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Quantifying habitat requirements of four freshwater species at risk in Canada: Northern Madtom, Spotted Gar, Lake Chubsucker, and Pugnose Shiner

Quantification des besoins en matière d'habitat de quatre espèces d'eau douce en péril au Canada : le chat-fou du Nord, le lépisosté tacheté, le sucet de lac et le méné camus

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ABSTRACT

Estimating the amount of suitable habitat needed to provide high probabilities of persistence in species at risk requires population-based recovery targets and a relationship between area and abundance in particular environments. In this paper, we define minimum area for population viability (*MAPV*) as the amount of suitable habitat required for a demographically sustainable recovery target based on the concept of minimum viable population size (*MVP*). We use demographic analyses, multiple allometric approaches, and home range in a decision flow path to guide precautionary quantifications of habitat requirements for all life stages within discrete populations. We determine *MAPV* for the following four freshwater species at risk in Canada: Northern Madtom (*Noturus stigmosus*), Spotted Gar (*Lepisosteus oculatus*), Lake Chubsucker (*Erimyzon sucetta*), and Pugnose Shiner (*Notropis anogenus*). We also discuss the importance of considering aquatic and terrestrial buffer zones to complement protected habitat designations and provide effective guidance for species persistence.

RÉSUMÉ

La quantification de l’habitat nécessaire pour assurer de fortes probabilités de persistance à des espèces en péril nécessite l’établissement de cibles de rétablissement fondées sur la population et d’un lien entre la superficie d’habitat et l’abondance dans des environnements particuliers. Dans ce document, nous définissons la superficie minimale pour une population viable (SMPV) comme étant la superficie d’habitat approprié et exclusif nécessaire à l’atteinte d’une cible de rétablissement démographiquement viable, d’après le concept de population viable minimale (PMV). Nous appliquons des analyses démographiques, des approches allométriques multiples et un domaine vital au processus décisionnel utilisé pour quantifier, de façon prudente les besoins en matière d’habitat pour toutes les étapes du cycle de vie à l’intérieur de populations distinctes. La SMPV est précisée pour les quatre espèces d’eau douce en péril au Canada suivantes : le chat-fou du Nord (*Noturus stigmosus*), le lépisosté tacheté (*Lepisosteus oculatus*), le sucet de lac (*Erimyzon sucetta*) et le méné camus (*Notropis anogenus*). Nous discutons également de l’importance de la prise en considération des zones tampons terrestres et aquatiques pour compléter les désignations d’habitats protégés et formuler une orientation adéquate sur la persistance de ces espèces.

INTRODUCTION

Despite the importance of identifying and protecting the habitat of threatened or endangered species as part of any conservation plan (Bisson 1995), freshwater habitats are usually protected incidentally as part of terrestrial reserves (Saunders *et al.* 2002). There are very few examples of protected areas created specifically to protect freshwater fishes. The Ash Meadow National Wildlife Refuge, California, was created to protect a remnant population of Devil's Hole Pupfish (*Cyprionodon nevadensis*), where the entire habitat consists of a few square meters near an extensive subterranean cavern system (Vrijenhoek 2001). Conservation actions included purchasing land and prohibitions on the extraction of groundwater. Another remarkable example is represented by the Pacaya-Samira National Reserve in Peru, which was designated to protect the native fish *Arapaima gigas* and included the protection of rivers and alluvial plains (Bayley *et al.* 1991).

Defining critical habitat for species at risk requires determining a population-based recovery target, developing a relationship between habitat and abundance, and quantifying the amount of habitat required to accommodate a population at the recovery target (Rosenfeld and Hatfield 2006). We define minimum area for population viability (*MAPV*) as the amount of exclusive and suitable habitat required for a demographically sustainable recovery target based on minimum viable population size (*MVP*). Therefore, *MAPV* can be considered a quantitative metric of critical habitat that can assist the management and recovery of species at risk. Building on the methodology developed by Vélez-Espino and Koops (2008a, 2008b, 2008c), the minimum area for population viability (*MAPV*) of four freshwater fish species at risk in Canada was estimated following two approaches: (1) predictive equations developed for freshwater fishes relating area per individual to adult length; and, (2) an allometric equation between adult weight and density for aquatic organisms. Information on stable stage distributions was used to extend estimates of *MAPV* to the entire population. These approaches were applied to Northern Madtom (*Noturus stigmosus*) assessed as Endangered (COSEWIC 2002a), Spotted Gar (*Lepisosteus oculatus*) assessed as Threatened (COSEWIC 2005), Lake Chubsucker (*Erimyzon sucetta*) assessed as Threatened in 2001 (Vlasman and Staton 2007), and Pugnose Shiner (*Notropis anogenus*) assessed as Endangered (COSEWIC 2002b).

We first describe how recovery targets can be set based on a criterion of demographic sustainability, followed by a description of the methods used to calculate *MAPV* and an exploration of the relationship between *MAPV* and home range in these four fishes. Finally, we propose a decision flow path for quantifying habitat requirements and discuss the importance of aquatic and terrestrial buffer zones.

METHODS

RECOVERY TARGETS

With demographic sustainability (i.e., a population is self-sustaining over the long term) as an appropriate criterion, we used the allometry between population growth rate and minimum viable population size (*MVP*; Shaffer 1981) developed by Reed *et al.* (2003) to calculate recovery targets consistent with science advice on recovery targets for aquatic species in the context of the *Species at Risk Act* (DFO 2005). *MVP*, defined as the adult population size required for a 99% probability of persistence over 40 generations, was calculated using the predictive equation:

1) $\log_e MVP = 9.36 - 1.55 \log_e \lambda$

where λ is the population growth rate. Back-transformation of log-transformed *MVP* values was corrected for bias following Sprugel (1983). The term λ was computed separately for each species as the natural base of the intrinsic rate of increase (*r*). Blueweiss *et al.* (1978; also revised in Charnov 1993) showed that there is a strong relationship between the maximum intrinsic rate of increase and adult body weight across a broad range of taxa. We used a predictive equation developed specifically for freshwater fishes (equation 2; Randall and Minns 2000) that is based on the allometry between production per unit biomass (P/B) and adult body weight (*W* in grams). In a population dynamic context, maximum P/B is equivalent to the maximum intrinsic rate of increase (Peters 1983). Accordingly, P/B as a surrogate of *r* also varies inversely with fish size and longevity and is therefore appropriate for individual species and populations (Randall and Minns 2000).

2) $r = 2.64 W^{-0.35}$

MINIMUM AREA FOR POPULATION VIABILITY

The maximum number of individuals that can occupy an area is primarily a function of the size of the organism (Peters and Wassenberg 1983, Cyr *et al.* 1997). Two predictive equations of area per individual (*API*; m^2), based on body size and developed for freshwater fishes (Randall *et al.* 1995, Minns 2003), were used to determine minimum area for population viability (*MAPV*) in river (equation 3) and lake (equation 4) environments.

3) $API = e^{-13.28} \; L_{(mm)}^{2.904}$

4) $API = e^{-10.37} \; L_{(mm)}^{2.58}$

The use of separate equations for rivers and lakes is necessary because area per individual (Randall *et al.* 1995, Minns 2003) and home range (Minns 1995) are both significantly larger in lake environments.

This metric of required habitat (henceforth named $MAPV_1$) was calculated as the product of *MVP* and adult *API*. We provided estimates of $MAPV_1$ for mean adult weight (*W*). The term *W* was computed as the geometric mean of minimum and maximum values of adult body size reported in the literature. These values corresponded to the adult length at first maturity and at maximum realizable age, respectively.

Alternatively, we used the allometric equation for density-body weight in aquatic species obtained by Cyr *et al.* (1997) to estimate a second metric of required habitat, common to lake and river environments, henceforth named $MAPV_2$:

5) $\log_{10} D = 5.6 - 0.91 \log_{10} h$

where *D* is density (individuals/m^2) and *h* is the mean weight of adult fish expressed in micrograms. Back-transformation of log-transformed *D* was corrected for bias (Sprugel 1983) and minimum area for population viability ($MAPV_2$) was computed as:

6) $MAPV_2 = D^{-1} \, MVP$

where the inverse of density represents another metric of area per individual. Given that equation 5 was generated from density data in lakes (Cyr *et al.* 1997), an estimate of $MAPV_2$ for rivers was inferred from the proportionality between the lotic and lentic estimates of $MAPV_1$.

HOME RANGE

Estimates of *MAPV* based on area per individual may underestimate required habitat area in species displaying large home ranges because *API* is a function of population processes controlled by a saturation function of habitat supply (Minns *et al.* 1996) and not by species' movement. Although estimates of home range cannot be directly translated into *MAPV* without knowing the degree of overlap between individual home ranges for particular species, it may be informative to explore the relationship between *MAPV* and home range. A positive relationship between body size and home range has been demonstrated for fishes (McAllister *et al.* 1986). The allometry between body size (*L*; mm) and home range (*HR*; m^2) developed by Minns (1995) was applied to mean adult length following the same procedure as in mean adult weight:

7) $$\log_e HR = -2.907 + 1.651 \log_e L_{mm} + 3.137 * HAB$$

where *HAB* (river = 0, lake = 1) is a dummy variable referring to the kind of habitat used by the species. Again, back-transformation of log-transformed *HR* was corrected for bias (Sprugel 1983). In addition, the number of exclusive home ranges that could fit into the required habitat (HR_{MAPV}) was calculated in relation to the highest *MAPV* of the two metrics used. This final step can help to determine how well the estimated *MAPV*s represent long-range movements associated with a species ecology and life history.

EXTENDING *MAPV* TO ALL LIFE STAGES

Our metrics of required habitat (*MAPV*s) are based on the concept of demographic sustainability and pertain exclusively to the area requirements of a minimum viable number of adults using good quality habitat. *MAPV* does not specify the amount of habitat needed for juvenile fish or spawning in the case that spawning habitat is not within the adult habitat. Therefore, a complete description of required habitat, derived from our approach, still needs basic demographic data and knowledge of stage-specific habitat preferences to specify the juvenile and spawning (where required) habitat necessary to sustain the minimum viable adult population size (see Figure 1).

Abundances of young-of-the-year (YOY) and juvenile fish necessary to maintain a stable population at the *MVP* were estimated from the stable stage distributions of demographic matrices modelling the life cycle of each species. Each life cycle was represented by a stage-structured matrix **M** with 3 stages (Figure 2): young-of-the-year (YOY; stage 1; from egg to the end of the first year of life), juveniles (stage 2; from the end of the first year to the age of first maturity), and adults (stage 3; which covers the period from first reproduction to maximum observed age at reproduction). The elements of **M** included the fecundity coefficient of stage class *j* (F_j), the probability of surviving stage *j* and remaining in stage *j* (P_j), and the transition probability of surviving one stage and moving to the next (G_j). This stage-structured model required defining σ_j as the annual survival probability of an individual in stage *j*, and γ_j as the probability of moving from *j* to *j*+1 given σ_j. Then, the parameters P_j and G_j are defined as $\sigma_j(1- \gamma_j)$ and $\sigma_j \gamma_j$, respectively, where the term γ_j is calculated from a geometric distribution of $1/T_j$ in which T_j is the duration of stage j in years. The largest eigenvalue of projection matrix **M** represents the annual population growth rate ($\lambda = e^r$).

We used a post-breeding projection matrix (see Caswell 2001), in which the fecundity coefficient (F_j) depends on adult survival through the previous year as well as the stage-specific fertility f_j such that:

8) $$F_j = f_j P_j + f_{j+1} G_j$$

According to equation 8, juveniles moving into the adult stage the following year will contribute to the reproductive output because a post-breeding variant assumes the census is taken after spawning (Crowder *et al.* 1994); this is why an additional reproductive element appears in matrix **M** (Fig. 2b and 2c).

Fertility was estimated as $f_j = m\, b\, \varphi$, where m is the average number of eggs per reproductive clutch, b is the average number of reproductive clutches per year, and φ represents the proportion of eggs producing females (a balanced sex ratio was assumed). Juvenile and adult survival (σ_2 and σ_3, respectively) were estimated from estimates of natural mortality (M) provided in Fishbase (www.fishbase .org) as $\sigma_j = e^{-M_j}$. Young-of-the-year survival (σ_1) was calculated for each species by solving for population growth rate according to equation 2 without altering any other matrix parameter. This involved an iterative process through direct perturbation of the projection matrices (Vélez-Espino *et al.* 2006).

The right eigenvector w of **M** represents the stable stage distribution, which indicates the proportion (p_j) of the population in stage j once sufficient time has passed to dampen fluctuations due to initial conditions (de Kroon *et al.* 1986). This vector satisfies the equation:

9) $$\mathbf{M}\, w = \lambda\, w$$

where:

10) $$w = \begin{bmatrix} p_1 \\ p_2 \\ p_3 \end{bmatrix}$$

Abundances of YOY and juveniles needed to maintain a stable population of *MVP* adults were calculated as the product of stage proportions and *MVP*. The minimum area for population viability required for each stage ($MAPV_j$) was estimated as the product of each stage's abundance and its corresponding *API*s. Length at age was estimated from the von Bertalanffy growth equations provided for the species in Fishbase (www.fishbase .org). Area per individual was estimated as the geometric mean area per individual at the points delimiting the stage: emergent fry (*API* = 0.001) and age 1 for YOY, and age-1 and age at first maturity for juveniles. When all stages share the same habitat, the size of a discrete area representing the minimum area for population viability of the entire population ($MAPV^*$) would be the sum of all $MAPV_j$. When different life stages use different habitats, the $MAPV_j$ would represent the allocation of habitat required for individual stages.

DATA
Values of adult body size and generation time, and habitat information to compute required habitat and home range from allometric relationships were extracted from several sources (Table 1). For species where adult weight was unknown, we used the allometry between length and weight ($W = aL^b$) provided for the species or genus in Fishbase (www.fishbase .org). For species using both lake and river habitats, $MAPV_1$, $MAPV_2$, and home range were estimated separately for each habitat type. Trait and vital rate values for the matrix models were extracted from different sources (Table 2).

RESULTS

Results are summarized in table 3. Minimum viable adult population size varied from 628 adult Pugnose Shiner to 8 127 adult Lake Chubsucker. Based on information on area per individual, minimum area for population viability ($MAPV_1$) ranged from 151 m^2 to 321.6 ha in rivers and from 735 m^2 to 686.9 ha in lakes for Pugnose Shiner and Spotted Gar respectively. Using the approach based on allometric density, minimum area for population viability ($MAPV_2$) ranged from 75 m^2 for Pugnose Shiner to 112.0 ha for Spotted Gar in rivers and from 367 m^2 for Pugnose Shiner to 270.9 ha Lake Chubsucker in lakes. Home range was smaller than *MAPV* in all species, except for Pugnose Shiner in lake environments, and ranged from 48 m^2 to 3 527 m^2 in rivers and from 1 106 m^2 to 7.5 ha in lakes based on mean adult body size in Pugnose Shiner and Spotted Gar respectively. Lastly, the number of exclusive home ranges that could fit within a *MAPV* ranged from 3.1 to 1104.7 in rivers and from 0.7 to 133.4 in lakes.

Following a precautionary approach as recommended by Vélez-Espino and Koops (2008a, 2008b, 2008c), adult habitat should be at least 1.5 ha of river habitat or 6.1 ha of lake habitat for Northern Madtom, at least 321.6 ha of river habitat or 686.9 ha of lake habitat for Spotted Gar, at least 98.1 ha of river or 270.9 ha of lake habitat for Lake Chubsucker, and at least 151 m^2 of river habitat or 1 106 m^2 of lake habitat for Pugnose Shiner (Table 3). Further, minimum area for population viability based on area per individual ($MAPV_1$) produced the most precautionary values of required habitat for lakes and rivers in Spotted Gar and for rivers in Pugnose Shiner whereas the approach based on allometric density ($MAPV_2$) produced the most precautionary values for rivers and lakes in Northern Madtom and Lake Chubsucker. Home range generated the most precautionary area requirements in lakes for Pugnose Shiner.

The combination of information provided by stable stage distributions and minimum viable adult population size (*MVP*) allowed the estimation of minimum viable population sizes of all stages and ultimately of the entire population (Table 4). By combining these estimates with area per individual, the sum of the minimum area for population viability required for each stage ($MAPV_j$) indicated that the minimum area for population viability required for the entire population ($MAPV^*$) was 99% greater in rivers and 51% greater in lakes for Northern Madtom, relative to this species' adult *MAPV*. The $MAPV^*$ was three times larger in rivers and lakes for Spotted Gar, approximately two times larger for Lake Chubsucker, and it showed more than a ten-fold increase for Pugnose Shiner (Table 4).

DISCUSSION

Our recommendations for required habitat of these four fishes are based on the concept of minimum viable population size, which can be misinterpreted (Beissinger and McCullough 2002) and used as a reference point for exploitation or allowable harm purposes. The concept of *MVP* is meaningful for individual, discrete populations that function demographically as independent units, pertains exclusively to minimum abundance levels for high probabilities of long-term persistence within a recovery framework, and ignores the probability of catastrophic events. It is important to note that *MVP* refers exclusively to habitat requirements for the adult portion of the population. The inclusion of spawning habitat as a separate habitat unit is important if spawning habitat represents a discrete area and not only a small portion of the entire adult habitat. This is important given the effect that alterations to spawning habitat can have on egg-to-hatch survival from density-dependent mortality and low survival at sub-optimal spawning sites (Vélez-Espino and Koops 2007).

Knowledge of the stage structure of populations allowed us to extrapolate required habitat to include the entire population. This analysis needed additional life history data and knowledge of habitat preferences for each life stage, including the degree of habitat overlap (see also Rosenfeld and Hatfield 2006). *MVP* estimates are usually applied to populations exhibiting abundance levels below the minimum viable size, and are useful for optimizing efforts and resources by selecting those populations with greater need of recovery action. Thus, our estimates of required habitat should not be considered final recommendations for habitat protection for species at risk but rather a first step within a recovery process in which the amount of critical habitat would be adjusted with new recovery targets, perhaps moving from demographic sustainability to ecological function or historic baselines (see Sanderson 2006).

RELYING ON THE PRECAUTIONARY APPROACH

Uncertainty in age and size structure should suggest that a precautionary approach is appropriate, erring toward protection of sufficient habitat to contain minimum viable populations of large individuals given the positive relationship between adult body size and both *MVP* and *MAPV*. But even with a risk averse quantification of required habitat, it is still necessary to develop a decision path that incorporates additional habitat protection concerns such as home range size or minimum areas for species with small body sizes and small home ranges (Fig. 1). Efforts to increase the probability of persistence of species at risk should include knowledge of *MVP* and home range (Soulé 1987). Although individual home ranges were less than the minimum area for population viability in all studied species and environments, excepting *N. anogenus* in lakes, we suggest using home range as a surrogate of required habitat for those cases when *MAPV* is less than the home range; particularly for species that require large river or lake ranges to support self-sustaining populations. For instance, although based on area per individual calculations, a lake sturgeon (*Acipencer fulvescens*) population of 500 adults would require as much as 76 ha in rivers and 236 ha in lakes (Randall 2008), more than 200 km^2 of river and lake habitat could be needed to support self-sustaining populations (Auer 1996).

CRITICAL HABITAT AND BUFFER ZONES

Including terrestrial and aquatic buffers to complement habitat protection for species at risk is a conservation approach that has been proposed and applied for different aquatic species such as Nooksack Dace (*Rhinichthys cataractae*; National Recovery Team for

Nooksack Dace 2005), Grey Nurse Shark (*Carcharias taurus*; www.fisheries.nsw.gov.au), freshwater turtles (Burke and Gibbons 1995), and salamanders (Semlitsch 1998). A riparian buffer is an area along a shoreline, wetland, or stream where development is restricted or prohibited. For instance, a riparian forest buffer is an area of trees, usually accompanied by shrubs and other vegetation, along a stream, river, or shoreline that is managed to maintain the integrity of the waterway, to reduce pollution, and to provide food, habitat, and thermal protection for fish and wildlife (Davis and Nelson 1994, Burke and Gibbons 1995). Riparian buffers of 30 m have been recommended to maintain fish habitat in streams (Hickman and Raleigh 1982, Raleigh *et al.* 1986, Jones *et al.* 1988) and some studies have found that widths of 10-50 m are sufficient to maintain stream temperatures and retain sediments and nutrients (Osborne and Kovacic 1993). The maintenance of shoreline buffer zones in lakes and wetlands is also important to reduce edge effects on aquatic species (Kipp and Calaway 2003). The Ontario Ministry of Natural Resources (OMNR) recommends a minimum 15 m buffer for water quality protection around lakes and streams supporting warmwater species and a 30 m buffer where the waterbody supports coldwater species in areas where the proposed land use adjacent to a waterbody is residential (OMNR 1994). Where the proposed adjacent land use is forestry, OMNR establishes a 120 m area of concern with a minimum 30 m no cut zone and a 90 m modified cut zone depending on slope (OMNR 1999).

The definition of aquatic buffers has been more elusive and receives significantly less research compared to riparian buffers. Aquatic buffer zones of 800 m have been implemented around the marine critical habitat of Grey Nurse Shark populations in Australia (www.fisheries.nsw.gov.au). Other studies indicate that aquatic buffer requirements in wetlands are met with surrounding areas ranging from 60 m to 164 m (Semlitsch and Jensen 2001). Proposed critical habitat for Nooksack Dace (*Rhinichthys cataractae*) in British Columbia's Fraser Valley consists of reaches that contain or are known to have previously contained Nooksack Dace and have more than 10% riffle by length. It includes riparian buffer strips of native vegetation on both banks for the entire length of the reach (National Recovery Team for Nooksack Dace 2005).

The protection of aquatic habitat may require incorporating both aquatic and terrestrial (where applicable) buffer zones. Buffer zones can complement river and lake (or wetland) habitat protection, but defining buffer zones may be easier in streams than in lakes or wetlands (Fig. 3). The concept of stream reach could be used to determine the limits of aquatic buffer zones. Stream reach is defined as a natural unit of river length that ranges from hundreds to thousands of meters in length, includes a riffle portion delimited by meander pools, and is characterized by unique water residence times (Frissell *et al.* 1986). In addition, the reach scale frequently corresponds closely to that of land ownership and, consequently, can be appropriate for recovery actions (National Recovery Team for Nooksack Dace 2005). Aquatic buffer zones in river environments could be defined by the limits of the stream reaches containing the required habitat (Fig. 4). For lake or wetland environments, the definition of aquatic buffer zones is more elusive but shoreline buffers could have similar widths to those recommended for riparian buffers (Fig. 3).

The use of allometric relationships to estimate area requirements for population viability produced extremely small *MAPV* for adult Pugnose Shiner, which exhibit the smallest body size and display the smallest home range among the studied species. However, *MAPV* of the entire population (i.e., including YOY, juveniles, and adults) was 38 times larger in lotic environments and 10 times larger in lentic environments than the area computed for adults only. This fact favours the conservation of a larger area per population because all life stages share the same habitat (COSEWIC 2002b). Yet, guidelines defining minimum areas for conservation of aquatic habitat in rivers, wetlands, and lakes still need to be developed. These guidelines could transcend ecological criteria (which are already considered in the quantitative analyses presented here) and consider the feasibility of practical conservation measures, basically answering the question: what is the minimum area that should be considered for the implementation of a feasible recovery strategy? The definition of these minimum areas for conservation of aquatic habitat could be generic and rely on expert opinion or could be species-specific, based on the ecology of individual species. At any rate, the inclusion of aquatic buffer zones is therefore of major importance for the conservation of aquatic species whose area requirements, estimated through ours or other methodologies, are extremely small. This implementation would be necessary to effectively protect aquatic habitat against edge effects.

ADDITIONAL CONSIDERATIONS

The use of allometric relationships to quantify required habitat relies on the premise that area as a function of body size are estimated for suitable (good quality) habitat and do not address the differences in habitat quantity necessary to contain viable populations derived from changes in habitat quality. High quality habitat will generally have higher survival rates, resulting in higher density and a steeper abundance–area relationship (Rosenfeld and Hatfield 2006). The loss or contraction of habitat for species at risk can impact population dynamics and demographic parameters through various mechanisms, including reduced survival rates (Minns *et al.* 1996), decreased somatic growth rates (Van Winkle *et al.* 1993) or increased propensity to emigrate to less suitable habitat (Grant and Kramer 1990). It does not seem unfeasible to generalize quantity-quality habitat relationships but there is no doubt that habitat quality can be as important as habitat quantity in defining habitat preserves (Rodwell *et al.* 2003). Considerations of habitat quality will have to be implemented on a case-by-case basis after empirically or experimentally determining specific relationships between some habitat component (biotic or abiotic) and population attributes (e.g., Hayes *et al.* 1996; Rodwell *et al.* 2003; Eby *et al.* 2005).

Our treatment of allometric relationships, stage structure and its implications on minimum areas for population viability was deterministic. Additional work is needed to examine whether variation in life history traits, and stochastic variation in vital rates, lead to significant changes in the amount of required habitat. Sources of stochastic variation will be of particular concern if our framework is adapted to project the efficacy of protecting habitat to cope with environmental edge effects and random catastrophes.

Finally, another consideration when protecting habitat is the relative importance of stage-specific habitat on population fitness. More specifically, by combining demography with information on stage-specific habitat preferences and knowledge of the relationship between habitat demand and availability it is possible to determine the life stage most sensitive to habitat loss and how losses or gains in habitat for this stage could affect population growth rates. This habitat-explicit approach was used by Vélez-Espino and Koops (2007) to define the sensitivity of Black Redhorse (*Moxostoma duquesnei*) population growth rates to stage-specific habitat loss. Analyses indicated that the population dynamics of Black Redhorse is particularly sensitive to the loss of young-of-the-year habitat. Using a similar approach, Levin and Stunz (2005) found that most of the variability in population growth rates of the Red Drum (*Sciaenops ocellatus*) is explained by larval and juvenile survival rates, therefore recommending the protection and restoration of marshes and seagrass habitats used by these life stages. Levin and Stunz

(2005) used the term “essential fish habitat” to describe the habitat whose restoration and protection (or loss and contraction for that matter) will have the greatest impact on population fitness. Preserving the habitat of fish species at risk would benefit from scientific advice not only on the required habitat for a viable population but also on essential fish habitat. Although this approach would generate robust guidance, data requirements may still limit its application in all conservation settings.

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Table 1. Information sources for habitat and life history information of four fish species at risk.

Species	Adult length	Adult weight	Generation time	Habitat
Northen Madtom	COSEWIC 2002a	Fishbase (genus)	COSEWIC 2002a	COSEWIC 2002a
Spotted Gar	COSEWIC 2005	Fishbase (species)	Fishbase (species)	COSEWIC 2005
Lake Chubsucker	Vlasman and Staton 2007 Coker *et al.* 2001	Fishbase (genus)	Coker *et al.* 2001	Vlasman and Staton 2007
Pugnose Shiner	COSEWIC 2002b	Fishbase (genus)	COSEWIC 2002b	COSEWIC 2002b

Table 2. Trait and vital rate values used to construct matrix models of studied species. Letters represent information sources and additional methodological details.

	Traits				Vital rates			
Species	Age at maturity	Longevity	# of eggs/ clutch	# of clutchs	YOY survival	Juvenile survival	Adult survival	Fertility
Northern madtom	1	3	100	3	0.0124	NA	0.196	150
	c	c	a	b2	e	f	c3	g
Spotted gar	4	18	20000	1	0.0001	0.691	0.852	10000
	a, c	a, c	d	b2	e	c2	c1	g
Lakechub sucker	3	8	12000	1	0.00035	0.631	0.819	6000
	a	a,c	a	b1	e	c2	c1	g
Pugnose shiner	1	3	900	2	0.008	NA	0.141	900
	c	a, c	a	b2	e	f	c3	g

a COSEWIC Reports.
b_1 Species information from Winemiller and Rose (1992).
b_2 Genus average from Winemiller and Rose (1992).
c Fishbase (www.fishbase.org).
c_1 Survival estimated from lower bound of natural mortality provided in Fishbase (www.fishbase.org).
c_2 Survival estimated from upper bound of natural mortality provided in Fishbase (www.fishbase.org).
c_3 Survival estimated from mean natural mortality provided in Fishbase (www.fishbase.org).
d http://www.tpwd.state.tx.us/huntwild/wild/species/spottedgar/
e Value generated by solving for matrix **M** at λ_{max}.
f For species maturing at age 2 there is not a juvenile stage.
g A balanced sex ratio (0.5 : 0.5) was assumed.

Table 3. Body size, minimum viable adult population size (*MVP*), and required habitat by adults of four freshwater fishes at risk in Canada in lotic (upper row) and lentic (lower row) environments. *MAPV*: minimum area for population viability. *HR*: home range. HR_{MAPV}: number of exclusive home ranges that fit within the most precautionary *MAPV*. The most precautionary area values are shown in bold.

Species	Adult *W* (g)	Adult *L* (mm)	*MVP* #	$MAPV_1$ (ha)	$MAPV_2$ (ha)	*HR* (ha)	HR_{MAPV}
Noturus stigmosus	29.1	104	3 996	0.49	**1.51**	0.012	125.8
				2.01	**6.15**	0.28	22.0
Lepisosteus oculatus	760.1	764.6	7 966	**321.61**	112.00	0.326	986.5
				686.90	239.22	7.525	91.3
Erimyzon sucetta	816.1	346	8 127	32.81	**98.10**	0.089	1102.0
				90.60	**270.90**	2.03	133.0
Notropis anogenus	0.8	59.2	628	**0.015**	0.008	0.005	3.1
				0.074	0.037	**0.111**	1.0

Table 4. Stable stage distribution (*SSD*), stage-specific minimum viable population size inferred from the *SSD* (MVP_{SSD}), and area per individual (*API*: m^2) and most precautionary estimates of minimum area for population viability ($MAPV_P$) in river and lake environments for each life stage (m^2) and the entire population (ha) in each studied species.

Species	Stage	*SSD*	*MVPSSD*	*API*		*MAPVP*	
				River	Lake	River	Lake
Northen Madtom	YOY/Juvenile	0.9934	601459	0.025	0.052	15036	31276
	Adult	0.0066	3996	3.8	15.4	15063	61477
	All		*605455*			*3*	*9.3*
Spotted Gar	YOY	0.9999	256594408	0.024	0.053	6158266	13599504
	Juvenile	0.0001	25662	8.94	30.03	229418	770630
	Adult	3.104E-05	7966	403.7	862.3	3216113	6869002
	All		*2.57E+08*			*960.4*	*2123.9*
Lake Chubsucker	YOY	0.9995	40614683	0.042	0.084	1705817	3411633
	Juvenile	0.0003	12191	6.67	22.52	81314	274541
	Adult	0.0002	8127	120.7	333.3	981004	2709000
	All		*40635001*			*276.8*	*639.5*
Pugnose Shiner	YOY/Juvenile	0.9989	570281	0.01	0.02	5703	11406
	Adult	0.0011	628	0.2	1.8	151	1106
	All		*570909*			*0.6*	*1.1*

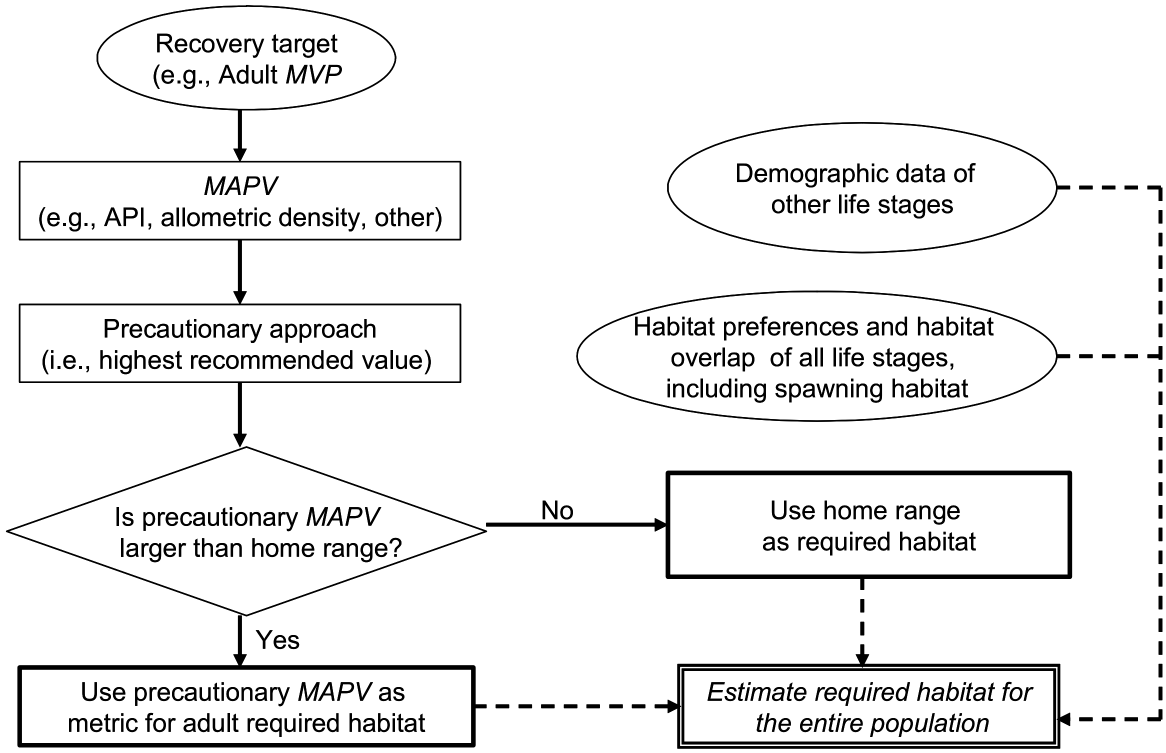
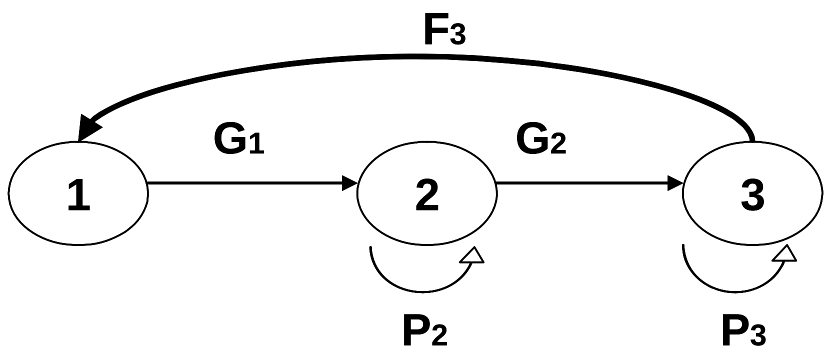


Figure 1. Decision flow diagram for required habitat based on a precautionary approach to demographic sustainability as defined by minimum viable adult population size (*MVP*), minimum area for population viability (*MAPV*), and home range.

(*a*)



(*b*)

$$\mathbf{M} = \begin{pmatrix} 0 & F_2 & F_3 \\ G_1 & P_2 & 0 \\ 0 & G_2 & P_3 \end{pmatrix}$$

(*c*)

$$\mathbf{M} = \begin{pmatrix} 0 & f_3\,\sigma_2\,\gamma_2 & f_3\,\sigma_3\,(1-\gamma_3) \\ \sigma_1\,\gamma_1 & \sigma_2\,(1-\gamma_2) & 0 \\ 0 & \sigma_2\,\gamma_2 & \sigma_3\,(1-\gamma_3) \end{pmatrix}$$

Figure 2. Generalized life cycle (a), corresponding stage-structured projection matrix (b), and formulas applied to calculate matrix elements (c) used to model the population dynamics of redside dace. The life cycle was dived into three stages: young-of-the-year, juvenile, and adult. F_j represents the stage-specific fecundity coefficient, P_j the probability of surviving and remaining in the same stage, and G_j the probability of surviving and moving to the next stage. The annual survival probability of an individual in stage *j* is σ_j, and the probability of growth from *j* to *j*+1 given σ_j is γ_j. (f_j): stage-specific fertility.

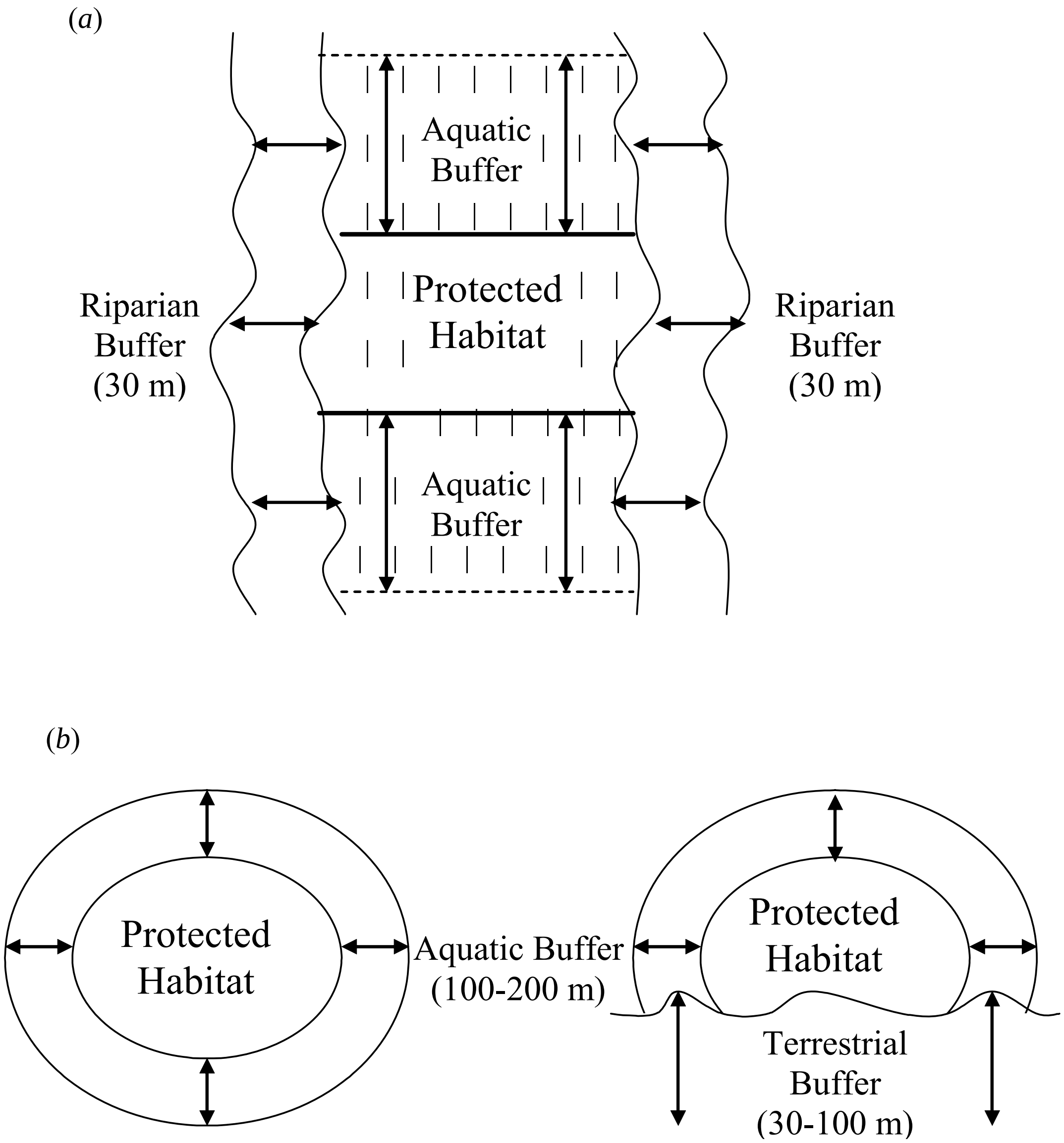


Figure 3. The incorporation of terrestrial and aquatic buffer zones to protect habitat of freshwater aquatic species in river (*a*) and lake-wetland (*b*) environments.

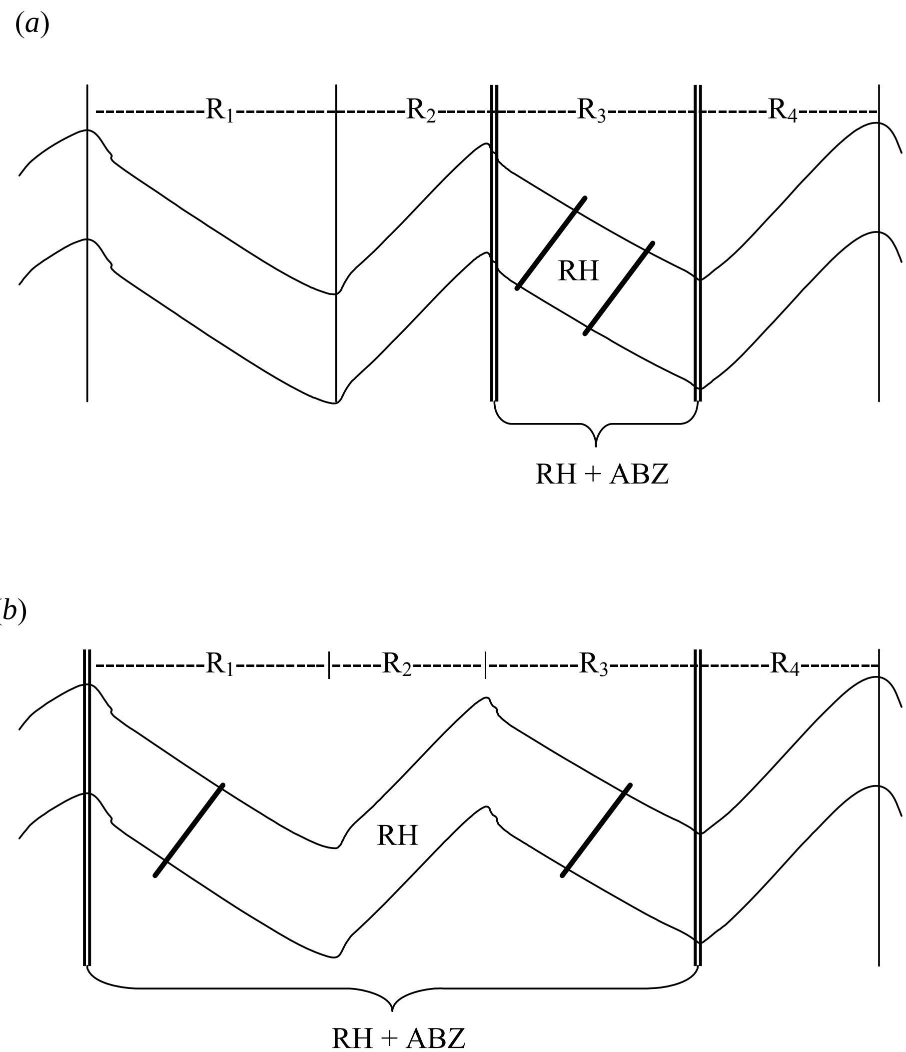


Figure 4. Required habitat (RH) with aquatic buffer zones (ABZ) delimited by the stream reach (R_i) encompassing required habitat when this is smaller than the reach (*a*) or by the outer limits of the stream reaches adjacent to the required habitat when this includes one or more stream reaches (*b*). Riparian buffers are not depicted.