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Identification of Critical Habitat for Sympatric Stickleback Species Pairs and the Misty Lake Parapatric Stickleback Species Pair

Définition de l'habitat essentiel des paires d'espèces sympatriques de l'épinoche et des paires d'espèces parapatriques de l'épinoche du lac Misty

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Abstract

In this paper recommendations are provided for defining critical habitat for stickleback species pairs in British Columbia, based on a weight of evidence approach. Recommendations are made for the proportion of existing habitat that can be considered critical, but no effort has yet gone into delineating specific areas in the wild. Critical habitat recommendations were developed using the framework suggested in Rosenfeld and Hatfield (2006). Population targets are explored and supported using multiple approaches, including simple population viability analyses, rules of thumb, and genetic considerations. Simple population viability analyses indicate that stickleback are resilient to environmental stochasticity even when populations are at low abundance. I used two quasi-extinction thresholds, based on environmental and genetic considerations. Population models could be improved considerably with additional information on stickleback vital rates, but population-specific data are unlikely to be available soon. Habitat required to meet proposed population targets varied from 5% to 100% of existing habitat depending on the modeling approach.

There are two key components of habitat for benthic-limnetic and lake-stream species pairs: 1) habitat features that control the abundance of limnetics and benthics (i.e., population size), and 2) features of the environment that ensure proper mate recognition and assortative mating. Therefore, habitat needs for species pairs include features whose alteration or loss will lead to reduction in abundance to an unviable population level, or breakdown of reproductive barriers sufficient to cause collapse into a hybrid swarm. These habitat features are reviewed briefly here.

Most defensible approaches indicate that a considerable portion of existing habitat is critical, and the dependence of species pair co-existence on reproductive isolation indicates that the habitat attributes required for persistence must be maintained at the ecosystem scale, i.e. that in each case the entire lake plus a riparian buffer should be designated as critical habitat. Recommended critical habitat for benthic-limnetic pairs includes the entire lake for each pair and a riparian buffer of 15 to 30 m width surrounding the wetted perimeter of each species pair lake and all ephemeral and perennial streams flowing into the lakes.

Recommended critical habitat for the Misty Lake pair includes the entire lake, the wetted area of the entire inlet stream, and the wetted area of the outlet stream as far downstream as the lower limit of currently occupied habitat (presently estimated at 2.3 km downstream of the lake). Also included as critical for the Misty Pair is a riparian buffer of 15 to 30 m width on the lake and both inlet and outlet streams, plus any perennial or ephemeral tributaries.

Résume

Ce document présente des recommandations en vue de définir l'habitat essentiel des espèces sympatriques de l'épinoche en Colombie-Britannique, en utilisant une approche fondée sur le poids de la preuve. Les recommandations faites ont trait à la proportion de l'habitat pouvant être considéré comme essentiel, mais aucune désignation de zones spécifiques dans la nature n'a été entreprise. Les recommandations en matière d'habitat essentiel ont été élaborées au moyen du cadre proposé par Rosenfeld et Hatfield (2006). Des cibles en matière de population ont été examinées et soutenues par diverses approches, notamment des analyses simples de viabilité de la population, des règles empiriques et des considérations d'ordre génétique. Les analyses de viabilité de la population indiquent que l'épinoche est résistante à la stochasticité environnementale, y compris lorsque les populations sont peu abondantes. J'ai utilisé deux seuils de quasi-extinction basés sur des considérations environnementales et génétiques. Les modèles de population pourraient être considérablement améliorés par l'apport de données supplémentaires sur les taux démographiques de l'épinoche. Il est cependant peu probable que ces données spécifiques des populations soient disponibles sous peu. L'habitat requis pour répondre aux propositions de cibles de population variait de 5 à 100 % de l'habitat existant, selon le modèle utilisé.

L'habitat des paires d'espèces benthiques-limnétiques et lacustres-fluviales comporte deux éléments clés : 1) des caractéristiques d'habitat qui limitent l'abondance des espèces benthiques et limnétiques (c'est-à-dire, la taille des populations) et 2) des caractéristiques environnementales propices à la reconnaissance des partenaires et à l'homogamie. Ainsi, les besoins d'habitat des paires d'espèces renvoient à des caractéristiques dont l'altération ou la perte mènera à une diminution de l'abondance jusqu'à atteindre un niveau de population non viable, ou à une dislocation des barrières reproductives suffisante pour causer l'effondrement de ces espèces en faveur d'un essaim d'hybrides. Ces caractéristiques d'habitat sont ici brièvement examinées.

La plupart des approches défendables indiquent qu'une part considérable de l'habitat existant est essentielle, et le fait que la coexistence de la paire d'espèces dépend de son isolement reproductif indique que les caractéristiques d'habitat requises en vue de la persistance des espèces doivent être soutenues à l'échelle écosystémique, c'est-à-dire que dans tous les cas l'habitat désigné comme essentiel devrait comprendre le lac dans son intégralité plus une zone riveraine tampon. Il est recommandé que l'habitat essentiel pour les paires benthiques-limnétiques comprenne le lac dans son intégralité pour chaque paire, une zone riveraine tampon de 15 à 30 mètres de large autour du périmètre mouillé du lac de chaque paire d'espèces, ainsi que la totalité des cours d'eau saisonniers et pérennes affluents de ces lacs.

Il est recommandé que l'habitat essentiel de la paire du lac Misty comprenne le lac dans sa totalité, la surface mouillée de l'intégralité du cours d'eau affluent, ainsi que la surface mouillée du cours d'eau effluent jusqu'à la limite inférieure de l'habitat actuellement occupé (que les estimations actuelles situent à 2,3 km en aval du lac). Pour la paire du lac Misty, on devrait également considérer comme habitat essentiel une zone riveraine tampon de 15 à 30 m de large autour du lac, des cours d'eau affluents et effluents, ainsi que toute autre artère secondaire pérenne ou saisonnière.

1. PREAMBLE

Defining critical habitat is one of the most challenging aspects of species management, yet it is vital to ensuring a species' long-term survival. This rationale is central to endangered species legislation in general, and specifically to the Species at Risk Act (SARA), where critical habitat is defined as:

"…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." [s. 2(1)]

Despite its complexity, the core issue is the same for all species: to determine the role of habitat in population limitation, and to answer the question, "How much habitat is required to maintain one or more viable populations?"

I separate the issue of defining critical habitat from its "identification," the term used in SARA. Definition of critical habitat is a scientific and technical process that determines how much habitat is required and where it is located (the "biological" definition or assessment of critical habitat). This document is concerned solely with the biological definition of critical habitat. Identification of critical habitat (the "legal" definition) is a subsequent step that is beyond the scope of this document.

2. APPROACH TO DEFINING CRITICAL HABITAT

Rosenfeld and Hatfield (2006) present a framework for defining critical habitat. They suggest that, for those species where habitat plays a key role in population limitation, the logical steps involved in identifying critical habitat are to:

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.

For species with multiple life stages that use different habitats, these steps need to be repeated for each life stage. A similar approach is suggested by Environment Canada (2005). In this document I adhere to this three-step procedure to define critical habitat for stickleback species pairs, to the extent that present information will allow. Additional data that would allow fuller definitions of critical habitat are identified in a schedule of studies.

3. DISTINCTION BETWEEN HABITAT NEEDS FOR SPECIES PAIRS AND SOLITARY POPULATIONS

Solitary stickleback populations (i.e., those populations for which a single form inhabits a lake or stream) are widely distributed and generally tolerant of significant changes in habitat or water quality. In contrast, stickleback species pairs are highly restricted in their distribution and very sensitive to changes in habitat or other environmental factors. As evolutionarily young species that are not yet intrinsically reproductively isolated from one another (i.e., they can produce viable hybrids), environmental changes can disrupt other pre-existing barriers to reproduction and lead to higher hybridization rates and collapse of co-existing species into a hybrid swarm.

Therefore, critical habitat for stickleback species pairs includes the same features that limit size or viability of solitary populations (e.g., juvenile rearing area, nesting habitat area), but also includes those features of the environment that prevent hybridization. These additional environmental features are part of critical habitat because alteration or loss would cause species collapse, as has recently occurred in Enos Lake (Kraak et al. 2001).

4. GENERAL LIFE HISTORY AND HABITAT USE

I begin by providing some context for discussions of habitat use by stickleback species pairs by summarizing the general life history and habitat needs of freshwater populations of threespine sticklebacks in general, and stickleback species pairs in particular.

The threespine stickleback (*Gasterosteus aculeatus*) is a small (usually 35-55 mm) fish that is common in coastal marine and fresh water throughout the northern hemisphere. The marine form is assumed to be the ancestral form to most freshwater forms, and is usually anadromous, meaning it returns to freshwater to reproduce (Schluter and McPhail 1992, 1993, McKinnon and Rundle 2002). *G. aculeatus* has a laterally compressed body with delicate pectoral and caudal fins. Individuals in most populations are well-armoured with retractable pelvic and dorsal spines, and calcified lateral plates (Wooton 1976, Reimchen 1994). Freshwater populations are variable in extent of armour but usually have less than the marine form (Reimchen 1994). Body color varies from silvery to mottled green and brown. Sexually mature males develop bright red throats during the breeding season, although in a few freshwater populations males turn completely black instead (McPhail 1969, Reimchen 1989).

Marine sticklebacks are phenotypically similar throughout their range, whereas freshwater sticklebacks are ecologically, behaviourally and morphologically variable (McPhail 1994). Three sets of genetically and morphologically divergent populations are known from coastal British Columbia (McPhail 1994): anadromous and stream-resident populations, sympatric limnetic and benthic populations (i.e. spatial distribution is entirely or mostly overlapping), and parapatric lake and stream populations (i.e. spatial distribution is contiguous and only overlapping in a relatively small area of contact),. In each case they may be referred to as “species pairs” since the populations are sympatric or parapatric in their distribution. An anadromous and stream-resident pair was studied in detail and described by Hagen (1967) and similar pairs exist in many coastal, low gradient streams in British Columbia. Anadromous and stream-resident stickleback populations are in contact during the breeding season, yet despite overlap in timing and location of breeding the two forms maintain their genetic and morphological distinctiveness and there is apparently little interbreeding (Hagen 1967, McPhail 1994). Most anadromous and stream-resident pairs were likely derived independently (McPhail 1994), so most pairs are evolutionarily and ecologically unique. Nevertheless, this radiation has been replicated so many times, they have generally not been deemed in need of protection.

Sympatric, reproductively isolated, limnetic and benthic populations have been discovered in seven lakes on islands in a restricted area of the Strait of Georgia (McPhail 1984, 1992, Schluter and McPhail 1992, McPhail 1993, 1994, Gow et al. 2008). In each case, limnetics primarily exploit plankton, and have morphological traits such as a fusiform body, narrow mouth and many, long gill rakers, which are traits considered adaptations to a zooplankton-consuming lifestyle (Schluter and McPhail 1992, 1993). Benthics mainly eat benthic invertebrates in the littoral zone, and have a robust body form, wide gape and few, short gill rakers, traits considered to be advantageous in benthic feeding (Schluter and McPhail 1992, 1993). The pattern of morphological and ecological divergence is similar in each of the lakes (Schluter and McPhail

1992, Gow et al. 2008), such that limnetics all look alike, as do all benthics. Despite similar appearance, phylogenies based on molecular genetic data strongly indicate that the pairs are independently derived (Taylor and McPhail 2000). Thus, benthics from different watersheds should be considered separate species, and the same for limnetics. Benthic-limnetic pairs are found in Paxton Lake and the Vananda Creek watershed (Spectacle [sometimes known as Balkwill], Priest, and Emily Lakes) on Texada Island, and Little Quarry Lake on Nelson Island. Two other pairs have recently been extirpated (Hadley Lake on Lasqueti Island, Hatfield 2001a) or collapsed through hybridization (Enos Lake on Vancouver Island, Kraak et al. 2001, Taylor et al. 2006) , so that 40% of recorded limnetic-benthic species pairs have been extirpated in the wild. Sympatric pairs have been designated endangered by COSEWIC and listed as endangered under SARA, with two exceptions. The Hadley Lake pair is listed as extinct, and the Little Quarry Lake pair has not yet been assessed. (Note: the formal status of the Enos Lake pair is uncertain pending re-assessment by COSEWIC.)

A third type of species pair is found in several other lakes in British Columbia: parapatric lake-stream pairs. Allopatric lake- and stream-dwelling sticklebacks are common, and have consistent morphological differences, with the lake forms having slimmer bodies, and more and longer gill rakers than stream-dwelling forms (McPhail 1994). Parapatric pairs are relatively rare and have been well-described for three lakes in BC: Mayer and Drizzle Lakes on the Queen Charlotte Islands (Moodie 1972, Stinson 1983, Moodie 1984, Reimchen et al. 1985) and Misty Lake on northern Vancouver Island (Lavin and McPhail 1993, McPhail 1994). Lake and stream parapatric pairs occur in other British Columbia watersheds (A. Hendry, McGill University, personal communication, Berner et al. 2008), but the Mayer, Drizzle and Misty pairs have been the best-described, are demonstrably divergent, and are almost certainly independently derived (Lavin and McPhail 1993). The Misty Lake stickleback complex includes a lake-dwelling form, an inlet stream-dwelling form, and an outlet stream-dwelling form. The two stream-dwelling populations are morphologically and ecologically similar. Although they are often referred to as a pair, the Misty Lake sticklebacks are perhaps more properly referred to as a triplet, since the two stream-dwelling populations are separate and do not interact directly. The Misty Lake pair has been designated endangered by COSEWIC, but a listing decision has not yet occurred under SARA.

4.1 Benthic-Limnetic Pairs

Benthic and limnetic sticklebacks have similar life histories, but different habitat requirements (McPhail 1993, 1994). These requirements vary throughout the year, and critical habitat should be identified for each life stage. In general, benthic-limnetic pairs spawn in littoral areas in the spring, rear in littoral and pelagic areas in spring and summer, and overwinter in deep water habitats during the fall and winter. Limnetics are thought to mature on average as one year-olds, and rarely live beyond a single breeding season. Benthics delay sexual maturation relative to limnetics; although some individuals likely mate in their first year, many may delay mating until they are two year-olds. They may live up to about five years, and mate in several breeding seasons. The species' life history timing is presented in Table **1**; detailed descriptions of habitat use are presented below.

Table 1. Life history timing for benthic-limnetic stickleback species pairs.

Species	Life Stage	Jan				Feb				Mar				Apr				May				Jun				Jul				Aug				Sep				Oct				Nov				Dec			
		1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Limnetic	Spawning													x	x	x		x	x	x	x	x																									
	Incubation														x	x		x	x	x	x	x	x																							
	Juvenile rearing															x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x											
	Adult rearing						x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x											
	Overwintering	x	x	x	x	x	x																													x	x	x	x	x	x	x	x	x	x	x	x
Benthic	Spawning										x	x		x	x	x	x	x	x																											
	Incubation										x			x	x	x	x	x	x	x																											
	Juvenile rearing													x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x											
	Adult rearing						x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x											
	Overwintering	x	x	x	x	x	x																													x	x	x	x	x	x	x	x	x	x	x	x
		1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
		Jan				Feb				Mar				Apr				May				Jun				Jul				Aug				Sep				Oct				Nov				Dec			

Spawning habitat – Benthic-limnetic pairs spawn in the shallow littoral area of lakes (McPhail 1994). Males construct nests, which they guard and defend, until fry are about a week old. The nests and contents remain vulnerable to predators of different kinds (Foster 1994). Benthics build their nests under cover of macrophytes or other structure; Limnetics tend to spawn in open habitats (McPhail 1994, Hatfield and Schluter 1996).

The extent of available spawning habitat may conceivably limit populations in some lakes where shallow littoral areas are uncommon. Although spawning habitat may limit limnetic or benthic abundance when spawning populations are very large, the total area of littoral habitat available for spawning appears to be extensive in each species pair lake, at least under present conditions (Hatfield 2001b, Hatfield and Ptolemy 2001).

A more important issue is the potential for changes in the quality of littoral habitat to affect reproductive isolation of the two species. Homogeneous littoral habitats may preclude the ability of limnetics and benthics to exercise preferences for specific microhabitats (Hatfield and Schluter 1996, Boughman 2001). For example, loss of macrophyte beds may lead to limnetics and benthics nesting in close proximity, possibly increasing the likelihood of hybridization between the two species (Hatfield and Schluter 1996). Females may be less able to differentiate between males of different species if nesting habitat preferences cannot be exercised. Species pair lakes naturally have abundant macrophytes, presumably facilitating assortative mating through expression of differences in male nesting habitat selection. The loss of littoral macrophyte cover from introduced crayfish is one of the mechanisms hypothesized as a primary cause of species collapse in Enos Lake (Taylor et al. 2006, Rosenfeld et al. 2008).

Juvenile rearing habitat – Immediately after leaving the protection of paternal care, both limnetic and benthic fry utilize the littoral zone, where there is abundant food and cover from predators. The extent of habitat partitioning by benthic and limnetic fry is not understood well, but limnetic juveniles are common along steep, rocky, unvegetated littoral shoreline compared to benthic juveniles, which shelter around macrophytes (Gow personal communication). Eventually, limnetics move offshore to feed in pelagic areas (Schluter 1995). The timing of movement into the pelagic region by limnetic juveniles is likely dictated by a combination of relative growth rates and predation risk in littoral and pelagic habitats (Schluter 2003), which may vary among lakes and among years. Benthic juveniles rear only in littoral areas.

Availability of suitable rearing habitat for juveniles may limit benthic and limnetic stickleback adult population size, although it is unclear when this is the case. Species pair lakes (with the recent exception of Enos Lake) have abundant macrophytes, but the extent of suitable beds

may affect survival of juvenile benthic and limnetic sticklebacks. Altering the relative abundance of benthic and planktonic prey may also alter the selective environment for sticklebacks (Schluter and McPhail 1993, Schluter 1994, 1995, Vamosi et al. 2000, Schluter 2003). For example, loss of suitable rearing habitat for benthics may increase the relative fitness of hybrids or limnetics at the expense of the benthic species, possibly facilitating hybridization and species collapse. On the other hand, studies of the collapse of the Enos Lake pair indicate an increase in hybrids at the expense of limnetics (Gow et al. 2006, Behm et al. in review). This suggests that the disappearance of species-specific juvenile habitat is likely less important in promoting hybridization than the impact the same habitat modifications may have on the breakdown of pre-zygotic reproductive barriers between species.

Adult rearing habitat – Adult limnetics (with the exception of nesting males) feed on zooplankton in the pelagic zone of the lake, whereas adult benthics feed on benthic invertebrates in the littoral zone (Schluter 1995). Productive littoral and pelagic habitats are required for the persistence of benthic-limnetic pairs. Maintenance of relative productivity between pelagic and littoral habitat is also thought to be important.

Overwintering habitat – By late summer individuals begin moving to deeper water habitats where they overwinter. Little is known about habitat requirements of limnetics and benthics during this stage, except that trapping and seining consistently indicate use of deeper water by early fall.

4.2 Misty Lake Parapatric Pair

Studies of Misty Lake sticklebacks have focussed on evolutionary processes (Lavin and McPhail 1993, McPhail 1994, Hendry et al. 2002, Hendry and Taylor 2004, Moore and Hendry 2005, Moore et al. 2007), and there is relatively little information on the Misty Lake pair from in situ ecological or behavioural studies. However, differences between the lake and stream forms have a genetic basis (Sharpe et al. 2008), and it is likely reasonable to assume their biology is similar to other stream- and lake-dwelling populations (see Wooton 1976, Bell and Foster 1994) and similar to that reviewed above for benthic-limnetic pairs. Both the lake and stream form in Misty Lake breed from April through June (McPhail 1994). The darkly stained water of Misty Lake has made observation of nests difficult, but it is assumed that stream forms breed predominantly in the stream and the lake form predominantly in the lake (Lavin and McPhail 1993, McPhail 1994). There is assortative mating in the wild (Delcourt et al. 2008), but there is also measurable gene flow between lake and stream populations (Hendry et al. 2002, Hendry and Taylor 2004, Moore and Hendry 2005, Moore et al. 2007). Gravid females of both forms were caught in the swampy transition zone between the lake and the stream, and it is likely that both forms breed in this area (McPhail 1994). Life span of Misty Lake sticklebacks have been estimated only from size-frequency plots. Fish from the inlet appear to live up to two years, whereas lake and outlet fish can reach three years. Within the entire system, breeding fish appear to be one to three years old (John Baker, Clark University, personal communication).

Diets are not well-studied, but morphology and some direct study indicates that adults of the lake form feed in the surface waters of the lake on zooplankton and insect larvae (Berner et al. 2008). The stream form is assumed to forage in relatively quiescent portions of the stream for benthos and allochthonous inputs. Nothing is known about diets during the initial life stages of the two forms, but older juveniles likely feed in similar habitats and on similar items as adults.

5. ADDITIONAL HABITAT NEEDS OF STICKLEBACK SPECIES PAIRS

There are two key components of habitat for benthic-limnetic and lake-stream species pairs:

1. habitat features that control the abundance of limnetics and benthics (i.e., population size), and
2. features of the environment that ensure proper mate recognition.

Therefore, habitat needs for species pairs include features whose alteration or loss will lead to reduction in abundance to an unviable population level, or breakdown of reproductive barriers sufficient to cause collapse into a hybrid swarm. These features are reviewed briefly here.

Ecological community.

Sympatric stickleback species pairs have evolved and persisted in the presence of only one other fish species, cutthroat trout (Oncorhynchus clarki; Vamosi 2003). Maintaining a simple ecological community is necessary if the sympatric pairs are to be retained, as underscored by the rapid extinction of the Hadley Lake species pair following introduction of brown bullhead (*Ameiurus nebulosus*; Hatfield 2001a) and the collapse of the Enos pair following invasion by introduced signal crayfish (*Pacifastacus leniusculus*).

Misty Lake sticklebacks co-occur with several other fish species. Coastal cutthroat trout (*Oncorhynchus clarki clarki*), rainbow trout (*O. mykiss*), coho salmon (*O. kisutch*), Dolly Varden (*Salvelinus malma*) and prickly sculpin (*Cottus asper*) occur in the watershed and juvenile and adult sticklebacks are probably prey for these species. The inlet stream form is known to coexist with cutthroat, coho and Dolly Varden (COSEWIC 2006).

Water quality and pelagic habitat.

Basic parameters. When water quality degrades beyond specific thresholds for oxygen, temperature, pH, or pollutants, aquatic species will be at risk. As a group, sticklebacks are tolerant of a fairly large range of water quality conditions. The precise needs of species pairs are unknown, but are not believed to be outside the limits of other stickleback species.

Light transmission. A significant issue for maintaining benthic-limnetic pairs is the relation between water quality and reproductive isolation (Boughman 2001). Differences in breeding colouration between benthics and limnetics are key breeding cues used in mate discrimination (Boughman 2001). Rapid collapse of the Lake Victoria African cichlids into a hybrid swarm was directly attributed to impaired mate colour recognition caused by increased turbidity associated with eutrophication (Seehausen et al. 1997). Changes in concentration of suspended solids, dissolved organic carbon (e.g., tannins), or other aspects of water chemistry that affect light transmission may disrupt mate recognition. For example, the collapse of the species pair in Enos Lake is associated with reduced macrophyte coverage after introduction of crayfish and with altered land use, which may have influenced turbidity or water colour and thereby affected mate recognition (Taylor et al. 2006).

It is not known whether this same constraint exists for the Misty Lake pair, but there are reasons to doubt that it is of the same importance. The water in Misty Lake is darkly stained with tannins, and light transmission properties are substantially different than in lakes with sympatric pairs. For example, Secchi depth in Misty Lake is less than 1 m (Lavin and McPhail 1993). Furthermore, the Misty forms are parapatric, meaning that only a small portion of each population is in contact during reproduction (McPhail 1994).

Nutrients. Solitary stickleback populations exist across a broad range of lake productivities in British Columbia (Lavin and McPhail 1985, 1986, 1987). In contrast, benthic-limnetic pairs are found only in lakes with relatively high productivity, typically with calcareous bedrock present in the watershed (McPhail 1994; Schluter unpublished data). Altered nutrient status may lead to demographic collapse, or hybridization between the two species by altering the relative fitness of limnetics, benthics, or hybrids.

Littoral habitat.

Extent of littoral habitat. Persistence of benthic sticklebacks depends on littoral zone production sufficient to support a large population of benthic individuals. The physical extent of the littoral zone depends on both the shape of the lake basin and the amount of water in the basin. The bathymetric profile of a lake is geomorphically fixed and not readily amenable to human alteration. The amount of water in the basin is determined by climate, but also is subject to human influence through the construction of dams and the extraction of water. Water licences currently allow substantial volumes to be extracted on several lakes with stickleback species pairs – in some cases annual extraction volumes exceed the volume of the lake (National Recovery Team for Stickleback Species Pairs 2007).

Productivity of littoral areas is determined by physical and biological factors, including depth of the euphotic zone, presence of macrophytes, soil types, nutrient levels, area available for colonization by benthos, and interactions among species. Littoral production is confined to shallow areas along the lake margin, where light penetration is sufficient to support significant macrophyte and algal production. In practical terms, the depth of the littoral zone rarely exceeds 10 m in most lakes, with the majority of photosynthetic production occurring in depths less than 3 m.

Extent of macrophyte beds. As noted earlier, macrophyte beds are the primary nesting locations for benthics, key rearing habitats for juveniles of both species, and foraging habitat for adult benthics. Macrophytes are a key feature mediating mate recognition, because differential nest site selection with respect to macrophyte cover maintains some degree of spatial isolation between limnetic and benthic spawners (McPhail 1994, Hatfield and Schluter 1996). Macrophytes also contribute significantly to the production of benthic macroinvertebrates that support the benthic stickleback species. Macrophytes may also stabilize substrate and maintain low levels of turbidity (an important factor for accurate mate recognition). Macrophytes are therefore important in limiting hybridization of benthic-limnetic pairs, and play a significant role in maintaining the balance of benthic and invertebrate production that is critical for maintenance of benthics and limnetics. Given the key role that macrophytes appear to have in mediating processes that maintain reproductive isolation between limnetic and benthic species, macrophyte beds warrant inclusion in a definition of critical habitat within sympatric pair lakes. Support for this is provided in part by the observation that hybridization and collapse of the Enos Lake species pair coincided with the introduction of crayfish and the loss of macrophytes (Taylor et al. 2006).

The natural temporal range in distribution and abundance of macrophyte beds over time is not known. The specific extent of macrophyte loss that can be sustained before hybridization rates reach a level that causes the species to collapse into a hybrid swarm is also not known. I therefore recommend that macrophyte abundance and distribution be maintained within the natural range within each lake with benthic-limnetic pairs.

6. POPULATION TARGETS

The first step in defining critical habitat is assigning a population target for the species of interest (Rosenfeld and Hatfield 2006). I first discuss existing population abundance, then use a variety of techniques to develop target population sizes for long-term conservation.

6.1 Current Abundance

6.1.1 Benthic-Limnetic Pairs

Based on the extent and quality of existing habitat there is no a priori reason to expect that historic abundance was significantly greater than it is at present. Good, empirically-derived population estimates do not exist for most of the stickleback species pairs. McPhail (1989) suggested that population sizes were on the order of 100,000 for each of the species in Enos Lake, prior to their collapse, but this was not a direct estimate based on captures, and more recent data suggest this may be generous, at least for individuals one year and older.

Matthews et al. (2001) estimated population sizes in Enos Lake, based on multiple mark-recaptures and a Bayesian estimation technique (Gazey and Staley 1986), but these estimates were confounded by species identification problems due to substantial hybridization between limnetics and benthics that had occurred by that time (i.e., the inability of the study team to distinguish between limnetics, benthics and hybrids).

Nomura (2005) completed abundance estimates of the Paxton species pair using mark-recapture methods, and the modified Peterson estimator (Table 2). Estimates were made separately in June, July and September of 2005, but were considered most robust for June, due to poor recapture rates in the later samples. Low recapture rates of limnetics contributed to relatively poor confidence in estimates of limnetic abundance. Estimates were made only for males in reproductive condition (i.e., in nuptial colouration). I assume a 1:1 sex ratio when using these estimates to assess total population sizes of mature individuals.

Table 2. June 2005 abundance estimates of Paxton Lake limnetic and benthic mature males (i.e., males in nuptial colour, aged 1+). Estimates are from a mark-recapture study (Nomura 2005) using the modified Peterson estimator and confidence intervals based on the Poisson distribution. (Note: To obtain estimates of total mature individuals, I assumed a 1:1 sex ratio and simply doubled Nomura's estimates for reproductive males. The true level of uncertainty for total mature limnetics and benthics is not known.)

	Benthic		**Limnetic**	
	Reproductive Males	**Total Mature**	**Reproductive Males**	**Total Mature**
N	3,332	6,664	45,853	91,706
lower CI	2,243	4,486	25,806	26,612
upper CI	5,305	10,610	83,981	167,962

Abundance estimates for both Enos and Paxton Lakes are based on standard mark-recapture techniques, which have a number of assumptions, such as closed population, sufficient longevity of marks, equal survival of marked and unmarked individuals, and capture success that is unrelated to presence of a mark or prior capture. Specifically in the case of sticklebacks, these estimates apply to individuals that can be caught with Gee traps and therefore exclude young of the year (fish less than 1 year old). This method of capture likely underestimates

abundance of limnetics, especially limnetic females, which tend to be somewhat trap shy and utilize primarily pelagic habitats. The estimates for Paxton Lake are considered reasonably good for mature benthics, but are less accurate for limnetics. These are the best available abundance estimates from direct study, but the fact remains that the estimates are based on a single study and some caution is warranted.

Therefore, there is only one somewhat imperfect study that can be used to indirectly estimate abundance of limnetics and benthics in each of the species pair lakes. Estimates could be projected to other lakes using a variety of assumptions, but the simplest is to base estimates on lake size (Table 3). Lake area was therefore used to extrapolate abundance of limnetics from Paxton Lake to other lakes, and lake perimeter was used to extrapolate numbers of benthics. In reality, each lake will have many differences (e.g., productivity, available habitat, predation), the accuracy of physical data is unknown, and abundance is based on a single estimate. But data are lacking with which to make appropriate adjustments and since the lakes have many features in common (e.g., size, biogeoclimatic zone, ecological community) the errors are probably acceptable for this purpose. I have used the abundance data from Paxton Lake, since this system is less-disturbed at present than Enos Lake and does not suffer from the identification complications brought on by massive hybridization. Abundance estimates for all lakes are presented in Table 4.

Table 3. Physical features of species pair lakes, based on existing data. The accuracy of these data is not known, but may pre-date construction of low head dams on some lakes. Data are from provincial sources (available online at http://www.env.gov.bc.ca/habwiz/) and are assumed to be accurate; values in italics are assumed, based on measurements from maps or averages of other lakes.

lake	area (ha)	mean depth (m)	max depth (m)	perimeter (m)	volume (m^3)
Hadley	6.7	*5.9*	-	1130	*392,453*
Enos	16.2	5.5	10.7	1609	891,000
Paxton	11.2	6.2	13.1	2277	694,400
Priest	44.3	5.43	17.3	3868	2,405,490
Spectacle	11.5	6.3	14.3	2268	724,500
Emily	7.2	*5.9*	-	1091	*421,740*
Little Quarry	29.8	*5.9*	-	*2600*	*1,772,169*

Table 4. Total abundance estimates for species pair lakes. These projected estimates are based on a single mark-recapture study in Paxton Lake in June 2005. All estimates, including 95% confidence intervals, are calculated by multiplying the Paxton Lake estimates by a factor that corrects for lake surface area in the case of limnetics, and lake perimeter in the case of benthics. Total abundance values are a sum of average abundance of each species estimate. (Note: the true level of uncertainty of abundance estimates for lakes other than Paxton is not known – the average, lower CI and upper CI are all extrapolated from the Paxton estimate.)

			limnetic			benthic			both species
lake	area (ha)	perimeter (m)	N	lower CI	upper CI	N	lower CI	upper CI	total
Hadley	6.7	1130	35,175	20,765	61,194	14,580	2,194	19,469	49,755
Enos	16.2	1609	85,050	50,208	147,962	20,761	3,124	27,721	105,811
Paxton	11.2	2277	58,800	34,712	102,295	29,380	4,421	39,230	88,180
Priest	44.3	3868	232,575	137,298	404,613	49,909	7,510	66,641	282,484
Spectacle	11.5	2268	60,375	35,642	105,035	29,264	4,404	39,075	89,639
Emily	7.2	1091	37,800	22,315	65,761	14,077	2,118	18,797	51,877
Little Quarry	29.8	2600	156,400	92.359	272,178	33,548	5,048	44,795	189,998

Estimates of total abundance provide some context for discussions of population targets, but the value of greatest importance is usually abundance of mature individuals. Nomura (2005) provided separate estimates for mature males, which were distinguished based on nuptial coloration. These estimates indicated an abundance of mature benthic males that was lower than originally anticipated. The estimate itself appears to be robust since it has fairly good confidence limits (Table 2). The same logic used to provide estimates of total abundance was used to provide estimates of reproductive benthics for each of the species pair lakes (Table 5).

Table 5. Estimates of mature benthics for each of the species pair lakes. These projected estimates are based on a single mark-recapture estimate of mature benthic males in Paxton Lake in June 2005. All estimates, including 95% confidence intervals, are calculated by multiplying the Paxton Lake estimates by a factor that corrects for lake perimeter, and multiplying by 2 to account for both sexes.

lake	perimeter (m)	mature benthic	lower CI	upper CI
Hadley	1130	3,307	2,226	5,266
Enos	1609	4,708	3,170	7,498
Paxton	2277	6,663	4,486	10,610
Priest	3868	11,319	7,620	18,024
Spectacle	2268	6,637	4,468	10,568
Emily	1091	3,193	2,149	5,084
Little Quarry	2600	7,608	5,122	12,115

A second method for estimating population size is based on effective population size (N_e) calculated from genetic studies, in conjunction with N_e:N ratios from the literature (summarized in Frankham 1995). Gow et al. (2006) have estimated N_e for limnetics and benthics in Paxton, Priest and Enos Lakes. N_e was estimated as 1160 for Paxton benthics, and 1330 for Priest benthics. If we assume 6600 mature benthics in Paxton (based on mark-recapture estimates) this translates into an N_e:N ratio of 0.176, not far off the average N_e:N of 0.1 from Frankham (1995). Despite the potential limitations of both approaches there is remarkable congruence between the mark-recapture estimate and the one based on N_e estimates.

6.1.2 Misty Lake Parapatric Pair

Based on the extent and quality of existing habitat there is no a priori reason to expect that historic abundance of Misty Lake sticklebacks was significantly greater than it is at present. The Misty Lake population is believed to be considerably larger than either of the stream populations (Hendry and Taylor 2004), but there have been no empirical population estimates of the lake or stream forms. Catch rates have generally been high in both lake and stream environments: a thousand fish in a single day of trapping with 30 traps in the lake, sometimes more than a hundred in a single trap, and several hundred fish in a single section of stream (A. Hendry, McGill University, personal communication). Hendry (personal communication) believes population sizes exceed 5,000 for the inlet, and more than 10,000 in the lake. Moore (personal communication cited in COSEWIC 2006) suggested about 2500 adults occupy the inlet and more than 4000 occupy the outlet, but these estimates are based on occasional captures rather than strict population estimation methods. Mark-recapture studies have been conducted in the inlet and outlet stream, but the study design was focussed on dispersal, and the results are therefore inappropriate to use as a census. Nevertheless, the results indicate population sizes of a few thousand fish in each stream.

A second method for estimating population size, as noted in Section 6.1.1, is based on effective population size (N_e) calculated from genetic studies of the Misty Lake populations and N_e:N ratios from the literature (summarized in Frankham 1995). Eric Taylor (University of British Columbia, personal communication) calculated N_e for the inlet and lake populations based on analysis of five microsatellite loci and two methods (Waples 1989, Bartley et al. 1992). Results are summarized in Table 6 and, although preliminary, suggest effective population sizes in the low hundreds. Using an average N_e:N from Frankham (1995) of 0.1, gives abundance estimates of mature fish in the low thousands. These estimates of N_e are considerably lower than longer term estimates generated for Paxton or Priest Lakes (Gow et al. 2006).[1]

[1] Values in Table 6 are based on analysis of 5 microsatellite loci in 30 fish from Misty Lake in 2004, 128 fish from Misty Lake in 2007, and 90 fish from Misty Lake inlet in 2005. Additional analyses are ongoing, which will allow these estimates of N_e to be updated. The approach taken here is to concentrate on analytic methods that allow the best extrapolation to *current* census numbers from estimates of N_e over short time frames (within a single generation or between a small number of generations). The linkage disequilibrium approach estimates N_e based on a single sample of animals and makes no assumptions regarding trends in N_e and does not compare N_e among different time periods. Estimates of N_e are also provided in Hendry et al. (2002) and Hendry and Taylor (2004) and indicate higher N_e values than shown in Table 6. The previously published values, however, were derived from different data and different methods and were calculated for different purposes (estimating "long term evolutionary" N_e over perhaps thousand of generations).

Table 6. Estimates of effective population size (N_e) for the inlet and lake populations, based on analysis of five loci using the temporal and linkage disequilibrium methods. Population estimates are calculated assuming an N_e:N ratio of 0.1 (Frankham 1995).

Population	N_e	95% C.I.	Method	N	95% C.I.
Inlet	296	132 – ∞	linkage disequilibrium	2,960	1320 – ∞
Lake	280	184 – 556	linkage disequilibrium	2,800	1840 – 5560
Lake	155	83 – 402	temporal	1,550	830 – 4020

The abundance estimates based on N_e are approximately congruent with the estimates for the inlet given in COSEWIC (2006). The estimates for the lake population are thought to be too low (A. Hendry, personal communication). A useful comparison may be drawn from population estimates from Drizzle Lake, another similar lake stickleback system (Reimchen 1990). Drizzle Lake is similar to Misty Lake, in that it has another of the known parapatric lake-stream pairs, is darkly stained and relatively shallow. Based on mark-recapture methods, Reimchen (1990) estimated that Drizzle Lake had about 75,000 adult sticklebacks (30,000 to 120,000). Drizzle Lake is about three times larger than Misty Lake (112 ha vs. 36 ha), but even at a third of this amount, the estimates differ by about an order of magnitude.

Unlike the population estimates for Paxton Lake, those derived from extrapolation from mark-recapture results and those from genetic data are highly discordant for Misty Lake. In contrast to the estimates from Paxton Lake, both data sets used to estimate Misty Lake abundances have considerable weaknesses: the mark-recapture data are from another lake system 100s of km away, and the genetic study used only a small number of genetic markers on a sample of fish not randomly collected from throughout the lake. Additional work is required to obtain a more confident abundance estimate for Misty Lake sticklebacks.

6.2 Current Habitat Availability

6.2.1 Benthic-Limnetic Pairs

Bathymetry is available from the provincial database for Paxton, Priest, and Spectacle Lakes, based on depth transects collected in 1970. Included on the bathymetry maps are the original depth transects used to create the bathymetric profile. According to annotations on the chart, the lake outlines were determined from air photos.

I developed a georeferenced digital elevation model (DEM) for Paxton Lake, which required as inputs a geo-referenced perimeter of the lake and a series of geo-referenced depth measurements. Unfortunately, the available bathymetry and depth measurements (available as a plan view bathymetric map from the provincial database) are not georeferenced. To georeference the depth measurements required overlaying the bathymetric map onto the provincial standard geo-referenced digital data base (Terrain Resource Information Management or TRIM) to create a georeferenced grid. The lake perimeter and transect data were digitized and projected onto the TRIM grid to create a DEM.

When developing the DEM for Paxton Lake I found that the match between lake perimeter from the existing bathymetry map and the TRIM outline of the lake was poor. The consequence is that there is likely some error in the DEM, however, it is not possible to quantify this error.

The DEM can be used to calculate a number of physical values, such as perimeter, littoral area, and volume, for any elevation band, or to model habitat availability at different water levels. I

used the DEM to calculate available habitat for limnetics and benthics in Paxton Lake, and to extrapolate these values to other species pair lakes. All calculations were done using GIS software at 0.1 m intervals. More accurate estimates of current habitat availability may be possible with additional depth surveys and more recent air photos.

Habitats were defined based on the following definitions, which in turn are based on expert opinion and available literature[2]:

1. littoral foraging habitat is all littoral area of 0.5 m to 3 m depth
2. pelagic foraging habitat is total lake area overlying lake depths >3 m
3. habitat for young of year individuals is 0.2 m to 1 m depth, with macrophyte cover
4. nesting habitat for benthics is 1 m to 3 m depth, with macrophyte cover
5. nesting habitat for limnetics is 0.5 m to 1.5 m depth, with no macrophyte cover
6. emergent and submerged macrophytes are assumed to cover 50% of available littoral area

Paxton calculations were based on the DEM of Paxton Lake. Values for other lakes are extrapolated from Paxton Lake, based on ratios of lake perimeter (for littoral area calculations) and on ratios with lake area (for pelagic area calculations), with the assumption that perimeter is most closely related to littoral habitat area and lake area is most closely related to pelagic foraging area. This is the same logic used to extrapolate abundance of limnetics and benthics from Paxton Lake to all other lakes (see Table 4 and Table 5). Habitat areas are presented in Table 7. There are no data available pertaining to habitat quality differences among lakes, so equivalence is assumed.

Table 7. Calculated habitat areas (ha) for different life stages of stickleback species pairs. Values for Paxton Lake were derived from a DEM; values for other lakes are extrapolated from Paxton Lake based on lake perimeter and area. (YOY = young of year)

Lake	Lake area	littoral foraging area	pelagic foraging area	YOY habitat	benthic nesting habitat	limnetic nesting habitat
Paxton	11.2	3.5225	4.6781	.7014	1.3668	0.7675
Priest	44.3	5.9838	18.5036	1.1915	2.3218	1.3038
Spectacle	11.5	3.5086	4.8034	0.6986	1.3614	0.7645
Emily	7.2	1.6878	3.0074	0.3361	0.6549	0.3677
Enos	16.2	2.4891	6.7665	0.4956	0.9658	0.5423
Hadley	6.7	1.7481	2.7985	0.3481	0.6783	0.3809
Little Quarry	29.8	4.0222	12.4471	0.8009	1.5607	0.8764

The match between lake perimeter from the existing bathymetry map of Paxton Lake and the TRIM outline of the lake was poor. Based on personal experience on the lake, the TRIM base appears to be a more accurate depiction of the true lake shape. Therefore developing an updated DEM for Paxton Lake, and possibly for the other species pair lakes, may provide better support for critical habitat definitions for all species pair lakes. As part of the bathymetric survey

[2] Recovery Team for BC Non-game Freshwater Fish (see National Recovery Team for Stickleback Species Pairs 2007and references therein).

it would be useful to also survey for macrophyte coverage, since these values are important in the calculated habitat areas in Table 7. On the other hand, the calculated value of benthic nesting habitat when combined with an abundance estimate of 3,300 males, translates to a density of one nesting benthic male per 4.14 m^2, which seems within the generally observed densities in the lake (personal observation).

6.2.2 Misty Lake Parapatric Pair

Surveys of habitat availability have not been conducted for Misty Lake and the inlet and outlet. The lake is relatively shallow, with a maximum depth of 6.7 m, and mean depth of 1.7 m (Province of BC 2008). The lake is deeply stained, oligotrophic, and dense growths of *Potamogeton* and *Nuphar* occur in the summer (Province of BC 2008, Lavin and McPhail 1993, COSEWIC 2006). The inlet and outlet stream join the lake through extended swampy transition zones of several hundred metres (COSEWIC 2006). Habitat areas based on the Paxton DEM are shown in Table 8. The shallow bathymetry of the lake ensures abundant spawning habitat for the lake form, likely in excess of the amount extrapolated from the Paxton Lake DEM.

Table 8. Calculated habitat areas (ha) for different life stages of sticklebacks in Misty Lake, based on a DEM for Paxton Lake and extrapolated based on lake perimeter and area.

Lake	Lake area	littoral foraging area	pelagic foraging area	YOY habitat	nesting habitat
Misty	35.86	4.33	14.98	8.63	2.62

Upstream and downstream limits of the stream forms are not known, but captures have been made about 2.3 km downstream and about 2.0 km upstream of the lake. The inlet stream has a mean wetted width of 3 m, total length of 5.3 km, mean gradient of 1.5%; the outlet has a mean wetted width of 3 m, length of 2.3 km and mean gradient of 1.0% (Irvine and Johnston 1992 cited in COSEWIC 2006). The two forms co-occur in the transition areas between lake and stream, especially during the breeding season (Lavin and McPhail 1993). Surveys of habitat availability within the streams have not been conducted, but given their low gradients useable habitat is likely high. Maximum habitat areas are ~6000 m^2 for the inlet and ~6600 m^2 for the outlet, based on mean stream width and capture extent. Presumably a lesser amount of habitat is useable as spawning and rearing habitat.

6.3 Abundance Targets

6.3.1 Background

In setting abundance targets for conservation one must consider external threats to the population, and inherent causes of population vulnerability. External threats tend to affect mean vital rates and carrying capacity. For example, mean fecundity and survival may be lower due to pollution, carrying capacity may be less due to habitat destruction, or harvest may affect the abundance of mature individuals. These factors are clearly important and must be addressed to meet conservation targets of threatened and endangered species. However, factors affecting temporal variability in vital rates must also be considered when setting abundance targets for long-term conservation. Both natural and threatened populations face temporal variability in vital rates, but such variability is generally a greater concern at low abundance. Some years (and individuals, habitats, etc.) tend to be better than others and this can have a substantial influence on population trajectories and overall population recovery probabilities.

There are multiple causes of temporal variability in vital rates, but they generally fall into the categories of demographic, environmental and genetic stochasticity. Demographic stochasticity is temporal variation in population growth driven by chance variation within years in the fates of individuals (Morris and Doak 2002). The effects of demographic stochasticity are strongly dependent on population size, and are generally not a significant concern at moderately large abundance. Some have suggested that demographic stochasticity is only a significant concern when populations are smaller than about 20 individuals, although others have suggested that the effect can be ignored only at significantly larger population sizes. In virtually all conceivable scenarios for stickleback species pairs, demographic stochasticity is expected to be a minor concern at most, and is henceforth ignored.

Environmental stochasticity can be defined as among-year variation in vital rates caused by changes in environmental factors. Population viability analyses (PVAs) tend to focus on effects of environmental stochasticity on survival and reproduction rates, and population-level processes, such as density-dependence, because these are the main sources of temporal variability in population vulnerability over the medium term. Special cases of environmental stochasticity include long term trends in environmental factors, and bonanzas and catastrophes — especially good or especially bad years that are outside the normal range of variation.

Genetic stochasticity is also a source of temporal variability in population vulnerability. Typically, genetic factors are a concern over longer time frames and require more individuals in a population to offset negative influences, such as inbreeding and mutation accumulation. An early rule of thumb was the "50:500" rule , which stated that a minimum of 50 individuals are required to offset short-term risks from inbreeding, whereas 500 individuals are required to maintain heterozygosity over the long term. More recent evidence indicates thresholds may be considerably higher (N_e of at least 1000) to ensure genetic viability over the long term (Lynch and Lande 1998, Allendorf and Ryman 2002).

Converting N_e to N can be done directly, or can be based on published N_e to N ratios, which average around 0.1 for a wide range of wildlife species (Frankham 1995). A population target based on N_e = 1000 should therefore be around 10,000 reproductively mature individuals. Gow et al. (2006) have estimated N_e for limnetics and benthics in Paxton, Priest and Enos Lakes. N_e was estimated as 1160 for Paxton benthics, and 1330 for Priest benthics; approximate 95% confidence intervals were 1110 – 1178 and 1272 – 1356, respectively. If we assume 6600 mature benthics in Paxton (based on mark-recapture estimates) this translates into a ratio of 0.176. Thus, an N_e of 1000 translates into 5690 mature individuals, or only marginally less than the estimated current population size for Paxton benthics. If we use the 95% confidence intervals for N_e (Gow et al. 2006) and the 95% confidence intervals for the mark-recapture estimate (Table 2) I calculate it would take a population of about 3808 to 9559 mature benthics to attain an N_e of 1000. The current population estimate of about 6600 sits comfortably inside this range, and further supports the notion that it would take the entire lake to meet this target.

Rules of Thumb for Minimum Viable Populations.— Since I have scarce data on vital rates of stickleback species pairs it is useful to consider some "rules of thumb" that have been developed in the literature. In a review of population variability in relation to population persistence, Thomas (1990) concluded that a population of "1,000 is adequate for species of normal variability, and 10,000 should permit medium- to long-term persistence of most of the most variable birds and mammals." In a more formal review of PVA results, Reed et al. (2003) found that MVPs for vertebrates tend to be on the order of 1,000 to 10,000 breeding pairs in single closed populations. They suggest a population target of 7,000 adults is appropriate for long-term persistence. As noted earlier, recent studies indicate that a threshold of $N_e \geq 1000$ is

necessary to ensure genetic viability over the long term. There are often good reasons to extend recovery targets beyond the MVP; for example, to account for restricted geographic distribution or to accommodate additional safety factors to offset threats.

6.3.2 Population Viability Analyses

6.3.2.1 Benthic-Limnetic Pairs

In this section I explore several simple population viability tools to assess population targets for benthic-limnetic pairs. I chose to concentrate on simple PVA tools because the data are lacking to support more complex models. Even these simple approaches require data on vital rates that are generally lacking. Vital rates have been used that seem reasonable given knowledge of the species, but I acknowledge that there is uncertainty in these rates, and changes in the vital rates would likely affect conclusions regarding appropriate population targets. Information on vital rates is a key data gap.

In addition to vital rates, it is necessary to supply a value for "quasi-extinction" (QET), a threshold above absolute extinction, but below which the processes of demographic stochasticity and depensatory population dynamics become important and at which the population becomes "effectively extinct." I chose a QET of 500 mature individuals, which is likely higher than for most species. A relatively high QET was selected because it is believed that hybridization rates in stickleback species pairs are density- and frequency-dependent, and even modest rates of hybridization are capable of causing collapse of the species pairs into a hybrid swarm. Selection of this QET is necessarily subjective due to the lack of applicable data, but is about two orders of magnitude lower than current population estimates in most lakes (see Table 4). Selection of a QET affects calculated probabilities, but not the general trends observed in PVA analyses.

Geometric Population Model.— The first model I explored is one of the simplest, a discrete-time geometric population model:

$$N_{t+1} = \lambda_t N_t$$

where N is total abundance, t is time in years, and λ is the population growth rate. In the absence of density-dependence or environmental variation, populations will grow if $\lambda > 1$, decline if $\lambda < 1$, or stay the same if $\lambda=1$. Environmental variation can be incorporated by specifying variance in λ. This model was analysed for a time horizon of 100 years using a variety of parameter values: ($\lambda = 0.9$ to 1.1, st. dev. = 0.05 to 0.2, initial population size = 500 to 5,000). Results are summarized in Figure 1 and indicate that probability of quasi-extinction increases with higher environmental stochasticity and lower population growth rates. High abundance provides a buffer against extinction risk over the short term, but any population with $\lambda < 1$ will decline and eventually go extinct. This buffer may be effective only when environmental stochasticity is low, and is unlikely to provide protection from catastrophes such as an exotic species introduction.

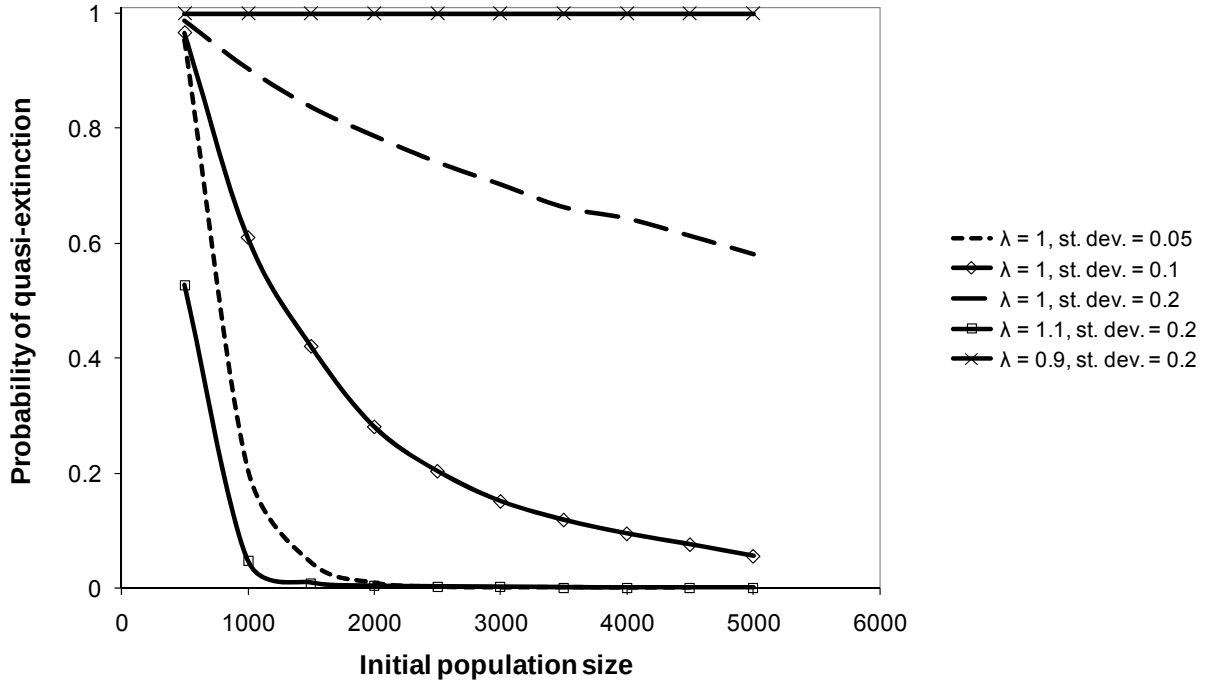

Figure 1. Summary of results from the exponential growth model. Model runs were for 100 generations, with input parameters as indicated in the legend.

This model is useful as an exploratory tool to demonstrate the effect of environmental stochasticity, however, since population variability data are lacking for all benthic-limnetic pairs it is difficult to use this quantitatively. Population variance is 0.2 for Cultus sockeye (Bradford and Wood 2004), but I do not know whether variance is similar in stickleback populations. Nevertheless, the model predicts that population abundance typical of most species pairs (Table 4) amply exceeds the population sizes where extinction probabilities are high. Stated another way, if abundances decline to levels well-below their current values, this model indicates that environmental stochasticity may present a concern over the short to medium term. A strong caveat is required, however, that the model does not consider the probability or potential effects of exotic species introductions, which are the primary threat to these highly endemic species.

Age-Structured Population Model.— In addition to the exponential growth model, I created a simple age-structured population model, based on methods in Morris and Doak (2002). The model uses projection matrices to simulate population trajectories, and can be run with a variety of values as parameter inputs. I focused on Paxton Lake benthics, since this is the population for which I have most information on vital rates (Table 9). To the extent possible I relied on existing estimates of vital rates from the literature, but since data are lacking for most parameters I had to also rely on expert opinion. Among-year environmental stochasticity was incorporated by using lognormally distributed errors for survival and normally distributed errors for fecundity. Standard deviations of errors were calculated assuming among-year coefficient of variation of 10 to 20%. Density-dependence data are lacking for sticklebacks, so this was modeled as "ceiling density dependence," in which abundance is limited to a maximum of carrying capacity, but no density dependence occurs below this level. I assumed that density dependence acted to limit recruits, but did not affect individuals >1 years old. This is the simplest form of density dependence to model. No correlations were assumed among variables; autocorrelations were also assumed to be absent. In exploring this model I used two

QET values: the original QET of 500 and a second QET corresponding to N_e of 1000, or 5690 mature individuals.

Survival was estimated for benthics, based on abundance estimates in Nomura (2005) and some simplifying assumptions. Assuming the sex ratio of benthics is 1:1, there are approximately 15,000 individuals of each sex in Paxton Lake. Of 15,000 males there are approximately 3,300 mature males, and by subtraction 11,700 immature 1 year old males. If we assume that benthics live about 5 years and reproduce starting in their 2nd year, there are 3,300 males distributed among the 2, 3 and 4 year old age classes. Assuming a constant survival after age 1 year, this translates into a survival rate of approximately 0.22 per year. Survival rates are likely similar for males and females.

Table 9. Inputs for an age-structured population model of Paxton Lake benthics. EO = expert opinion.

Variable	Description	Value	Source
years	length of population trajectories to simulate	100	EO
K	carrying capacity of individuals ≥1 years old	30,000	Nomura (2005)
sex ratio	ratio of males to females	0.5	EO
clutches	annual number of clutches laid by females	2	Baker (1994) and EO
clutch size	number of eggs per clutch produced by a female	150	Baker (1994) and EO
age at first reproduction	age at which females produce their first clutch	2	EO
maximum age	age by which all individuals die	5	EO
survival1	survival from egg to 1 year old	0.05	EO
survival2	annual survival rate of individuals ≥1 years old	0.22	Nomura (2005)

The initial projection matrix used was,

0	0	75	75	75
0.05	0	0	0	0
0	0.22	0	0	0
0	0	0.22	0	0
0	0	0	0.22	0

To introduce environmental stochasticity this matrix was modified at each time step with random variation in fecundity and survival. The model was run for 100 time steps (years), and 1000 iterations. Population totals tracked individuals ≥ 2 years old, which correspond to mature adults. All runs were seeded with a starting abundance equivalent to a fairly stable age structure near the carrying capacity.

The age-structured model suggests that benthic sticklebacks may be resilient to population perturbations from environmental stochasticity. With inputs as indicated in Table 9 and a coefficient of variation of 20%, the population trajectories did not come close to the QET boundary of 500 (Figure 2). Trajectories crossed the QET of 5690 only 9 times out of 1000 (Figure 2). One caveat is that we know that species with short lifespans are vulnerable to extended periods of poor recruitment (King and McFarlane 2003), but this model assumed that environmental stochasticity was not autocorrelated. Modeling environmental stochasticity to allow for more protracted “bad” periods may produce different results.

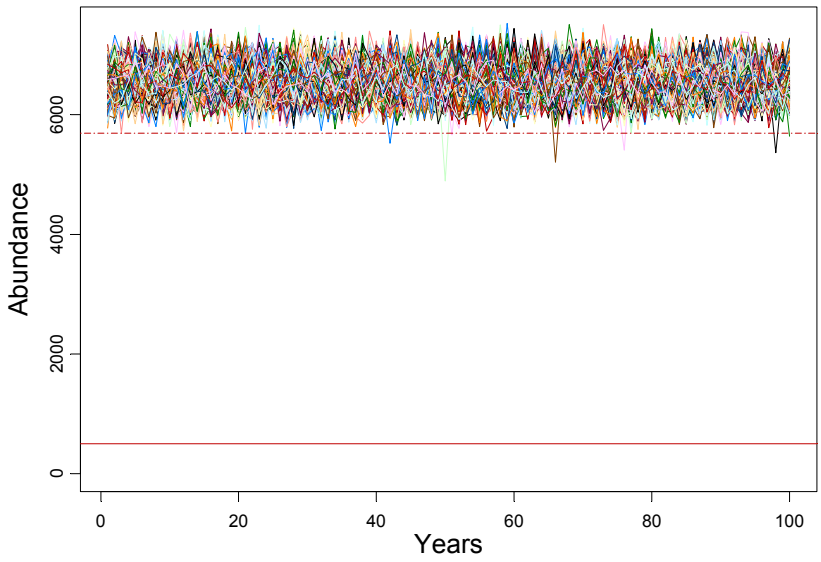

Figure 2. Population trajectories of mature Paxton benthics (age 2+) simulated over 100 years, assuming inputs as noted in Table 9. QETs of 500 and 5690 are indicated by solid and dashed red lines, respectively. Populations hover around the current estimate of 6,600.

There are essentially two ways to model habitat impacts with this model, and they work in slightly different ways. The first is to lower carrying capacity. This would be equivalent to removing habitat that supports growth and survival of benthics — essentially removing sections of the littoral region of a lake. The second way to model a habitat impact is to affect only nesting habitat. This type of impact would conceivably occur with the removal of preferred nesting areas in the lake. This might occur through impacts to *Chara* beds, the preferred nesting area of benthics. It is conceivable that such an impact would lower the number of reproducing individuals while having little or no impact on the overall carrying capacity. In the present model, this is modeled as having a direct impact on fecundity, since fewer nests means lower realized fecundity.

Modeling impacts to habitat in these two ways has quite different effects. Reducing carrying capacity has the effect of simply lowering total abundance (Figure 3). Given a constant QET then, lowering carrying capacity brings the population closer to the threshold, until at some level of carrying capacity it crosses the boundary (Figure 4). To assess the probability of extinction, one can tally the proportion of iterations that cross the QET. A relationship between carrying capacity and probability of quasi-extinction (Figure 4) suggests that carrying capacity of about 2700 benthics (all age classes) would produce a quasi-extinction probability of about 1%.

Modeling habitat impacts as reductions in available nesting habitat has a substantially different effect, which is equivalent to altering the vital rates of the population. Essentially this lowers a population's ability to respond to environmentally induced population reductions, leading to more variable population trajectories (Figure 5) and ultimately to extinction, due to an inability to replace the current population (Figure 6).

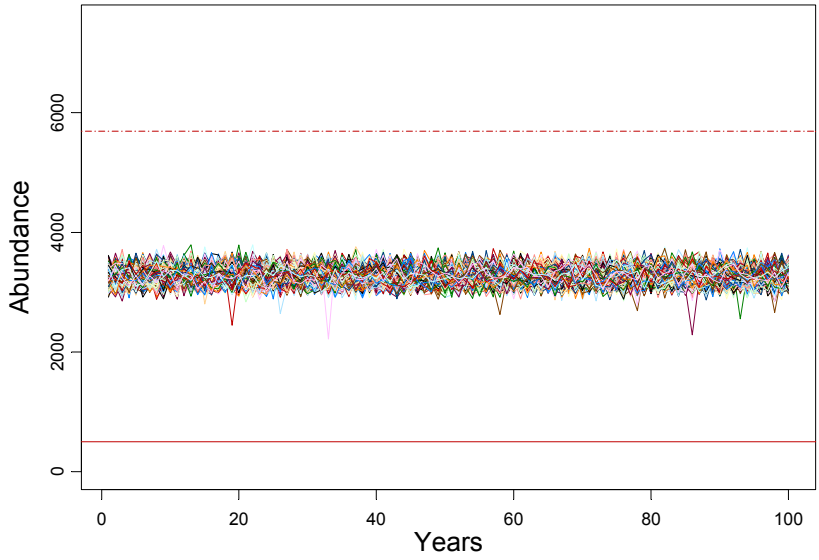

Figure 3. Population trajectories of mature Paxton benthics (age 2+) simulated over 100 years, assuming inputs as noted in Table 9 and a total carrying capacity of 15,000 (half of the current estimate, see Nomura 2005). QETs of 500 and 5690 are indicated by solid and dashed red lines, respectively. Populations hover around 3,300, or half the current estimate.

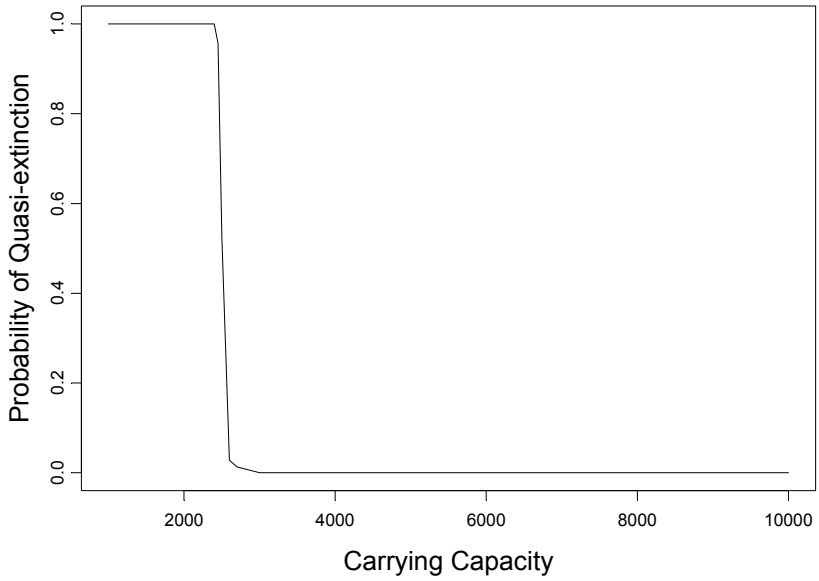

Figure 4. Probability of quasi-extinction vs. carrying capacity based on an age-structured population model. Quasi-extinction is defined as a threshold of 500 mature benthic individuals, carrying capacity is defined as the maximum population size of 1+ benthics. Probability of quasi-extinction is simply the proportion of iterations that cross the QET. Therefore , a reduction in carrying capacity to approximately 2700 mature benthics produces a probability of about 1% over 100 years.

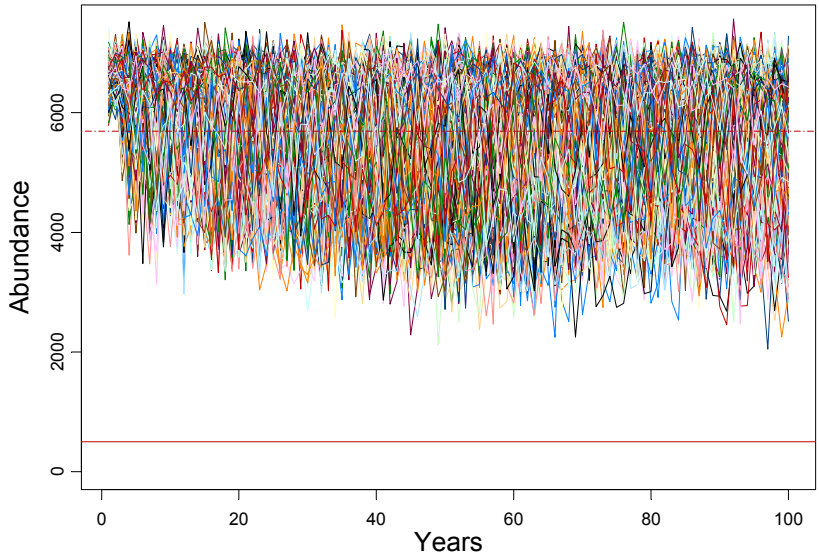

Figure 5. Population trajectories of mature Paxton benthics (age 2+) simulated over 100 years, assuming inputs as noted in Table 9 and half the available nesting habitat. QETs of 500 and 5690 are indicated by solid and dashed red lines, respectively.

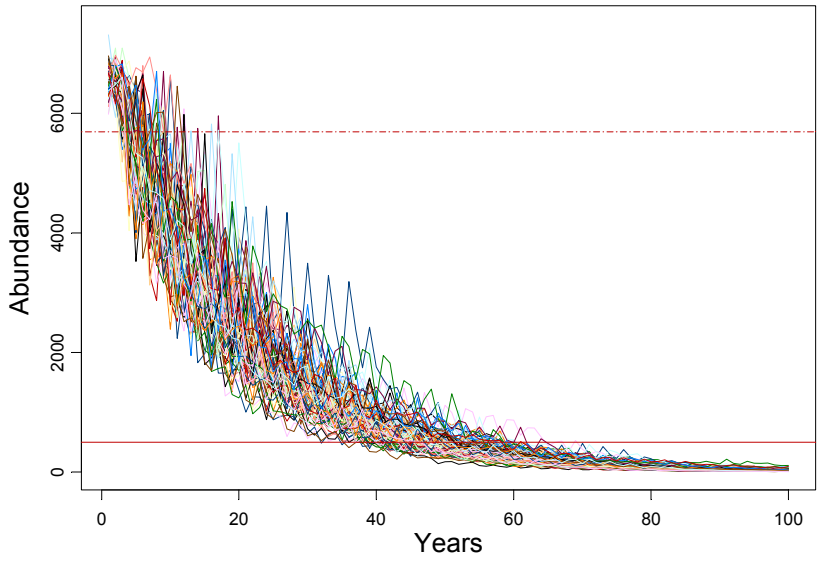

Figure 6. Population trajectories of mature Paxton benthics (age 2+) simulated over 100 years, assuming inputs as noted in Table 9 and 40% of available nesting habitat. QETs of 500 and 5690 are indicated by solid and dashed red lines, respectively.

6.3.2.2 Misty Lake Parapatric Pair

No unique PVA was conducted for the Misty Lake species pair. Results from the PVA for benthic-limnetic pairs can be used as context for discussing population targets for the Misty Lake pair.

Calculations of N_e (see Section 6.1.2) indicate fairly modest abundance within the lake, inlet and outlet. The estimates of N_e and N are below the rules of thumb for minimum viable populations (see Section 6.3.1).

7. ABUNDANCE VS. HABITAT RELATIONSHIPS

Rosenfeld and Hatfield (2006) note that the second step in identifying critical habitat is to define a quantitative relationship between habitat and population size. This can be done empirically by contrasting habitat availability and abundance across several populations or by manipulating habitat and assessing the response in abundance. An abundance-habitat relationship can also be assumed, based on expert judgement or theory.

There is little information available to compare habitat availability and abundance across stickleback populations, and there are no data on specific habitat features that are related to habitat quality. I have therefore assumed a linear relationship between habitat availability and population size. This relationship can be updated as information becomes available, and adjustments to critical habitat definitions can be made if required. A linear relationship is assumed for benthic-limnetic pairs and for the Misty Lake pair.

8. HABITAT REQUIRED TO MEET ABUNDANCE TARGETS

8.1 Benthic-Limnetic Pairs

Given the information presented on existing abundance and habitat availability, population targets, and the assumed linear relationship of habitat vs. abundance, it is possible to define critical habitat in general terms. For the present I have decided to focus the definition on benthic sticklebacks with the assumption that defining critical habitat for benthics will provide protection to all life stages of both species. The focus on benthics and their habitat is based on the following logic:

- benthics have lower natural abundance than limnetics,
- benthics delay reproduction and have lower reproductive potential than limnetics (and therefore slower population response to perturbations),
- benthic habitat is more likely to be affected by development such as shoreline construction or water extraction,
- changes to water quality would affect both species.

The proportion of existing habitat that should be defined as critical was calculated for five different abundance targets (Table 10). Most of the values indicate that a substantial portion of species pair lakes should be defined as critical habitat. The range of values spans from 62% to 100%, but most values indicate a large proportion.

The age structured model was used to calculate the effect of habitat impacts based on a decline in carrying capacity or a decline in available spawning habitat. Decline in overall carrying

capacity did not cause population trajectories to cross the QET of 500 mature individuals until total population size was reduced to a little more than 2700. Using estimates of current population as noted in Table 4, and an assumed habitat-abundance relationship that is linear, one can calculate how much of the current habitat would be required to reach this population level. This value is different for different lakes, because current habitat availability differs.

When habitat impacts are modeled as a decline in reproductive rate the results are somewhat different, in that when fecundity reaches approximately 45% of its current value the population is unable to maintain itself and declines to extinction. This result is somewhat unrealistic in that it suggests populations will reach this point at habitat availability levels that are higher in some lakes than others (i.e., 45% of existing habitat regardless of lake size). One would expect that the absolute amount of required spawning habitat would be similar across lakes, rather than the relative amount. This type of habitat impact is therefore likely better modeled with true density-dependence (i.e., not ceiling type DD). Additional data on the form of density-dependence would be required to build this into the model.

Table 10. Proportion of current benthic habitat that is deemed critical under different population targets, assuming equal habitat quality. Values for N_e1 were calculated directly for Paxton and Priest estimates of N_e. 95% confidence intervals in parentheses are based on confidence intervals for N_e. Values for N_e2 assume a target N_e of 1000 and an Ne:N ratio of 0.1, effectively making this a population target of 10,000 mature individuals. 95% confidence intervals in parentheses are based on confidence intervals for N as indicated in Table 5. Values for MVP targets were calculated from abundance estimates in Table 5.

Lake	N_e1 = 1000	N_e2 = 1000 (N_e:N = 0.1)	MVP = 7,000	MVP = 10,000
Paxton	0.862 (0.849 – 0.901)	1.0 (0.943 – 2.229)	1.0 (0.660 – 1.560)	1.0 (0.943 – 2.229)
Priest	0.752 (0.737 – 0.786)	0.883 (0.555 – 1.312)	0.618 (0.388 – 0.919)	0.883 (0.555 – 1.312)
Spectacle	-	1.0 (0.946 – 2.238)	1.0 (0.662 – 1.567)	1.0 (0.946 – 2.238)
Emily	-	1.0 (1.967 – 4.653)	1.0 (1.377 – 3.257)	1.0 (1.967 – 4.653)
Enos	-	1.0 1.334 – 3.155)	1.0 (0.934 – 2.208)	1.0 1.334 – 3.155)
Hadley	-	1.0 (1.899 – 4.492)	1.0 (1.329 -3.145)	1.0 (1.899 – 4.492)
Little Quarry	-	1.0 (0.825 – 1.952)	0.920 (0.578 – 1.367)	1.0 (0.825 – 1.952)

The age structured population model produced the lowest values, but this is not surprising. First, this model does not consider genetic effects, which typically require higher population levels than are required for purely demographic reasons. Second, the model considers density-dependence only as a single deflection point and population growth up to the carrying capacity is not inhibited. This likely overestimates a population's resilience following perturbation. Third, environmental variance is expressed as a simple statistical form. In practice, environmental variance often has substantial autocorrelation, such that perturbations last for more than one year. For example, a physical habitat disturbance is likely to last longer than a single year. Other disturbances, like species introductions, would have even longer lasting effects. Population targets based on genetic considerations and / or more complete species-specific population dynamics considerations are likely more realistic, and consideration of the realistic nature of potential environmental disturbances are required.

For the present, I suggest focussing on the population target of $N_e \geq 1000$, and using the average published N_e:N of 0.1 (Frankham 1995). (This measure is thus identical to the MVP =

10,000 rule of thumb.) This is a reasonably objective criterion, based on population genetic theory and does not require adjusting based on species-specific vital rates. Meta-analyses of PVA trends for other species are useful as approximate guides, but necessarily ignore species-specific issues and are dominated by long-lived terrestrial species. Many of these PVA results may be quite different than those for sticklebacks, if appropriate data were available. If information becomes available, a more detailed PVA can be developed for each of the stickleback species pairs, and population targets can be adjusted as necessary.

Values in Table 10 for the population target of $N_e \geq 1000$ and an $N_e:N$ of 0.1 in all cases span the full extent of available habitat in each lake. Within the lakes there are habitats of different quality and detailed surveys of all littoral areas would be required to refine recommendations further, including macrophyte distribution by species, habitat quality information, and habitat capability ratings for different species of macrophytes. Throughout my analyses I have assumed that preferred spawning habitats for limnetics are likely to be protected through designations of benthic critical habitat. This assumption remains unvalidated, but requires testing if less than the entire lake is designated as critical.

Other considerations.— The above analysis focuses on physical habitat and its effects on population limitation, and indicates on this basis alone that a substantial portion of existing habitat should be designated as critical. In Section 5 I noted that in addition to certain locations in a lake, there are also aspects of habitat quality such as ecological community and water quality that are essential components of critical habitat for benthic-limnetic pairs. To ignore these other factors places undue risk on the species pairs. The importance of these factors (and others noted in Section 5) is underscored by what we know about the collapse of the Enos Lake pair, where alteration of the ecological community, benthic habitat and water quality likely played roles in breakdown of reproductive isolation (Gow et al. 2006).

For benthic-limnetic pairs, habitat plays a role in species persistence other than simply limiting population size. Benthic and limnetic species coexist with limited gene flow because of strong reproductive isolation associated with accurate mate recognition and reduced hybrid fitness. Hybrids are fertile but selected against because they are less fit than either parental type, owing to intermediate morphology and lower reproductive success (Schluter 1995, Hatfield and Schluter 1996, 1999, Vamosi and Schluter 1999, Vamosi et al. 2000, Gow et al. 2007). 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, which is a key factor in mate recognition (Nagel and Schluter 1998).

Recently, hybridization rates in Enos Lake have increased to the extent that the species pair has collapsed into an undifferentiated hybrid swarm (Kraak et al. 2001, Gow et al. 2006, Taylor et al. 2006). Habitat changes caused by non-native crayfish are suspected as the primary cause of the collapse. Habitat changes include loss of macrophyte beds, potential loss of differential productivity between benthic and limnetic habitats, loss of nest site segregation, and possibly changes in water turbidity, and each has been implicated as a potential factor contributing to breakdown of reproductive isolation (Taylor et al. 2006, Rosenfeld et al. 2008). For instance, loss of macrophytes may destroy physical cues that limnetics and benthics use for segregation of their nests, leading to hybridization. In this scenario, introduction of an alien species is the ultimate driver of hybridization, but impacts are mediated through habitat change, and critical habitat designation for stickleback species pairs needs to include consideration of the role of habitat in maintaining reproductive isolation.

Benthic-limnetic pairs have co-evolved in only a handful of lakes, and thus are extreme endemics. Rosenfeld and Hatfield (2006) discuss some of the theoretical and practical issues surrounding critical habitat definitions for extreme endemics like the species pairs. They suggest that identification of areas of habitat larger than the absolute minimum required for species persistence may be warranted when: (i) excluding occupied habitat from protection increases extinction risk for extreme endemics; (ii) when a critical habitat area is small, and the economic consequences (in terms of lost opportunity costs) of protecting the whole area vs. a subset are small; (iii) when protecting areas at extremely small spatial scales becomes problematic for management purposes; and (iv) edge effects may render very small critical habitats ineffectual. Each of these points is valid for species pair lakes, but the last point is especially germane.

There are solid, logical reasons to identify the whole of each lake plus a riparian buffer as critical habitat. The open, contiguous nature of the littoral and pelagic habitat is the primary rationale. Protecting a portion of the pelagic or littoral area of a small lake affords little to no protection from potential disturbances in the other portion. If hybridization is initiated in one portion of a lake because of habitat degradation that removes reproductive barriers, increased abundance of hybrids may have a population level effect throughout the lake. Similarly, protection of riparian on a portion of the lake will not provide sufficient protection if the other portion is disturbed or destroyed and initiates increased hybridization. Designating only a part of the lake, say an amount sufficient to protect stickleback based on population limitation alone, would leave the entire species pair vulnerable to collapse through hybridzation by allowing habitat alterations outside of the protected portion of habitat. The potential for substantial edge effects require buffers to be incorporated into critical habitat designations if they are to be effective.

An additional reason to conclude that existing information is sufficient to designate the entire lake is the considerable time and expense required to arrive at a more spatially refined definition of critical habitat, and the large degree of uncertainty in such a refined assessment should it be produced. More specifically, identifying the exact location and area of critical habitat would require targeted research to collect much additional demographic, life history, and habitat use information. The considerable time and resources to do this research may not be available, nor is it at all certain that it would greatly increase the confidence with which the exact subset of habitats required for species persistence could be designated. Given the considerable rationale that already exists for protecting existing habitat within the lakes, and the significant potential for hybridization to propagate beyond smaller protected habitat patches, the benefits of an extensive research program to reduce and refine the spatial location of critical habitat patches within the lakes are tenuous.

Riparian buffers.— Riparian zones form a physical transition zone between aquatic and terrestrial ecosystems, and there are often strong physical and biological interactions between the two. For fish, riparian zones offer three important functions: streambank and lakeshore stability (e.g., roots bind soils and prevent erosion or sloughing), instream cover (e.g., large and small woody debris, overhanging vegetation), and food (e.g., insect fall and contribution to invertebrate food sources). There are abundant data demonstrating the importance of riparian areas to physical processes, general ecology, and fish populations in lakes and streams (e.g., France et al. 1996, Schindler et al. 2000, Francis and Schindler 2006, Sass et al. 2006, Francis et al. 2007, Rotha et al. 2007, Richardson et al. 2009), though admittedly there is considerably more information available for streams than for lakes. Riparian areas on lakes contribute to the energy base of aquatic ecosystems through inputs of leaves, dissolved nutrients and insect fall, and such allochthonous inputs can amount to up to half of the carbon base of lake ecosystems

(Pace et al. 2004), particularly in small lakes with large perimeter:area ratios. Typically the contribution is less than half, but has been measureable in many studies (e.g., France and Peters 1995, France et al. 1996, France and Steedman 1996). Riparian zones provide inputs of terrestrial invertebrates that are directly consumed by fish, and large woody debris inputs from the riparian zone provide substrate for invertebrates and structural heterogeneity that strongly influences fish abundance and the ecology of the littoral zone (Schindler et al. 2000, Christensen et al. 2006). Indeed, it is this direct contribution to the functioning and integrity of lake and stream ecosystems that led to the establishment of the Riparian Areas Regulation (under the Fish Protection Act) in British Columbia, and equivalent legislation protecting riparian habitats in other jurisdictions. Despite the relative paucity of studies for lakes, the legislation has protected lakes in a manner equivalent to streams, accepting that the logic of riparian protection extends equally to streams and lakes. This legislation represents a de facto, multi-jurisdictional consensus on the importance of the riparian zone to aquatic species, and reflects the strength of the science it is based on. Of special significance to stickleback species pairs is the role of the riparian zone in preventing sediment inputs from activities (e.g., logging) that disturb surface sediments which may be transported to the lake in surface runoff, since it is these sediment inputs that have the potential to trigger increased hybridization event if they occur during the breeding season.

Riparian areas are required to maintain adequate habitat conditions in species pair lakes and the tributaries flowing into them, and these habitats are included in the biological definitions of critical habitat provided here. Which upland habitats are required, the extent of each, and the width of riparian buffers to prevent harmful sedimentation or erosion would require onsite assessments from a qualified professional. A detailed geotechnical assessment of this sort has been completed for Crown land in the Priest, Spectacle, and Emily watersheds under the B.C. Ministry of Forests and Range Identified Wildlife Habitat Area program (Wood 2007). This Wildlife Habitat Area (WHA) is pending revision based on additional habitat information for Emily Lake. The concerns described above with respect to sediment inputs from logging on riparian crown land, particularly in the context of the irreversibility of a hybridization event, resulted in the inclusion of 90 m riparian buffers on lakes, 50 m buffers on primary tributaries, and 30m buffers on secondary tributaries, totalling an area of 72 ha of Crown land. These recommended buffer widths under the WHA are wider than those normally recommended under the provincial Riparian Areas Regulations (RAR), but it should be noted that recommended buffer widths under the RAR are intended to afford protection to normal populations of fishes, particularly salmonids, that are not at risk of extinction through hybridization. The potential sensitivity of stickleback species pairs to hybridization through sediment inputs and other disturbances, the irreversibility of these impacts, and their status as an endangered species indicate that RAR buffer widths should be viewed as a minimum requirement for species protection. The geotechnical analysis also identified an additional 162 ha of upslope forested crown land with the potential to generate significant quantities of sediment based on the underlying hydrology and geology (Wood 2007). In the absence of detailed assessment by a qualified professional, such as that presented in Wood (2007), the Riparian Areas Regulation and supporting methodologies provide guidance for recommending riparian buffer widths. For lakes and wetlands where the existing or potential vegetation type is trees (the case for all lakes discussed here) the recommended widths are 30 m for shade, 15 m for large woody debris supply, and 15 m for litter fall and insect drop. For sticklebacks, woody debris supply and litter and insect drop are probably more important than shade. Riparian buffer widths of 15 to 30 m on the lake are thus reasonable at this time, or until additional site-specific information indicates otherwise, although these widths are considerably narrower than those established under the WHA. Given the concerns over sediment inputs to these lakes, these buffers should be extended to all ephemeral and perennial streams flowing into the lakes (Wood 2007). In all cases riparian

critical habitat should be managed to maintain its ecological function with respect to lake ecology, in particular minimizing the potential for sediment inputs that could trigger increased hybridization.

Water Quality.— At present I suggest that water quality objectives for stickleback species pairs use the provincial guidelines for protection of aquatic life. At this time, it seems logical to address management of these and other habitat features by managing threats to the species and their habitats, while focusing on delineating physical areas of lakes and riparian areas as critical habitat. Ongoing recovery activities are attempting to manage these and other threats to the stickleback species pairs.

8.2 Misty Lake parapatric pair

For the present, I suggest focussing on the population target of $N_e \geq 1000$. This is a reasonably objective criterion, based on population genetic theory and does not require adjustment based on species-specific vital rates. Current estimates of N_e and N for the inlet and lake are below these thresholds (Table 1) and therefore indicate that 100% of the stream and lake habitat should be defined as critical habitat.

Other considerations.— The above analysis is focussed on physical habitat and its effects on population limitation, and indicates on this basis alone that 100% of existing occupied habitat should be designated as critical for the Misty Lake sticklebacks. In Section 5 I noted that in addition to certain locations in a lake or stream, there are also aspects of habitat quality such as ecological community and water quality that are essential components of critical habitat.

Some portions of upland or ancillary habitat are required to maintain adequate habitat conditions in the lake and streams. For example, riparian buffers may be required to prevent harmful amounts of sediment input and erosion. Which upland habitats are required and the extent of each requires onsite assessments from a qualified professional. The riparian areas regulation (under the BC *Fish Protection Act*) and supporting methodologies provide some guidance for recommending riparian buffer widths. For lakes and wetlands where the existing or potential vegetation type is trees (the case for lake and stream areas supporting the Misty pair) the recommended widths are 30 m for shade, 15 m for large woody debris supply, and 15 m for litter fall and insect drop. Riparian buffer widths of 15 to 30 m on the lake and stream are thus reasonable at this time, or until additional site-specific information indicates otherwise. Given the concerns over sediment inputs to these lakes, these buffers should be extended to all ephemeral and perennial streams flowing into the lake. This methodology can also be used to identify upstream areas of the inlet stream that are presently unoccupied by sticklebacks, but require some protection to ensure that water quality in occupied habitat is maintained.

Habitat change leading to hybridization of lake and inlet/outlet species is a concern in Misty Lake, but less so than it is for limnetic and benthic species, since the lake and stream forms in Misty Lake are more spatially separated in rearing and reproductive habitat.

9. SUMMARY OF CRITICAL HABITAT RECOMMENDATIONS

9.1 Benthic-limnetic pairs

Critical habitat for benthic-limnetic pairs includes the entire lake for each pair, a riparian buffer of 15 to 30 m width surrounding the wetted perimeter of the lakes, and a riparian buffer of 15 to 30 m width surrounding all ephemeral and perennial streams flowing into the species pair lakes.

9.2 Misty Lake parapatric pair

Critical habitat for the Misty Lake pair includes the entire lake, a riparian buffer of 15 to 30 m width surrounding the wetted perimeter of the lake, and a riparian buffer of 15 to 30 m width surrounding all ephemeral and perennial streams flowing into the lake. Critical habitat includes the full length of the inlet stream including areas upstream of currently occupied habitat, and a riparian buffer of 15 to 30 m width surrounding the wetted perimeter of the inlet stream. Critical habitat for the outlet stream extends to the lower limit of currently occupied habitat (presently estimated at 2.3 km downstream of the lake), and a riparian buffer of 15 to 30 m width surrounding the wetted perimeter of the inlet stream.

10. ACTIVITIES THAT ARE LIKELY TO RESULT IN DESTRUCTION OF CRITICAL HABITAT

Activities that are likely to permanently or temporarily destroy critical habitat for benthic-limnetic pairs and the Misty Lake parapatric pair include, but are not limited to the following:

- introduction of non-native species, especially fish and crayfish (where “non-native” is defined as not native to one or more lakes with benthic-limnetic pairs)
- impoundment or water withdrawals that result in water level fluctuations that are greater than those occurring naturally on an annual basis, particularly drawdowns during the period of reproduction
- destruction of macrophyte beds or littoral habitat
- land use (or other) effects on productive littoral area or productive pelagic volume
- release of deleterious substances (e.g., hydrocarbons, sediment-laden water, pollutants and toxins)
- riparian vegetation removal within the defined buffer areas around the lake and inflowing streams, or activities that degrade the normal function of riparian zones, in particular activities that generate sediment inputs to adjacent waterbodies.

11. SCHEDULE OF STUDIES

A series of tasks is proposed here, which if completed would improve our understanding of the sympatric and parapatric species pairs, and thereby increase confidence in the biological definition of critical habitat for these species. The precise nature of each task will be developed in one or more Action Plans, which are required under recovery planning initiatives under SARA.

- improve information base on vital rates of all stickleback species pairs, to improve accuracy of population viability modeling,
- determine the natural range of lake levels (especially for lakes with relatively large extant water licences),

- improve abundance estimates for sympatric and parapatric pairs,
- improve understanding of habitat use by juveniles (especially in lakes with sympatric pairs),
- extend baseline surveys of macrophyte coverage to all species pair lakes and monitor changes in coverage,
- develop an improved digital elevation model for Paxton Lake and possibly for the other species pair lakes. This may provide better support for critical habitat definitions for all species pair lakes.

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