landscape, a finer resolution of habitat associations and critical habitat may be appropriate. Many studies have demonstrated that variance in abundance is related to variance in habitat type and quality (e.g., Pess et al. 2002), and critical habitat designations should occur at a scale that reflects this. The required resolution of habitat–abundance relationships and critical habitat designation will ultimately depend on the biology of the species being examined, and the spatial and temporal variation in its habitat. For example, designation of spawning habitat at the reach scale may be more appropriate than the channel unit scale if discrete riffle locations are periodically altered by floods.

The role of habitat in population limitation can best be understood by considering habitat effects at three spatial scales. At the smallest spatial scale, habitat type and quality affect the fitness (growth, survival, fecundity, reproductive success) of individuals. Understanding how habitat affects the performance of individuals is key for differentiating critical and noncritical habitat and for understanding the mechanisms whereby habitat change causes population-level effects (Hayes et al. 1996). At a larger spatial scale, the relative availability of habitat for different life history stages will determine the primary limiting habitat factor for a population, which life history stage it operates on, and the specific identity of critical habitat. For species with multiple populations, the size and spatial configuration of different habitats at a landscape scale and their status as sources or sinks will determine which habitats and subpopulations are critical for the persistence of the species as a metapopulation. The information required to define critical habitat and establish habitat–abundance relationships at any of these scales will depend on the biology and distribution of the species of interest, as described below.

Habitat effects on individual performance: assessing habitat quality

Habitat quality is a widely used but loosely defined concept in fish and wildlife management and is generally understood to represent the ability of a habitat to sustain
individuals of a particular species and support population growth (Garshelis 2000). The biological response to habitat is then used to infer which features of habitat are important for organism growth and survival. Habitat quality is a function of the availability of prey, the abundance of competitors, predators, refuges, and a suite of other environmental attributes. Credible metrics of habitat quality (i.e., the density-independent biological response to habitat) are fundamental to the identification of critical habitat as well as most other stages of recovery planning. The best indices of habitat quality are direct measures of the fitness consequences to individuals (growth, survival, fecundity, reproductive success) of using different habitat types (Sogard 1994; Railsback et al. 2003) in the absence of competition (i.e., at low density). Production is the emergent population-level measure of habitat quality that integrates the effects of individual growth and survival (Randall and Minns 2000). Unfortunately, these metrics are often difficult to obtain, and biologists typically use more easily measured surrogates of habitat quality, such as presence or abundance.

The presence or absence of individuals in different habitat types is the simplest metric of habitat quality. However, it is potentially misleading (Garshelis 2000); for instance, Able (1999) found the presence of large numbers of subtropical juvenile fish in a New Jersey estuary to be a poor indicator of suitable rearing habitat, since most died at low fall and winter temperatures. Presence data may fail to distinguish between source and sink habitats (e.g., Able 1999), and provides no information on variation in quality of occupied habitats.

Measures of abundance (e.g., density, frequency of use, catch per unit effort) contain more information on habitat quality than presence or absence. Under the assumptions of Ideal Free Distribution theory (Fretwell and Lucas 1970), organisms should select habitats that maximize their fitness, resulting in the highest densities in high-quality habitat. However, density and habitat use can also be misleading indicators of habitat quality (Van Horne 1983; Hobbs and Hanley 1990; Garshelis 2000). Caution should be used when inferring habitat quality based on habitat use, particularly when mechanisms such as territorial behaviour can displace subordinates into poor-quality habitat at high densities (Van Horne 1983; Messier et al. 1990; Railsback et al. 2003). The long-standing discussion on the usefulness of habitat suitability curves (Bovee 1982; Rubec et al. 1999; Parasiewicz and Dunbar 2001) documents many of the problems inherent in the application of habitat use as an index of habitat quality (Mathur et al. 1985; Railsback et al. 2003). Density and measures of habitat selection may be of great utility in the designation of critical habitat, but their reliability may require validation if aspects of species biology (e.g., territoriality) warrant it. Arguably, when the consequences of being wrong may lead to extinction, a greater level of confidence in assessment of habitat needs is desirable.

Direct measurements of individual (or population) growth, survival, and fecundity in different habitats are the most reliable indices of habitat quality (Sogard 1994; Railsback et al. 2003; Rosenfeld 2003). However, vital rates associated with specific habitats are usually much more difficult to estimate than abundance and must either be measured in different habitat types in the wild (correlative approach) or by measuring performance of individuals experimentally confined to different habitats. Because growth rates in the wild are often density dependent, experimental manipulations may be necessary to reliably assess habitat quality. Measuring individual performance in different habitat types will be easier in some ecosystems than others. While it may be feasible to monitor growth and survival of individual fish confined to different habitats in streams (e.g., Lonzarich and Quinn 1995; Rosenfeld and Boss 2001), for example, it may be extremely difficult in other systems (e.g., marine pelagic), requiring that inferences about critical habitat be made with less data than might be acceptable elsewhere (e.g., Gregr and Trites 2001).

### Limiting habitats for populations: habitat quantity

The relationship between population size and habitat illustrated in Fig. 1 is simplistic, but may adequately represent the dynamics of species where life stages share the same habitat. The ecology of most species is more complex, with different life stages often requiring different habitats (Fig. 2), which may or may not overlap in space (Schlosser 1991; Northcote 1997; Rieman and Dunham 2000). To meet a recovery target of adult animals, sufficient habitat must be available to support enough individuals to recruit to each sequential life stage. Critical habitat for each life stage can then be designated based on the quantity and quality of habitat necessary to achieve the recovery target. This is illustrated in Fig. 2, which shows population sizes and habitat–abundance relationships for three life history stages (eggs, juveniles, adults) of a hypothetical fish species. Understanding how habitat quality and quantity sequentially limit the abundance of different life stages is therefore fundamental to the identification of critical habitat (Imhof et al. 1996; Halpern et al. 2005). High-quality habitat will generally have higher survival rates, resulting in higher density and a steeper abundance–area relationship.

The probability that an individual will survive to reproduce will be the product of a series of stage-specific survival rates that depend on habitat conditions (quality) experienced by different life stages ($S_1$, $S_2$, $S_3$, ..., $S_n$; Moussalli and Hilborn 1986). Survival at any life stage will also depend on density (i.e., density dependence will reduce survival at high densities so that the number of individuals recruiting to the next life history stage has a ceiling determined by the capacity of the habitat). Severe habitat limitation implies strong density dependence and therefore lower stage-specific survival. Increasing either density-independent survival (by increasing habitat quality) or the amount of available habitat will shift population limitation to a different life history stage (Bradbury et al. 2001; Halpern et al. 2005).

We illustrate a scenario (Fig. 3a) where there are sufficient adults to saturate spawning habitat, adequate egg survival to saturate juvenile-rearing habitat, and sufficient juveniles recruiting to the adult population to saturate adult habitat (with saturation meaning habitat that is at capacity, i.e., the point where density-dependent increases in mortality limit additional recruitment). Because adult habitat is at capacity in this scenario (i.e., adult habitat is limiting), the population will not respond to any increase in the availability of spawning or juvenile-rearing habitat. Increasing the availability of adult habitat will result in a compensatory population re-
Fig. 3. Different scenarios of population limitation are illustrated for a hypothetical fish species with three distinct life history stages that use different habitats. The left panels illustrate the habitat–abundance relationship (solid line), stage-specific population target (horizontal broken line, $N_{target}$), and critical habitat area (vertical broken line, $H_{crit}$) for eggs; the middle panels illustrate this for juveniles and the right panels for adults. Figures represent abundance at a specific point in time, since densities of a cohort decrease over time. Egg to juvenile and juvenile to adult survivals are set at 25% and 40%, respectively, with an increase in stage-specific survival indicated by a broken arrow. (a) Habitats for all life history stages exist in an optimal ratio such that all habitats are at capacity (i.e., sufficient individuals recruit from each life history stage to saturate habitats for subsequent life stages to achieve the adult population recovery target). (b) Available juvenile rearing habitat ($H_{available}$, center panel) is insufficient to recruit enough juveniles ($N_{realized}$) to the adult life history stage to meet the adult recovery target (solid line). If it is impossible to increase the area of habitat available to juveniles, then increasing habitat quality (the slope of the habitat–abundance relationship; broken line) can increase juvenile recruitment to meet the recovery target. (c) In this scenario, the availability of spawning habitat is limiting the population below the recovery target. Increasing the area of habitat available to subsequent life history stages will have no effect because these habitats are unsaturated (under-recruited). However, increasing stage-specific survival (e.g., juvenile overwintering survival; broken arrow) will increase recruitment to the adult stage to meet the recovery target, despite habitat limitation at an earlier stage. This illustrates that populations can be limited by both habitat quantity and quality for different life history stages, providing an opportunity for multiple leverage points to achieve a recovery target.
sponse (release from density dependence; Rose et al. 2001) that quickly attenuates because of insufficient recruitment to saturate adult habitat (e.g., curved line in Fig. 1). Depending on the strength of density-dependent processes, any significant increase in the adult population will require proportionally increasing habitat availability (recruitment) for earlier life stages as well. The ideal proportion of habitats for a particular species can therefore be thought of as existing in an optimal habitat ratio, which can be defined as the relative proportions of habitats for different life stages where all are at capacity. Optimal habitat ratios represent a potentially useful approach for conceptualizing the habitat requirements of species and for developing rules of thumb for habitat restoration (e.g., Reeves et al. 1989; Rosenfeld 2003).

When habitat for one life stage is in short supply, then that life stage and its associated habitat represent a limiting bottleneck for the adult population (Minns et al. 1996a). This will occur, for example, when available juvenile habitat is inadequate to produce sufficient recruits to saturate adult habitat (Fig. 3b, solid lines). Increasing the size of the limiting juvenile cohort can be achieved through either increasing the area of juvenile habitat or by increasing the quality of existing habitat so that the original number of juveniles can be supported in a much smaller area (Fig. 3b, broken lines). This example illustrates three points that are relevant to both designation of critical habitat and recovery of degraded habitats. First, increasing the area of habitat available to a life stage before or after a limiting stage will have no effect on the adult population; correct identification of the limiting stage is therefore essential to effective population recovery. Second, habitats other than the limiting one may also qualify as critical because they will become limiting once the bottleneck is removed (therefore classified as potential habitat; National Recovery Working Group 2004). Third, increased numbers of a limiting life stage can be achieved either through increasing the quantity or quality of available habitat or through a combination of both. This latter point is extremely important because it introduces flexibility in approaches for both designating and restoring critical habitat.

The idea that a single habitat or life stage can be a bottleneck for a population is misleading; it implies that habitat conditions for life stages subsequent to the bottleneck will not influence adult population size. However, increasing habitat quality for life stages subsequent to a bottleneck may have a positive and potentially profound effect on the ultimate population size. A population may therefore be limited by habitat quality at multiple life stages even though limited by habitat quantity at a single life stage. For instance, consider a scenario where a population bottleneck is created by inadequate recruitment from limited spawning habitat (Fig. 3c, solid lines). Even though spawning habitat is limiting, an improvement in juvenile overwintering habitat quality (arrows, Fig. 3c) may increase juvenile survival enough to achieve the adult recovery target (broken line, Fig. 3c). It is important to understand that populations may be limited by habitat quality at more than one life stage and that this creates multiple leverage points to increase population size within a life history. Which habitats are the most practical and efficient to manipulate will depend on the specific circumstances of each species at risk. For instance, when increasing the quality or quantity of limiting habitat is not possible, increasing quality (survival) for a later life history stage may be a practical management option. Key information needs for species at risk therefore include the determinants of habitat quality, how to improve them, and understanding quantitative effects of habitat quality on growth, abundance, and survival.

In practice, it is very difficult to identify which habitats and life stages are limiting a population. For example, Nickelson et al. (1992) used density of juvenile coho salmon in different habitat types during winter high flows to infer that highly selected backwater refuges were limiting smolt production in coastal streams. This was confirmed by demonstrating increased smolt abundance in watersheds subject to restoration of high-quality overwintering habitat (Solazzi et al. 2000). This example illustrates several points: first, the careful use of habitat selection (density) data, in conjunction with a good knowledge of life history, can provide useful insight into limiting habitat factors. Second, the only way to unequivocally demonstrate that a habitat is limiting is to show population-level effects of habitat change, often an expensive, time-consuming, and difficult proposition.

Habitat-explicit population models may be a more practical alternative for identifying limiting habitat, potential impacts of habitat change, and leverage points for recovery actions (Akcakaya 2000; Bradbury et al. 2001; Haight et al. 2002). Models can then be used to guide habitat management, and management activities can be treated as adaptive experiments to test hypotheses about population limitation (Walters and Holling 1990; Jones et al. 1996; Minns et al. 1996b) and to generate more realistic model parameters for management. This approach may be particularly appropriate for species at risk, where there is more impetus for careful management because the consequences of incorrect management are more serious than for unlisted species. The sophistication of models and the information required to parameterize them (and even their need in the first place) will ultimately be driven by the specific context of endangerment (see Appendix A), as well as the quantity of data available.

Habitat models range from simple models that generate population estimates by extrapolating densities of animals in different habitat types to larger areas (Hankin 1984; Hankin and Reeves 1988) to habitat-explicit, size-structured population models (e.g., Nickelson and Lawson 1998; Akcakaya and Atwood 1997; Railsback et al. 2003). Habitat-explicit population models are the most realistic for exploring the potential of different habitat configurations to meet population recovery targets. These models have the additional advantage that they can be used to generate PVA by including stochastic effects on demographic rates to assess time to extinction.

Metapopulation considerations: assessing which populations are critical

For species that exist as a metapopulation (a group of spatially disjunct populations linked by migration), some populations may be disproportionately important for the survival of the species. If all populations are required to meet a recovery target (or when an explicit recovery goal is to maintain the original distribution of a species), then critical habitat should be designated for each population. If only a subset of populations are required to meet a recovery tar-
get, then it will be necessary to designate critical habitat only within this subset. One of the recovery tasks will therefore be to identify which populations are required along with their spatial configuration.

Distinguishing between source and sink populations is fundamental to identifying populations essential for species persistence. Failure to distinguish these may result in protection of sinks instead of sources, inappropriate identification of critical habitat, and underestimation of the probability of extinction. The subset of populations necessary for species persistence may include a combination of sources and sinks (Pulliam 1988; Pulliam and Danielson 1991) if sink habitats are corridors for dispersal or refuges for recolonizing source populations vulnerable to stochastic extinction. This is particularly relevant to species in streams and rivers (Schlosser 1995; Rieman and Dunham 2000; Labbe and Fausch 2000), which are likely to exhibit a metapopulation structure (i.e., subpopulations experiencing periodic extinction and recolonization). Sinks habitats may also qualify as critical if they can be transformed to source habitat through restoration or natural regeneration (Sinclair et al. 1995).

The importance of each population to species persistence will also depend on its size and associated threats. Extinction risk may arise from a suite of natural stochastic (e.g., climate extremes, floods) and anthropogenic events (e.g., pollution, urbanization, exotic species, etc.). On average, larger populations in high-quality habitat are less likely to go extinct from natural events than small populations in poor-quality habitat (Caughley 1994; Rieman and Dunham 2000). Unfortunately, human impacts are often concentrated in high-productivity habitats where populations would otherwise be most likely to persist (Kerr and Cihlar 2004; Harig et al. 2000; Allan 2004). In some cases (e.g., developed landscapes), the populations most likely to persist may very well be smaller low-productivity populations isolated from human impacts. Properly identifying threats for different populations is essential for determining which populations are critical for species persistence, and whether recovery actions need to focus on increasing population size and habitat quality or on reducing risk from human impacts.

Identifying critical habitat at the level of multiple populations may be most challenging when habitat loss is a minor factor in species endangerment, and when populations are limited by non-habitat factors such as overfishing or low ocean survival. Atlantic salmon (*Salmo salar*) on the east coast of Canada are a good example; there is abundant, unoccupied, freshwater rearing habitat for many (>30) discrete populations (Irvine et al. 2005), but it is unclear where to designate critical habitat in freshwater because of uncertainty in the spatial distribution of population recovery (should there be any). In the face of uncertainty, it may be appropriate to designate larger areas as critical than would be necessary if, for instance, freshwater rearing habitat was clearly limiting and there was reliable information on how different populations would contribute to meeting a recovery target. It should be noted that regulating fishing or otherwise increasing ocean survival is the conservation priority in this example, and critical habitat is largely irrelevant, especially if there are minimal threats to habitat. Critical habitat should eventually be defined so that if ocean survival increases, limiting habitat essential for population recovery is protected, but identifying critical habitat remains a secondary conservation priority in this scenario. Legal requirements aside, the effort that goes into defining critical habitat should be proportional to the benefit to the species.

Key information needs at the metapopulation scale therefore include (i) determining the status of discrete populations as sources or sinks, (ii) identifying corridors for dispersal and evaluating the probability of exchange between populations, and (iii) assessing the probability of subpopulation persistence based on risk of extinction from combined natural and anthropogenic impacts.

### Habitat required to achieve the recovery target

When relationships between limiting habitat and organism abundance have been developed, the quantity and location of habitat required to meet the recovery target can be determined. The population size that can be supported by any given habitat will be the product of habitat area (quantity) and animal density (quality, assuming habitat is saturated). For endemic species limited by scarce habitat, all available habitat may be required to meet the recovery target (see examples in Appendix A). For more abundant listed species with wider distributions, various combinations of habitat areas of differing quality may support the target population. In effect, different areas may be substitutable in terms of their contribution to a recovery target. This will be a key issue for both critical habitat identification and recovery planning, since it allows flexibility in designation of critical habitat, which will be particularly important for species in developed landscapes where there are significant social and economic costs to designating critical habitat.

Evaluating the substitutability of candidate habitat patches requires careful consideration of the roles that habitat quantity and quality play in population persistence. Changes in habitat quantity influence carrying capacity (target population size), whereas habitat quality affects population and individual vital rates (i.e., growth, survival, and fecundity) as well as capacity (Hayes et al. 1996). Population viability is influenced by both habitat capacity and productivity; larger populations are more resistant to extinction from demographic and genetic stochasticity, while populations in high productivity habitats are more resilient because growth rates are higher following population declines. Ludwig (1999) noted that catastrophic population declines are natural phenomena in real populations, that this issue is usually ignored in PVA, and that this can lead to the probability of extinction being underestimated. Protecting high-quality (productive) habitat may therefore be an important factor for maximizing long-term population persistence (Nickelson and Lawson 1998). Substituting different high-productivity habitats may not affect long-term persistence, but substituting a large area of low-quality habitat for a small area of high-quality habitat with equivalent capacity may significantly increase risk of extinction (Fig. 4). While socio-economic issues will influence which habitat configurations are feasible, and it may not always be possible or necessary to protect the highest quality habitat, the consequences of substituting lower quality habitat need to be carefully considered.

It is worth noting that the quantity of habitat available will also affect recovery rate following a perturbation. Density-dependent processes will slow population growth as it ap-
The spatial configuration or proximity of alternative habitat patches (habitat complementarity; Dunning et al. 1992; Kocik and Ferreri 1998) will also be an important consideration for critical habitat selection. This applies to candidate habitats used by a single life stage, as well as habitats used by different life stages (e.g., spawning vs. rearing habitat (Schlosser 1995; Kocik and Ferreri 1998)). For instance, juvenile-rearing habitat in close proximity to spawning habitat may function better than rearing habitat that is distant from spawning sites. Future threats from natural and anthropogenic factors should also be an important consideration when choosing among candidate critical habitats, since future threats will affect long-term average habitat value. For example, proximity to urban sprawl may compromise the future value of some candidate habitats, despite high quality in the present.

The appropriate scale of critical habitat designation will also depend on sensitivity of habitat quality to activities outside critical habitat boundaries. Species persistence may be compromised if habitat quality degrades from activities in the surrounding landscape (e.g., Sinclair et al. 1995; Fahrig 2001); this is a major concern for aquatic habitats that integrate impacts from the surrounding watershed. Regulation of activities outside of critical habitat must be sufficient to maintain quality inside critical habitat; when this is not possible, consideration should be given to expanding critical habitat boundaries to include the larger area. This is consistent with the Species at Risk Act, which permits critical designation for habitats that indirectly affect areas used by a listed species (Species at Risk Act 2002).

This highlights two opposite but complementary approaches to designating and managing habitat for species at risk: preservation vs. regulation. Preservation usually involves creating some form of protected area (with varying levels of effective protection; see Jamieson and Levings 2001; Bruner et al. 2001), while regulation is used for routine management of activities outside of protected areas. In most cases, the establishment of critical habitat over limited areas (preservation approach) will not ensure the persistence of a species, and regulation of activities in the broader habitat matrix surrounding critical habitat will be necessary (regulation approach). The issue becomes whether to designate as critical only those smaller habitats that will be preserved or to also include as critical habitat much larger areas in the surrounding matrix where activities will be permitted.

Key information needs for selection of specific critical habitat areas therefore include (i) sufficient information on habitat quality and complementarity to evaluate the substitutability of candidate habitat patches and (ii) the sensitivity of habitat quality to activities at different spatial scales (local vs. landscape), which will influence appropriate critical habitat patch size and acceptable activities inside and outside of critical habitat.

**Summary**

We have focused on the role of habitat limitation as the primary criteria for identifying critical habitat and advocated using some form of habitat–abundance relationship in conjunction with a population recovery target to define an appropriate area of critical habitat to support the target. We believe that this general framework will make critical habitat designations defensible, consistent, and transparent, all of which are essential elements for the management of species at risk.

Information requirements in this process framework can be summarized as follows:

(i) **Fundamental information needs**

1. Basic life history information, including identification of different life stages and their habitat associations
2. Availability of suitable habitat (present and potential)
3. Population recovery target

---

**Fig. 4.** Hypothetical landscapes where contours represent growth rate potential (habitat quality) for individuals or populations. Filled areas bounded by a dashed line represent candidate critical habitat areas. Right hand panels represent a shift in habitat quality associated with a stochastic climatic event or regime shift. In panel (a), a small area of high-quality habitat supports the same population as a large area of low-quality habitat, so that the patches appear to be superficially substitutable. However, when a large-scale climatic event reduces habitat quality equally across the landscape (panel b), the low-quality habitat becomes a sink with negative growth, while the high-quality habitat remains a source habitat, indicating poor substitutability. Panel (c) illustrates two high-quality patches that are truly substitutable, since habitat capacity is equivalent and both are equally resilient to stochastic changes in habitat quality (panel d).
(ii) Habitat–abundance relationships
(4) Reliable metrics of habitat quality for different life stages
(5) Relationships between habitat quality and quantity and abundance for each life stage

(iii) Habitat required to achieve the recovery target
(6) Estimates of survival for different life history stages or sufficient demographic and spatial data to parameterize a PVA
(7) Sufficient information on habitat quality and quantity to evaluate the substitutability and complementarity of candidate habitats
(8) Severity of present and future threats to different habitats and subpopulations
(9) Contribution of different subpopulations to species persistence

Informed management of fish and wildlife habitat must be based on an accurate understanding of habitat requirements, particularly for species at risk. Conservation efforts to protect critical habitat should be initiated with existing information to whatever extent possible; absence of information should not be an excuse for inaction (Ludwig et al. 1993; Pister 1999). Data acquisition to fill information gaps should clearly identify both short-term priorities (e.g., interim critical habitat designation) and long-term goals and applications (e.g., parameterizing a PVA). When it is necessary to make management decisions prior to filling key information gaps, established rules from the literature, information from similar species, or expert opinion may provide useful guidance (Randall et al. 2003; Martin et al. 2005). A precautionary approach will be appropriate when both uncertainty and the negative consequences of errors remain large. Even in relatively data-rich situations there may be considerable uncertainty, and it may be best to treat the relations used in various components of this process as hypotheses that should be tested and refined within an adaptive management framework.

Despite our emphasis on the role of habitat in population limitation, habitat may play a pivotal role in species persistence for reasons other than habitat limitation (e.g., maintenance of reproductive isolation between species). Critical habitat designation may be justified for a suite of reasons related to the biology and endangerment of particular species (see Appendix A, case 5).

Identifying critical habitat remains only one component in the broader process of managing endangered species. The other key component is the management of habitat and human activities outside of critical habitat. Activities beyond critical habitat boundaries will have a pervasive influence on species persistence for several reasons. First, habitat patches are intimately linked to their surrounding landscapes; activities in the broader habitat matrix often profoundly influence the quality of habitat in adjacent areas, particularly in aquatic systems. Second, protecting discrete habitats will fail to ensure their persistence if the landscape-level processes that create and maintain them (e.g., peak flows in streams) are not protected (Barinaga 1996; Fausch et al. 2002). If critical habitat areas are to be effective tools for species persistence, they must be complemented by careful management of land use in the broader landscape they are part of.

Acknowledgements

We thank Tom Johnston and Eric Parkinson for particularly astute advice on an early version of this paper and the B.C. Non-Game Fish Recovery Team for their insight during the recovery planning process. Funding for this work was provided by the Save the Salish Sucker Foundation.

References


© 2006 NRC Canada


Appendix A. Example taxa with contrasting informational requirements for identifying critical habitat.

A key issue with respect to identifying critical habitat is deciding on the necessary level of information to make a credible designation. Below we illustrate application of appropriate levels of rigour by considering scenarios for species along a gradient of increasing information need.

(1) Endemic species with highly restricted distributions

Many endangered species are listed because of highly restricted geographic distributions, which make them extremely vulnerable to extinction from stochastic events. The hotwater physa (*Physella wrighti*), a freshwater snail endemic to the Liard Hot Springs in British Columbia (Remigio et al. © 2006 NRC Canada
2001), is a good example. It is restricted to several hundred metres of stream and pool habitat (Te and Clarke 1985) and is thus highly vulnerable to habitat destruction or toxic contamination. In this example, simple distributional information is sufficient to infer the extent and location of critical habitat (i.e., presence or absence gives adequate information about habitat quality). Additional information in terms of density and vital rates within the occupied habitat is largely irrelevant for the identification of critical habitat, and the entire area warrants designation as critical for several well-defined reasons: (i) excluding occupied habitat from protection significantly increases extinction risk for extreme endemics; (ii) when a critical habitat area is small, the economic consequences (in terms of lost opportunity costs) of protecting the whole area vs. a subset are trivial; (iii) edge effects may render very small critical habitats ineffectual; and (iv) protecting areas at extremely small spatial scales (e.g., less than 30 m resolution) becomes problematic for management purposes.

Additional reasons to define habitat requirements beyond identifying the current distribution for an extreme endemic might include situations where (i) monitoring indicates the population is in decline, and the underlying mechanism is unknown; (ii) trends in climate are anticipated that might alter habitat quality and therefore population viability; (iii) there are plans to establish a population elsewhere, and information on habitat needs is essential for proper site selection and successful introduction (Harig and Fausch 2002). However, for the purposes of defining critical habitat, the known distribution of an extreme endemic should be sufficient.

(2) Broader endemic species where presence or absence gives inadequate information on habitat quality

For species that are not globally restricted to an extremely small area and are more widespread within one or several watersheds, it may not be desirable or necessary to designate as critical all habitats where the species is known to occur. Salish sucker (Catostomus sp.), which are endemic to 10 small watersheds in the lower Fraser Valley of British Columbia, are a good example; although widely distributed, they are only abundant in a subset of habitats (Pearson and Healey 2003). Because aquatic organisms often occur in sink or low-productivity habitats as a consequence of dispersal or displacement (e.g., Able 1999), presence alone may be an insufficient criterion for critical habitat identification and may potentially lead to the inadvertent inclusion of habitats that contribute little to species recovery. Worse still, it may lead to the inadvertent designation of sink habitats as critical. It may be appropriate to knowingly designate sink habitat as critical when there is an intention to restore sinks to sources as part of recovery planning (Sinclair et al. 1995), but this still requires the ability to differentiate between source and sink habitats. In this case, density or another abundance-based index of habitat quality is necessary to differentiate low- and high-capacity habitats and permit candidate critical habitats to be ranked in terms of their potential contribution to population recovery targets. For example, the density of Salish sucker was found to be consistently higher in deeper pool habitat, particularly marshes (Pearson 2004). In this case quantitative relationships between abundance and habitat features contribute essential information for identifying critical habitat and for informing appropriate design features for habitat restoration.

(3) Species where both presence or density are unreliable indicators of critical habitat

Under certain circumstances, both presence and abundance may be poor indicators of habitat quality. This will be the case when densities in the wild are too low for abundance to be a meaningful assay of habitat quality. This typically occurs when species are at risk because of recruitment failure, and an absence of larval and juvenile fish prevents reliable observations on early life history habitat associations.

Examples where low densities associated with recruitment failure complicate assessment of habitat needs include the razorback sucker (Xyrauchen texanus) and other endangered fishes endemic to the Colorado River (Minckley et al. 2003) and white sturgeon (Acipenser transmontanus) populations in the Kootenai River (Paragamian et al. 2001; Ireland et al. 2002). In both rivers, recruitment failure has been attributed to poor spawning success because of altered water quality, substrate, and flow regimes; predation on juveniles (particularly by alien species in the Colorado; Minckley et al. 1991); and habitat change. Evidence also implicates the importance of off-channel habitat for juvenile rearing, habitat that is now largely absent or unconnected with the river channel because of dikes and flood control downstream of dams.

When there are insufficient fish in the wild to infer habitat needs based on observed habitat use or when abundance is simply difficult to measure because of logistic constraints (e.g., challenges of sampling fish at low densities in very large rivers), some form of experimental manipulation may be required to assess habitat quality. These typically include observations of habitat selection by individuals released in the wild (e.g., using radiotelemetry) or individuals given the choice of alternate habitats in controlled experiments (Rosenfeld and Boss 2001), or by measuring growth or survival of fish experimentally confined to different habitat types (Rozas and Odum 1988; Lonzarich and Quinn 1995; White and Harvey 2001). Although radiotelemetry is an outstanding technique for identifying unique habitat such as spawning and overwintering sites, assessing frequency of habitat use through radiotracking is equivalent to using density (number of individuals found in a habitat type) as an index of habitat quality. Experimental releases of radio-tagged fish have been used on several occasions to assess habitat use by razorback sucker in the Colorado River (Gurtin et al. 2003; Mueller et al. 2003) and other endangered species (e.g., paddlefish, Polyodon spathula; Zigler et al. 2003). Experiments that measure actual growth and survival in different habitats tend to be more definitive in terms of understanding habitat quality because they directly quantify the fitness consequences of habitat use, but are more difficult to design and implement. Examples would include measuring growth and survival of fish experimentally confined to different habitat types in the wild (e.g., using enclosures or isolating fish in individual backwater habitats). Legal restrictions may preclude experiments that lead to mortality of endangered species, but the use of hatchery progeny (e.g., Ireland et al. 2002) or closely related species or populations not at risk may offer a partial solution to this problem. While the fitness consequences of habitat use to individuals provides
strong insight into the role of different habitats for endangered species, the most definitive understanding of which habitats are critical will come from adaptive management experiments that measure the population-level consequences of habitat manipulations (e.g., Solazzi et al. 2000; Minckley et al. 2003).

(4) Species where sufficient data exists to parameterize habitat-explicit, stage-structured population viability analysis (PVA)

For some species, sufficient information may exist on habitat-abundance, growth, mortality, and production relationships to parameterize models that can explore both the population size and viability consequences of habitat change. While habitat-explicit PVA models are the ideal tools for modeling alternative scenarios for identifying critical habitat, the level of information required will probably only be available for species with extensive research histories. This usually includes species with significant historical or current commercial value. Salmonid species are a good example, and the wealth of information and the potential to transfer parameters among species facilitates model construction. Nickelson and Lawson (1998) provide a good example of a full life cycle, habitat-explicit PVA for coho salmon (Oncorhynchus kisutch) that explores the consequences of habitat degradation for stock viability. Other examples include several for birds (e.g., Ackakaya and Atwood 1997), fish populations in the Great Lakes (e.g., Minns et al. 1996a), and Atlantic salmon (Salmo salar; Legault 2004), although very few account for spatial variation in habitat quality. While PVA may be the most sophisticated planning tool for identifying critical habitat that scientists and managers can work towards, most endangered species will initially have insufficient data to parameterize complex models, and interim critical habitat designation may be necessary based on available data.

(5) Species where critical habitat is unrelated to population limitation

In some instances, critical habitat will be unrelated to population limitation, and measures of fish abundance or performance in different habitat types may be of secondary importance to critical habitat identification. This will be the case when habitat plays a role in species persistence other than simply limiting population size. Endangered stickleback species pairs (Gasterosteus spp.) in British Columbia (Schluter and McPhail 1992; McPhail 1993) are a good example. Sympatric species of benthic and limnetic stickleback have co-evolved in a handful of lakes, where the benthic species has morphological and ecological adaptations for feeding on benthic invertebrates in the littoral zone, and the limnetic species has adapted to feeding on zooplankton in the pelagic zone. Benthic and limnetic species coexist with limited gene flow because of strong reproductive isolation associated with accurate mate recognition and reduced hybrid fitness. Benthic and limnetic breeding males have different breeding colours, in addition to differences in size (benthics are much larger) and morphology that females use to identify conspecifics. Hybrids are fertile but selected against because they are less fit than either parental type, owing to intermediate morphology and lower reproductive success (Hatfield and Schluter 1999). Habitat is thought to play a key role in maintaining reproductive isolation because benthic and limnetic species nest in different habitats, water clarity influences light transmission and perception of nuptial colours (Boughman 2001), and larger prey items in the littoral zone may contribute to the greater body size of benthic species (a key factor in mate recognition).

Recently, hybridization rates have increased to the extent that the species pair in one of the lakes appears to have collapsed into an undifferentiated hybrid swarm (Kraak et al. 2001). Although a definitive cause is still lacking, habitat change (loss of macrophyte beds, changes in water clarity) associated with introduced crayfish (Pacifastacus leniusculus) is suspected. Increases in turbidity, loss of differential productivity between benthic and limnetic habitats that maintains a size differential between reproductive individuals of different species, and loss of nest site segregation have all been implicated as potential factors contributing to breakdown of reproductive isolation (presently an area of active research). For instance, increased turbidity might impair detection of nuptial colours and cause increased hybridization independent of effects on population limitation (Seehausen et al. 1997; Boughman 2001; Wood 2003). In this scenario, introduction of an alien species is the ultimate driver of hybridization, but impacts are largely mediated through habitat change. While management priorities should address control of the alien crayfish, and habitat likely plays some role in population limitation, critical habitat designation for stickleback species pairs needs to be primarily based on the role of habitat in maintaining reproductive isolation.

Although we have emphasized the role of habitat in population limitation as the primary criteria for identifying critical habitat throughout this paper, this example emphasizes the importance to critical habitat designation of clearly identifying the cause of species endangerment (e.g., population limitation vs. hybridization) and the role (if any) that habitat plays in it. While limiting habitat will be the primary reason for designating critical habitat for most species, designation will remain justified for a wide range of reasons unique to the endangerment of different taxa.

Appendix references


© 2006 NRC Canada


