

Recovery Strategy for Paxton Lake, Enos Lake, and Vananda Creek Stickleback Species Pairs (*Gasterosteus* spp.) in Canada

Stickleback Species Pairs



July 2007



About the *Species at Risk Act* Recovery Strategy Series

What is the *Species at Risk Act* (SARA)?

SARA is the Act developed by the federal government as a key contribution to the common national effort to protect and conserve species at risk in Canada. SARA came into force in 2003 and one of its purposes is “to provide for the recovery of wildlife species that are extirpated, endangered or threatened as a result of human activity.”

What is recovery?

In the context of species at risk conservation, **recovery** is the process by which the decline of an endangered, threatened, or extirpated species is arrested or reversed and threats are removed or reduced to improve the likelihood of the species’ persistence in the wild. A species will be considered **recovered** when its long-term persistence in the wild has been secured.

What is a recovery strategy?

A recovery strategy is a planning document that identifies what needs to be done to arrest or reverse the decline of a species. It sets goals and objectives and identifies the main areas of activities to be undertaken. Detailed planning is done at the action plan stage.

Recovery strategy development is a commitment of all provinces and territories and of three federal agencies — Environment Canada, Parks Canada Agency, and Fisheries and Oceans Canada — under the Accord for the Protection of Species at Risk. Sections 37–46 of SARA (http://www.sararegistry.gc.ca/the_act/) outline both the required content and the process for developing recovery strategies published in this series.

Depending on the status of the species and when it was assessed, a recovery strategy has to be developed within one to two years after the species is added to the List of Wildlife Species at Risk. Three to four years is allowed for those species that were automatically listed when SARA came into force.

What’s next?

In most cases, one or more action plans will be developed to define and guide implementation of the recovery strategy. Nevertheless, directions set in the recovery strategy are sufficient to begin involving communities, land users, and conservationists in recovery implementation. Cost-effective measures to prevent the reduction or loss of the species should not be postponed for lack of full scientific certainty.

The series

This series presents the recovery strategies prepared or adopted by the federal government under SARA. New documents will be added regularly as species get listed and as strategies are updated.

To learn more

To learn more about the *Species at Risk Act* and recovery initiatives, please consult the SARA Public Registry (<http://www.sararegistry.gc.ca/>) and the Web site of the Recovery Secretariat (<http://www.speciesatrisk.gc.ca/recovery/>).

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Additional copies:

You can download additional copies from the SARA Public Registry (<http://www.sararegistry.gc.ca/>)

Cover illustration: Stickleback species pair from Paxton Lake, British Columbia. Gravid benthic top, gravid limnetic bottom. Photo by Todd Hatfield.

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DECLARATION

The recovery strategy for stickleback species pairs has been prepared by Fisheries and Oceans Canada and the British Columbia Ministry of Environment. Fisheries and Oceans Canada has reviewed and accepts this document as its recovery strategy for stickleback species pairs as required by the *Species at Risk Act*. The British Columbia Ministry of Environment has reviewed and accepts this document as scientific advice.

This document identifies the recovery strategies that are deemed necessary, based on the best available scientific and biological information, to recover stickleback species pairs in Canada. Success in the recovery of this species depends on the commitment and cooperation of many different constituencies that will be involved in implementing the directions set out in this strategy and will not be achieved by Fisheries and Oceans Canada or any other jurisdiction alone. In the spirit of the National Accord for the Protection of Species at Risk, the Minister of Fisheries and Oceans invites all Canadians to join Fisheries and Oceans Canada in supporting and implementing this strategy for the benefit of stickleback species pairs and Canadian society as a whole. Fisheries and Oceans Canada and the BC Ministry of Environment will support implementation of this strategy to the extent possible, given available resources and its overall responsibility for species at risk conservation. The Minister will report on progress within five years.

This strategy will be complemented by one or more action plans that will provide details on specific recovery measures to be taken to support conservation of the species. The Minister will take steps to ensure that, to the extent possible, Canadians interested in or affected by these measures will be consulted.

RESPONSIBLE JURISDICTIONS

The responsible jurisdiction for stickleback species pairs under the *Species at Risk Act* (SARA) is Fisheries and Oceans Canada. The Province of British Columbia co-lead the development of this recovery strategy.

AUTHORS

DFO and the Province of British Columbia cooperated in the development of this recovery strategy. A recovery team was assembled to provide science-based recommendations to government with respect to the recovery of the stickleback species pairs. Members of the Stickleback Species Pairs Recovery Team are listed below:

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ACKNOWLEDGMENTS

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STRATEGIC ENVIRONMENTAL ASSESSMENT STATEMENT

In accordance with the *Cabinet Directive on the Environmental Assessment of Policy, Plan and Program Proposals*, the purpose of a Strategic Environmental Assessment (SEA) is to incorporate environmental considerations into the development of public policies, plans, and program proposals to support environmentally-sound decision making.

Recovery planning is intended to benefit species at risk and biodiversity in general. However, it is recognized that strategies may also inadvertently lead to environmental effects beyond the intended benefits. The planning process based on national guidelines directly incorporates consideration of all environmental effects, with a particular focus on possible impacts on non-target species or habitats.

This recovery strategy will clearly benefit the environment by promoting the recovery of stickleback species pairs. The potential for the strategy to inadvertently lead to adverse effects on other species was considered. The SEA concluded that this strategy will clearly benefit the environment and will not entail any significant adverse effects. Refer to the following sections of the document in particular: Description of the Species – General Biology, Ecological Role; Recommended Approach/Scale for Recovery; and Potential Management Impacts for Other Species.

RESIDENCE

SARA defines residence as: “*a dwelling -place, such as a den, nest or other similar area or place, that is occupied or habitually occupied by one or more individuals during all or part of their life cycles, including breeding, rearing, staging, wintering, feeding or hibernating*” [SARA S2(1)].

Residence descriptions, or the rationale for why the residence concept does not apply to a given species, are posted on the SARA public registry:

http://www.sararegistry.gc.ca/plans/residence_e.cfm

PREFACE

The responsible jurisdiction for stickleback species under the *Species at Risk Act* (SARA) is Fisheries and Oceans Canada. Section 37 of SARA requires the competent minister to prepare recovery strategies for listed extirpated, endangered or threatened species. Paxton Lake and Vananda Creek stickleback species pairs were listed as endangered under SARA in June 2003, while Enos Lake stickleback species pairs were listed as endangered under SARA in January 2005. Fisheries and Oceans Canada – Pacific Region co-led the development of this recovery strategy with the British Columbia Ministry of Environment. The final strategy meets SARA requirements in terms of content and process (Sections 39-41).

EXECUTIVE SUMMARY

The fish known collectively as “stickleback species pairs” are small, freshwater fish descended from the marine threespine stickleback (*Gasterosteus aculeatus*). Their recent and unique evolutionary history has been of considerable scientific interest and value. Stickleback species pairs were known to exist in four watersheds in the Georgia Basin, British Columbia: two watersheds on Texada Island, and one each on Lasqueti and Vancouver Islands. Within the last decade the species pair on Lasqueti Island has been declared extinct, and the species pair in Enos Lake has collapsed into a single hybrid swarm. The present global range is therefore restricted to four small lakes in two watersheds on northern Texada Island.

The stickleback species pairs each consist of a separate benthic and limnetic form. The species 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. The lakes in which stickleback species pairs developed have abundant and productive littoral and pelagic habitat, and a simple fish community comprised only of stickleback and cutthroat trout. Specific environmental conditions required to maintain abundance and reproductive isolation of limnetic and benthic species include water quality, light transmission, nutrients, littoral habitat, and macrophytes.

The greatest known threats to stickleback species pairs are introductions of exotic species, and impacts from water management and land use. Immediate recovery efforts should focus on controlling and minimizing risks from these threats.

Defining critical habitat of stickleback species pairs is an important action required to meet the recovery objectives, and to help place acceptable bounds on activities that impact the species. Critical habitat will be a collection of environmental 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. Some proposed features of critical habitat are described in this recovery strategy. A series of research tasks to help identify critical habitat are also laid out in the strategy.

The goal of the recovery strategy is to secure the long-term viability of all remaining populations of stickleback species pairs. Recovery objectives include the maintenance of species pairs in Paxton Lake and the Vananda Creek watershed, recovery of the Enos Lake species pair, and re-establishment of a species pair in Hadley Lake. Strategies to achieve the recovery goal and objectives fall into three broad, complementary categories: stewardship, protection, and research. These strategies along with their associated actions, performance measures, and relative priority are outlined in detail in this recovery strategy.

Recovery of stickleback species pairs is deemed to be technically and biologically feasible, although they are likely to always be at some risk due to their naturally restricted distribution. Information gaps to be filled are related to species pairs biology, threats, recovery techniques, and the effectiveness of stewardship.

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SPECIES INFORMATION

The status report and assessment summary for stickleback species pairs is available from the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) Secretariat (www.cosewic.gc.ca).

Common Name: Threespine stickleback, species pairs denoted as “limnetic” and “benthic” species.

Scientific Name: *Gasterosteus* spp. (no formal taxonomic designation for the species pairs, although there is strong evidence that indicates the forms are true biological species independently derived from marine *Gasterosteus aculeatus*)

COSEWIC Assessment Summary:

Enos Lake species pair. November 2002

Hadley Lake species pair. May 2000

Paxton Lake species pair. May 2000

Vananda Creek (Balkwill, Priest and Emily Lakes) species pair. May 2000

COSEWIC Status:

Enos Lake species pair. Endangered

Hadley Lake species pair. Extinct

Paxton Lake species pair. Endangered

Vananda Creek species pair. Endangered

SARA Status:

Enos Lake species pair: Endangered, January 2005

Hadley Lake species pair: Extinct

Paxton Lake species pair: Endangered, June 2003

Vananda Creek species pair: Endangered, June 2003

COSEWIC Reason for Designation:

Enos Lake species pair. These fish are restricted to a single, small lake on Vancouver Island are experiencing severe decline in numbers due to deteriorating habitat quality and the introduction of exotics. Since the COSEWIC designation, the species pair has collapsed into a hybrid swarm. A captive breeding program is ongoing with pure limnetics and benthics.

Hadley Lake species pair. This Canadian endemic fish was known only from Hadley Lake, Lasqueti Island, British Columbia. It was lost as a result of nest predation by the introduced brown bullhead.

Paxton Lake species pair. This unique Canadian endemic is impacted by habitat loss and/or degradation from human disturbance. It is in danger of extinction by the introduction of exotic species.

Vananda Creek species pair. This unique Canadian endemic is impacted by habitat loss and/or degradation from human disturbance. It is in danger of extinction by the introduction of exotic species.

Canadian Occurrence: Stickleback species pairs are restricted to specific coastal lakes in the Georgia Basin, British Columbia. Present occurrence is four lakes (in two watersheds) on northern Texada Island. Historically, species pairs also existed in Hadley Lake, Lasqueti Island, and in Enos Lake, Vancouver Island. The species pair in Hadley Lake went extinct following introduction of brown bullhead, and the species pair in Enos Lake has been reduced to a hybrid swarm following introduction of signal crayfish.

COSEWIC Status history:

Enos Lake species pair. Original designation (including both Benthic and Limnetic species) was Threatened in April 1988. Split into two species when re-examined. Designated Endangered in November 2002. Last assessment based on an update status report.

Hadley Lake species pair. Designated Extinct in April 1999. Status confirmed in May 2000. Last assessment based on an existing status report.

Paxton Lake species pair. Designated Threatened in April 1998. Status re-examined and confirmed in April 1999. Status re-examined and uplisted to Endangered in May 2000. Last assessment based on an existing status report.

Vananda Creek species pair. Designated Threatened in April 1999. Status re-examined and uplisted to Endangered in May 2000. Last assessment based on an existing status report.

BACKGROUND

1. DESCRIPTION OF THE SPECIES

1.1 General Biology

Threespine stickleback (*Gasterosteus aculeatus*) are small (usually 35-55 mm) fish that are abundant in coastal marine and freshwater throughout the northern hemisphere. In general, *G. aculeatus* has a laterally compressed body and individuals in most populations are well-armoured with retractable pelvic and dorsal spines, and calcified lateral plates. Freshwater populations are variable in extent of armour but usually have less than the marine form. 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 stickleback are phenotypically similar throughout their range, whereas freshwater stickleback are ecologically, behaviourally and morphologically variable. Several lakes on islands in the Strait of Georgia are especially noteworthy because they each contain two distinct, reproductively-isolated species (McPhail 1984, 1992, 1993, 1994; Schluter and McPhail 1992; Figure 1). We refer to the two stickleback species in each lake as a "species pair."

In each case, one of the species (referred to as "limnetic") primarily exploits plankton, and has morphological traits such as a fusiform body, narrow mouth and many, long gill rakers. These traits are considered adaptations to a zooplankton-consuming lifestyle (Magnuson and Heitz 1971; Kliewer 1970; Sanderson et al. 1991; Schluter and McPhail 1992, 1993). The other species (referred to as "benthic") mainly eats benthic invertebrates in the littoral zone, and has 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), such that limnetics all look alike, as do all benthics. Despite similar appearance, phylogenies based on molecular genetics strongly indicate that the pairs are independently derived (Taylor and McPhail 2000). Thus, benthics from different lakes should be considered separate species, and the same for limnetics. There are thus at least eight separate species within the species pair complex—two in each of the four watersheds.

Limnetics mature early, usually after one year, and rarely live beyond two years. There is considerable sexual dimorphism: reproducing limnetic males tend to be bigger on average than gravid females. Large male size enables greater nest protection and territory defence (Rowland 1989). Typical fecundity is low, about 30-40 eggs per clutch for a gravid limnetic female, but they produce several clutches per season, usually in close succession if food availability is high.

Males are the sole providers of parental care. In the spring they acquire territories in the littoral region where they build nests and mate (sometimes with many females). Limnetics prefer non-vegetated, open nesting locations (McPhail 1994; Hatfield and Schluter 1996). They often nest in less than 1 m of water on submerged logs, in shallow bays with gravel or rocky substrates, and on firm muddy substrate. Preferred spawning habitat is not uniformly distributed in the littoral zone, so nesting males are often clumped in their distribution. Despite reproducing at the same time of year limnetics and benthics rarely interbreed (McPhail 1992).

Benthics differ from limnetics in a number of ways: they generally mature later, live longer and reproduce less often than limnetics. There is little or no sexual dimorphism. Fecundity is typically higher than for limnetics, about 150-250 eggs for a gravid benthic. Females usually produce only one or two clutches per season, regardless of food availability. Benthics prefer densely vegetated nesting locations, usually among beds of *Chara* (Hatfield and Schluter 1996), and their nests are highly concealed. They tend to nest in water of greater depth than limnetics, though usually less than 2 m depth. As with limnetics, preferred spawning habitat for benthics is not uniformly distributed, so nesting benthics are clumped in their

distribution. Benthics are similar to limnetics in most aspects of parental care and early development.

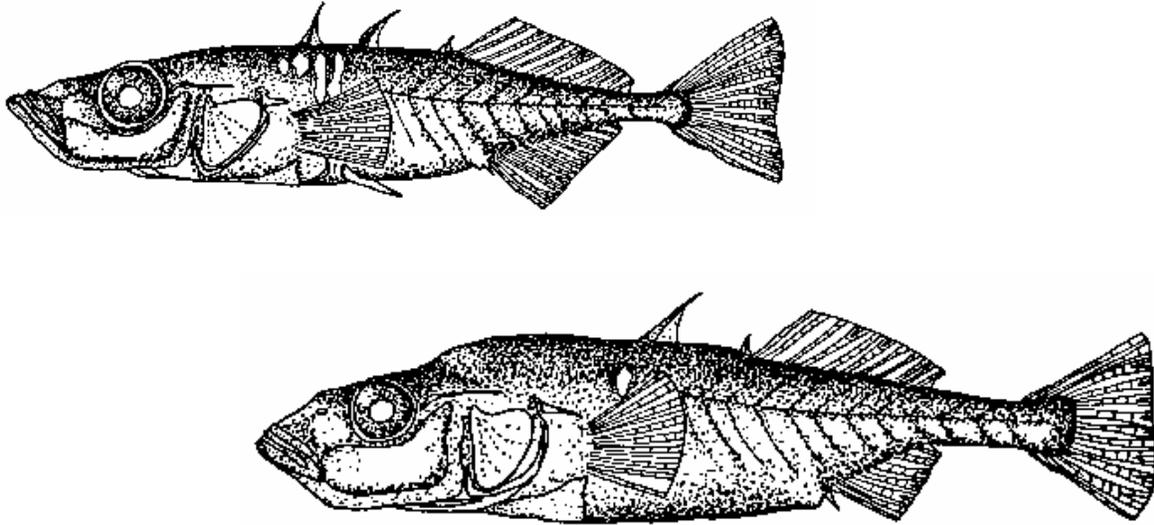


Figure 1. Paxton Lake stickleback species pair; limnetic species (top) and benthic species (bottom). Drawing by Laura Nagel.

As adults, limnetic and benthic stickleback eat quite different foods. Limnetics feed primarily in the surface waters away from the lake margins. There they hunt in loose schools for copepods, *Daphnia* and insect larvae. Males will often forage for benthos when nesting in the littoral zone. As young juveniles, limnetics feed at the lake edges among reeds and submerged plants where they can seek cover from predators.

Benthics on the other hand forage along the shallow margins of the lake for larger prey such as snails, clams, dragonfly nymphs, amphipods, and chironomids. These invertebrates are found among a variety of substrates including plants, rocks or mud. Benthics likely eat similar food types throughout their life, but gradually shift to larger prey as they grow.

Very little is known about diets during the initial life stages of the two species.

1.2 Distribution

Stickleback species pairs were known to exist in four watersheds in the Georgia Basin, British Columbia: two watersheds on Texada Island, and one each on Lasqueti Island and Vancouver Island (Figure 2). Evidence indicates that the species pairs evolved independently in each watershed, meaning that this is a multi-species complex rather than two species spread over multiple watersheds (Taylor and McPhail 1999). There are thus at least eight separate species within the species pair complex—two in each of the four watersheds. Benthics from different lakes should be considered separate species, and the same for limnetics.

Within the last decade the species pair in Hadley Lake on Lasqueti Island has been declared extinct (Hatfield 2001a), and the species pair in Enos Lake on Vancouver Island has collapsed into a single hybrid swarm (Kraak et al. 2001; D. Schluter and E. Taylor unpublished data). The present global range is therefore restricted to two watersheds on northern Texada Island – the Paxton Lake species pair in the Paxton watershed, and the Vananda Creek species pair in Balkwill, Priest and Emily Lakes.

The loss of the Hadley and Enos pairs represent a 50% reduction in the pool of distinct species pairs, and a 33% reduction in the total number of lakes with species pairs. It is possible that undiscovered species pairs currently exist elsewhere in BC, but this is unlikely given the thoroughness of past surveys (McPhail 1993). It is also possible that other pairs existed in the region but went extinct before being discovered.

Prior to the collapse of the Enos Lake stickleback species pair, a population of Enos Lake limnetics was established by adding wild fish in 1988 and 1999 (under permit from the Fisheries Branch of the British Columbia Ministry of Environment, Lands and Parks) to a pond in Murdo-Frazer Park in North Vancouver. A viable population was confirmed in spring 2002 (D. Schluter, unpublished data).

A captive breeding program is underway at UBC in an attempt to recover “pure” limnetics and benthics from the population in Murdo-Frazer Park and the hybrid swarm in Enos Lake. The ultimate success of this program is uncertain.



Figure 2. Map of southwestern British Columbia with historic distribution of stickleback species pairs indicated by red stars (upper: Textada Island, middle: Lasqueti Island, lower: Vancouver Island). These three locations are the only known sites to have had species pairs. Within the last decade the species pair on Lasqueti Island has been declared extinct, and the species pair in Enos Lake has collapsed into a single hybrid swarm.

1.3 Abundance

Prior to their collapse, McPhail (1989) suggested that population sizes were on the order of 100,000 for each of the species in Enos Lake. Since then Matthews et al. (2000) estimated population sizes at 22,000 limnetics and 37,000 benthics. These estimates are likely confounded by species identification problems due to substantial hybridization between limnetics and benthics that had occurred by the time of the survey. More recently, Nomura

(2005) completed abundance estimates of the Paxton species pair using mark-recapture methods, and the modified Peterson estimator. Low capture success of limnetics contributed to relatively poor confidence in estimates of limnetic abundance. The abundance estimate for mature benthics was 3,332 (2,243 – 5,305 95% confidence limit) indicating that some age classes may be considerably less abundant than previously imagined.

Since most of the species pairs' lakes are similar in size, McPhail's (1989) abundance estimate for Enos Lake may be sufficiently accurate for other lakes.

There has been no systematic monitoring of abundance in any of the lakes, so population trends are unknown (Hatfield 2001a, b; Hatfield and Ptolemy 2001). However, stickleback species pairs from Paxton and Priest Lakes have been intensively studied by zoologists at UBC for the last two decades (e.g., Schluter and McPhail 1992; McPhail 1994; Taylor and McPhail 1999). Throughout this time both species have remained abundant and easy to trap in large numbers in Gee traps (Hatfield 2001b; Hatfield and Ptolemy 2001).

1.4 Ecological Role

Stickleback species pairs occupy an intermediate trophic level (Reimchen 1992). Limnetics utilize pelagic areas of the lake for feeding and are able to influence the density of plankton in this zone. Benthics feed primarily in the littoral zone and likely influence the density of littoral invertebrates upon which they feed. Juvenile stickleback are prey for several species of carnivorous benthic invertebrates, and older stickleback are preyed upon by coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) and by piscivorous birds (e.g., herons (*Ardea herodias*), kingfishers (*Megaceryle alcyon*) and loons (*Gavia immer*)).

1.5 Importance to People

The significance of the stickleback species pairs is primarily aesthetic and scientific. Stickleback species pairs are widely regarded as a scientific treasure; they are as valuable to science as cichlid fish species in the Great Lakes of Africa, and Darwin's finches in the Galapagos Islands. In large part this is because they are among the youngest species on earth. The evolution of a new species is thought to usually take on the order of millions of years, but scientists believe the species pairs have evolved since the end of the last glaciation, a mere 13,000 years ago (McPhail 1994; Schluter and McPhail 1992). The speed with which these distinct fish species evolved has intrigued and excited scientists around the world. They are a remarkable research subject that will help us understand the biological and physical processes that give rise to the tremendous diversity of organisms we see around us. Newspapers, magazines and scientific journals have published the story of the discovery of these species, and have followed the results of ongoing scientific studies.

2. DESCRIPTION OF NEEDS OF THE SPECIES

A healthy lake ecosystem in which limnetic and benthic stickleback are expected to thrive has abundant littoral and pelagic habitat, with secondary productivity of these two major habitat types sufficient to support populations in the 10s of thousands for each species, and a simple fish community comprised of only stickleback and cutthroat trout. Specific environmental features required to maintain viable population levels and sustain reproductive isolation of limnetic and benthic species include: general water quality parameters (oxygen, temperature, pH, and pollutants), specific water quality parameters (light transmission and nutrients), littoral habitat (extent and productivity), and macrophytes. Lake levels and extent of macrophytes should be maintained within the natural range for species pair lakes.

2.1. Physical Habitat Requirements

Knowledge of habitat requirements comes mainly from observations in Paxton and Enos lakes, and is assumed to be representative of other species pairs. Habitat requirements vary throughout the year for each life stage. In general, stickleback species 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. The species' life history timing is presented in Table 1; detailed descriptions of habitat use are presented below.

Table 1. Life history timing for 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	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																		
	Overwintering	x	x	x	x	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																															
	Incubation													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																			
	Adult rearing													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	x	x	x	x					

Spawning habitat – Stickleback species 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 structures; 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 2001a; 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.

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. Macrophyte beds constitute both a source of food (benthic invertebrates associated with the lake bottom and macrophyte surfaces) and refuge from predation. The extent of habitat partitioning by benthic and limnetic fry within macrophyte beds is unknown, but it appears that both species use this general habitat type. As individuals grow, habitat partitioning likely increases, and 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 differentially affect survival of juvenile benthic and limnetic stickleback. Altering the relative abundance of benthic and planktonic prey may alter the selective environment for stickleback (Schluter and McPhail 1993; Schluter 1994, 1995, 2003; Vamosi et al. 2000). 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.

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 stickleback species pairs.

Abundance of benthic and limnetic stickleback is likely determined by many factors, but total area and secondary productivity of littoral and pelagic zones is assumed to have a strong effect. Habitat alterations that result in changes to body size (e.g., through lower growth rates or reduced size at maturity) may result in poorer mate discrimination and increased hybridization between limnetics and benthics, since body size is a key factor determining mate selection (Nagel and Schluter 1998).

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 and through the winter.

Fish community – The stickleback species pairs appear to have endured in the presence of only one other fish species, coastal cutthroat trout (Vamosi 2003). Maintaining a simple ecological community is necessary if the species 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 2001b).

Habitat productivity – High productivity of the two major habitats (in comparison with most other coastal lakes) is believed necessary for persistence of the species pairs. Furthermore, secondary production should be relatively similar in the two habitats (though the absolute and relative prey productivities necessary to maintain species pairs are unknown). Stickleback abundance is likely strongly correlated with available secondary production, and lower production will likely increase risk of extinction. Extinction risk is also believed to increase if the relative productivity of each habitat type is altered beyond its normal range. If productivity in one habitat declines substantially one or both species may be affected by increased hybridization (Figure 3).

Specific environmental features required to maintain safe population levels and promote reproductive isolation of limnetic and benthic species are identified below.

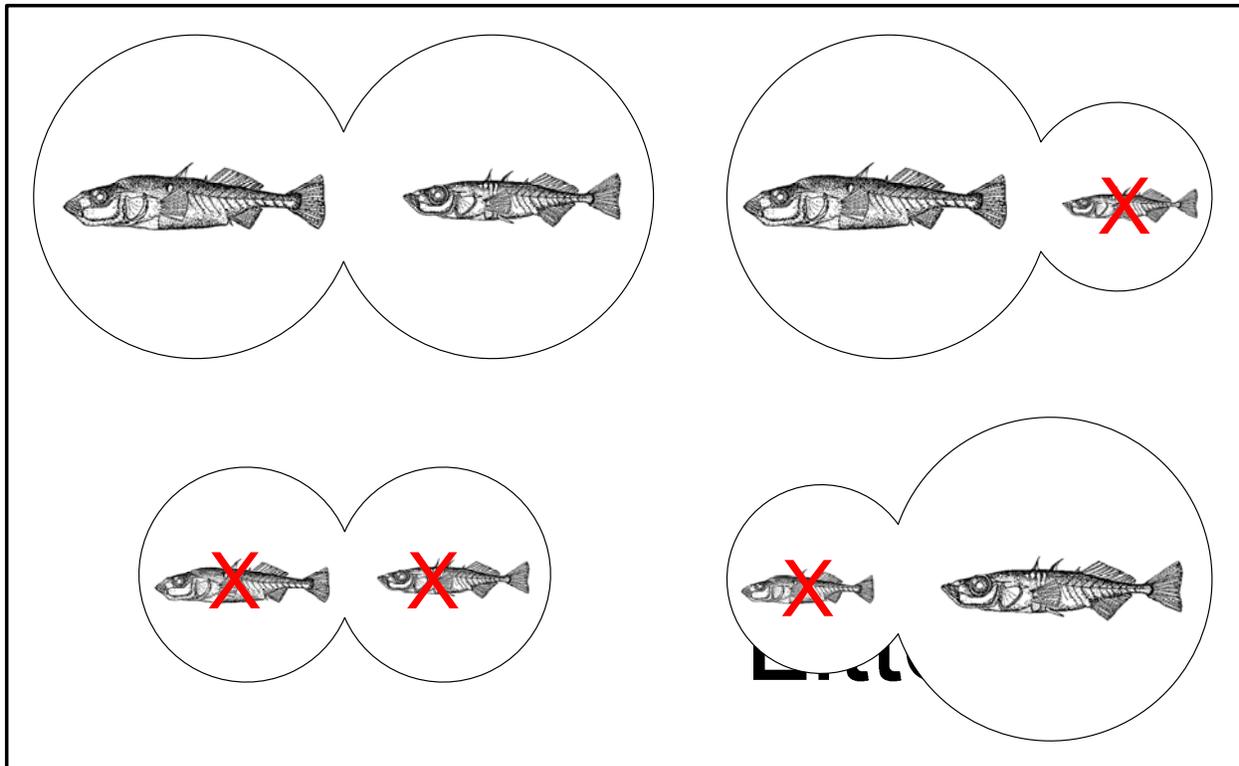


Figure 3. Types of benthic and pelagic productivities and the likely consequences for stickleback species pairs. Available secondary production (depicted by area of each circle) must be high and roughly equivalent in the two major habitats to avoid extinction (scenario A). As production declines in one or more habitats, extinction (shown as a red X) becomes more likely for one or both species (scenarios B to D).

2.2. Pelagic and Littoral Habitats

Water quality – Stickleback species pairs will be at risk when water quality degrades beyond certain levels for oxygen, temperature, pH, or pollutants. As a group, sticklebacks are tolerant of a fairly large range of water quality conditions. The current provincial water quality standards for the protection of aquatic life are appropriate guidelines for basic parameters of water quality in lakes with stickleback species pairs (see <http://srmwww.gov.bc.ca/risc/pubs/aquatic/interp/index.htm>). However, some aspects of water quality in species pair lakes need to be maintained in a much narrower range than that required for short-term individual survival, as described below.

Light transmission – A significant issue for stickleback species pairs is how changes in water quality may affect barriers to reproductive isolation (Boughman 2001). In particular, there is concern that increases in turbidity that alter transmission of different wavelengths of light may interfere with behavioural mechanisms that influence mate recognition and choice (cf. Seehausen et al. 1997). Differences in breeding colouration between benthics and limnetics are key breeding cues used in mate discrimination (Boughman 2001). 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.

Factors affecting light transmission therefore need to be maintained within the natural range of conditions present in species pair lakes. Changes in water quality that alter light transmission properties outside of this range may lead to impaired mate discrimination and

result in a higher frequency of hybridization, and possibly species collapse (cf. Seehausen et al. 1997).

Nutrients – Production of phytoplankton and benthic algae form the base of the aquatic food chain, and are driven by nutrient availability in the water column, which is itself determined by geology of the watershed. Solitary stickleback populations exist across a broad range of lake productivities in British Columbia (Lavin and McPhail 1985, 1986, 1987). In contrast, stickleback species pairs are found only in lakes with relatively high productivity, typically with calcareous bedrock present in the watershed (McPhail 1994; Schluter unpublished data). The evolution of stickleback species pairs is believed to have been possible only under specific levels of benthic and pelagic invertebrate production (see Figure 3), which facilitated exclusive adaptations to either a pelagic (zooplankton) or littoral (benthic invertebrate) food resource. Changes to nutrient status that alter the relative productivity of zooplankton and benthos could therefore alter the adaptive environment for stickleback species pairs (Schluter 1995; Vamosi et al. 2000). Altered nutrient status may lead to demographic collapse, or hybridization between the two species by altering the fitness of limnetics, benthics, or hybrids.

Increases in nutrients may alter the relative productivities of the benthic and pelagic zones, either by favouring production of unpalatable algae that cannot be consumed by zooplankton, or by phytoplankton blooms reducing macrophyte abundance through shading (Wetzel 2001). Land use practices that lead to lake eutrophication should be avoided, and nutrient levels (nitrogen, phosphorous, total alkalinity) need to be maintained within the natural range for lakes with stickleback species pairs.

Extent of littoral habitat – Persistence of benthic stickleback 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, which will influence the quantity of habitat available and therefore total population size of stickleback.

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. The compensation depth (the depth at which light level allows energy gain from photosynthesis to equal energy loss to respiration, the euphotic zone) is usually defined as the depth at which irradiance is 1% of surface irradiance (Wetzel 2001). In practical terms, the depth of the littoral zone is the maximum depth of rooted aquatic vegetation, which rarely exceeds 10m in most lakes, with the majority of photosynthetic production occurring in depths less than 3m.

Maintenance of the littoral zone is very important to the persistence of stickleback species pairs, and water level changes that are outside the natural range for the species pairs' lakes should be avoided. The relative extent of littoral habitat may affect reproductive isolation during nesting, growth and survival of juveniles of both species, adult abundance and individual size, as well as hybrid fitness. Variation in the extent of littoral habitat outside of the natural range will significantly increase the probability of species hybridization and collapse. Genetic evidence indicates that historic hybridization has been considerably higher in the Paxton Lake species than for the other species pairs (E. Taylor, unpublished data). This lake has had the greatest drawdowns from water abstraction, and there is an hypothesized link between the two.

Extent of macrophyte beds – As noted above, 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 are therefore important in limiting hybridization and play a significant role in maintaining the balance of benthic and invertebrate production that is essential for maintenance of the two species.

3. THREATS

A variety of specific threats can be described based on experience in other watersheds and prioritized based on professional judgement. The threats are summarized here and described in greater detail in Hatfield (2003). Immediate recovery efforts should focus on the issues identified below. By prioritizing threats there is no intent to imply that other threats are not significant or worthy of attention. Quantitative risk assessment is not currently possible when analyzing threats to stickleback species pairs due to absence of information on the effects of different threats on population vital rates (e.g. hybridization rates, growth, survival, reproductive success). A summary of population status and threats is presented in Table 2.

Table 2. Summary of status and threats to stickleback species pairs in their native lakes.

	Hadley Lake	Enos Lake	Paxton Lake	Vananda Cr. watershed
COSEWIC status	Extinct	Endangered	Endangered	Endangered
Current population status	Extinct	Hybrid swarm	Apparently Stable	Apparently Stable
Cutthroat trout present	assumed absent	No	rare	present
Exotic species	Brown bullhead	Signal crayfish	none	none
Water Management	<ul style="list-style-type: none"> lake outlet is regulated, unknown water use at present (assumed minor) 	<ul style="list-style-type: none"> lake outlet is regulated, unknown water use at present 	<ul style="list-style-type: none"> lake outlet is regulated, no water use at present, licensed amounts are large relative to lake volume and inflows 	<ul style="list-style-type: none"> some lake outlets are regulated, modest water use at present, licensed amounts are large relative to lake volume and inflows
Land Use - Forest harvest	assumed to be minor	<ul style="list-style-type: none"> minor at present, adjacent lands are private 	<ul style="list-style-type: none"> recent, adjacent lands are private 	<ul style="list-style-type: none"> some recent, adjacent lands are mixed crown and private
Other land use	<ul style="list-style-type: none"> some rural residential, road adjacent to lake outlet 	currently being developed for residential use	<ul style="list-style-type: none"> limestone quarry adjacent, historic mining in area 	<ul style="list-style-type: none"> some rural residential, roads and pipeline adjacent, historic mining in area

3.1. Exotic Species

The species pairs appear to depend critically on the maintenance of several ecological factors, including a simple fish community. Species pairs occur in lakes that naturally have only stickleback and cutthroat trout (Vamosi 2003).

The Hadley Lake species pair quickly became extinct following the introduction of brown bullhead (*Ameiurus nebulosus*), which likely preyed upon or interfered with nesting stickleback, ultimately leading to complete recruitment failure (Hatfield 2001a). Bullhead were introduced to Hadley Lake in the early 1990s and stickleback were absent by 1995 (Hatfield 2001a). This highlights the vulnerability of the stickleback and the speed with which a species pair can be affected by an introduced species. The Enos Lake species pair has collapsed due to hybridization (Kraak et al. 2001; D. Schluter and E. Taylor unpublished data), and the recent appearance of the signal crayfish (*Pacifastacus leniusculus*) is implicated in the collapse. The mechanism by which the crayfish are affecting stickleback may be direct (e.g., predation or displacement from nesting habitat) or indirect (e.g., competition for food resources, increased turbidity, altered macrophyte distribution), but the ultimate effects (e.g., severe population declines) of crayfish introductions on stickleback populations have been observed elsewhere (Foster et al. 2003).

The threat of species introductions applies to a number of other species that are in nearby lakes and spreading throughout the region. These species include largemouth and smallmouth bass (*Micropterus salmoides* and *M. dolomieu*), pumpkinseed sunfish (*Lepomis gibbosus*), and yellow perch (*Perca flavescens*), which are spread by anglers and other members of the public. Potential threats also include the spread of amphibians like the bullfrog (*Rana catesbeiana*) and invasive aquatic vegetation such as Eurasian milfoil (*Myriophyllum spicatum*) and purple loosestrife (*Lythrum salicaria*). Although the stickleback species pairs have co-evolved with coastal cutthroat trout (McPhail 1994), we do not know the extent to which the pairs would be affected by introduction of other native salmonids, such as rainbow trout (*Oncorhynchus mykiss*), or indigenous non-salmonids such as sculpins (*Cottus* sp.). This suite of potential invaders could affect stickleback species pairs through a number of mechanisms including, predation of adults, juveniles, or nests; competition for pelagic or littoral food resources; introduction of disease; or alterations to water quality, which may affect mating decisions or food resources.

3.2. Water Management

Concerns with development activities relate to water quality and water quantity, both of which can alter the ecology of a lake to the detriment of a species pair. Water licences dictate the parameters for diversion and storage and therefore have direct bearing on lake levels. Existing licences are large relative to volume of some of the lakes and size of the catchments. For example, existing water licences on Paxton Lake allow annual diversions of more than twice the volume of the lake, yet inflows are low due to small catchment area and limited precipitation. Severe drawdowns have occurred in the past as part of mining operations (Larson 1976).

Depending on the timing and duration, lake level drawdown may cause loss of effective littoral zone available for foraging and nesting. Large drawdowns can shrink lake volume and depth to such an extent that pelagic habitat essentially disappears and littoral habitat is all that remains. Water level increases associated with damming of lake outlets may also alter the extent of littoral habitat, depending on the morphology of the basin. Large fluctuations have impacts on littoral productivity and pelagic volume and likely have a direct effect on stickleback, severely limiting both spawning and feeding habitats.

3.3. Land Use

There have been numerous land-based development activities in watersheds inhabited by species pairs: forestry, mining, road building, pipeline construction, and housing developments (Larson 1976; McPhail 1994). The main concerns from such activities include cumulative impacts on water quality leading to eutrophication, sedimentation, and habitat destruction or alteration. The greatest of these risks appears to be introduction of suspended sediments (i.e., increased turbidity), but at present, the risk is difficult to gauge. The Enos Lake watershed is currently being developed for residential use, and increased turbidity has been observed as a consequence of construction and land-clearing.

3.4. Other

Additional impacts may occur from other activities, including fishing, recreation, disease, climate change, and pollution. These threats are of concern to the Recovery Team, but are believed to present a lower risk to the species pairs than other threats noted above. It may be possible to effectively manage many of these threats through the development and implementation of good stewardship practices.

4. HABITAT TRENDS

Trends in habitat quantity and quality vary among the species pairs' watersheds. Habitat trends can be assessed only qualitatively, since there has been no systematic monitoring in any of the lakes.

Texada Island – Existing water licences permit substantial water extraction from Paxton and Emily Lakes and moderate volumes from Priest Lake. Historical trends in water use cannot be determined directly because water use was not gauged on all these watersheds. Larson (1976) noted that water extractions from Paxton Lake caused severe drawdowns in the past. Nevertheless, industrial use of water has declined during the last 30 years due to a shift in mining activities from underground extraction of ores to open pit quarrying of limestone. The decline in water use has likely had a positive effect on stability and productivity of littoral and pelagic habitats. Land-based activities have the potential to negatively affect within-lake habitats. Mining and forest harvest have been most extensive in the Paxton Lake watershed. For the most part the influences of land use are difficult to quantify.

Lasqueti Island – Existing water licences for Hadley Lake permit substantial water storage and extraction relative to lake volume and inflow. Land-based development in the watershed includes roads, housing, and perhaps some minor forest harvest. These activities have the potential to negatively affect within-lake habitats, but are assumed to be of relatively minor consequence at present. It is possible that introduced brown bullhead have modified the littoral habitat, but the extent and magnitude of any change is unknown.

Vancouver Island – Recently issued water licences for Enos Lake permit substantial water storage and extraction and a new dam has been constructed at the lake outlet. Present and historic water use is unknown, as is its effect on stability and productivity of littoral and pelagic habitats. Changes in littoral habitat and nutrient status of the lake have likely occurred following raising of the lake level (Stockner et al. 2000). On-land activities are presently minimal, but will likely increase with the expansion of the Fairwinds development (a large residential / golf course development on the privately-owned land surrounding Enos Lake). The development's negative or positive influences on within-lake habitats are difficult to predict until the plans are assessed

in detail. Littoral macrophyte abundance seems to have declined considerably; it is possible that crayfish, which were introduced, have modified the littoral habitat.

5. HABITAT PROTECTION

At present none of the lands surrounding species pairs' lakes are formally protected, although the Vananda Creek species pair is listed as an Identified Wildlife species under the *Forest Practices and Range Act* (Wood et al. 2003) and prescriptions for a Wildlife Habitat Area are under development. The intention of the Wildlife Habitat Area and associated prescriptions will be to protect the species pair from potential adverse effects of forest harvest. Lands surrounding the Texada Island lakes should be considered highest priority for stewardship and habitat conservation programs.

6. CRITICAL HABITAT

The Recovery Team has developed biologically-based recommendations for defining critical habitat for stickleback species pairs. These recommendations have been prepared as a separate document (Hatfield 2006), which is available to the public upon request to the Recovery Team. The proposed critical habitat document will be submitted for external scientific peer review through the Pacific Science Advisory Review Committee. After the peer review process, a final version will form the biological recommendations for designating critical habitat. To conform with current policy on species at risk and recovery strategy content, the following discussion on critical habitat presents general habitat features that should be considered when defining and designating critical habitat, but does not make specific geospatial recommendations.

Critical habitat is defined in SARA as "habitat that is necessary for the survival or recovery of a listed wildlife species and that is identified as the species' critical habitat in the recovery strategy or in an action plan for the species." Stickleback species pairs utilize both the pelagic and littoral zones of the lakes they inhabit, for both reproduction and feeding (McPhail 1993, 1994). Defining critical habitat is an important action required to meet recovery objectives, and to help place acceptable bounds on activities that impact the species.

6.1. Distinction Between Species Pairs and Solitary Populations

Solitary stickleback populations (i.e., those populations for which a single form inhabits a lake) occur in a wide range of habitat conditions and are fairly resilient to habitat change (Wootton 1976; Bell and Foster 1994). Stickleback species pairs, on the other hand, are highly restricted in their distribution and are believed to have considerably more stringent habitat requirements, and to be much more sensitive to habitat change (e.g., Bentzen and McPhail 1984; Schluter and McPhail 1992). All lake-dwelling stickleback populations require spawning habitat (typically the benthic nearshore littoral zone), juvenile rearing habitat (typically the littoral zone), and adult rearing habitat (typically the littoral and pelagic zones) — habitat requirements that include most of the lake (Wootton 1976; Bell and Foster 1994). Critical habitat for species pairs should include these same aspects of habitat (i.e., spawning and rearing habitat), as well as the specific aspects of habitat that permit species to co-exist without collapsing into a hybrid swarm. In other words, loss of spawning and rearing habitat is of concern, but so too are small changes in turbidity (which may affect light transmission and therefore mate identification) or water chemistry (which may affect benthic or littoral productivity) because they may cause hybridization and species collapse. Specific ecological factors such as these do not usually form part of critical habitat definitions, but in the case of stickleback species pairs these components should be considered. The exact nature of these factors is still unknown, so additional research will be required to help define critical habitat for stickleback species pairs.

Since delineating critical habitat will take considerable effort and time, efforts should focus first on those components of habitat that act as barriers to hybridization and that are the most likely to be affected by human activities.

6.2. Specific Critical Habitat Features for Stickleback Species Pairs

There are two key components of potential critical habitat for stickleback species pairs:

1. Habitat features that control the abundance of limnetics and benthics, and
2. Features of the environment that ensure proper mate recognition.

Critical habitat then should be a collection of environmental 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.

The general needs of species pairs are described in detail in Section 2. Individual features that could be considered as part of critical habitat are presented below.

Extent of littoral habitat – A very substantial portion of the littoral zone could be identified as important to persistence of stickleback species pairs (Hatfield 2006). In general, water level changes that are outside the natural range for lakes with stickleback species pairs should be avoided. The relative extent of littoral habitat may affect reproductive isolation during nesting, growth and survival of juveniles of both species, adult abundance and individual size, as well as hybrid fitness. Variation in the extent of littoral habitat outside of the natural range will increase the probability of species hybridization and collapse. Genetic evidence indicates that historic hybridization has been considerably higher in the Paxton Lake species than for the other species pairs (E. Taylor, unpublished data). This lake has had the greatest drawdowns from water abstraction.

Extent of macrophyte beds – Macrophyte beds are habitats with high potential productivity given their key role as rearing and spawning habitat and also in mediating processes that maintain reproductive isolation between limnetic and benthic species. The natural temporal range in distribution and abundance of macrophyte beds over time is not currently 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. We therefore recommend that macrophyte abundance and distribution be maintained within the natural range present in lakes with stickleback species pairs.

Pelagic habitat – The pelagic zone is the prime rearing area for limnetics, and this habitat must be sufficient in area and quality to support a robust population of limnetics. The qualities of pelagic habitat that relate to this component of habitat with high potential productivity are captured under nutrient status, water quality, and littoral area (which is related to pelagic volume).

Overwintering habitat – Little is known about overwintering habitat, except that the species pairs appear to utilize deeper portions of the lakes. Additional work would be required to include a description of overwintering habitat as part of a critical habitat definition.

Fish community – The stickleback species pairs have evolved and endured in the presence of only one other fish species, coastal cutthroat trout (Vamosi 2003). This simple ecological community could be considered a component of critical habitat.

Basic water quality parameters – Water is essential for aquatic species, and aquatic species will be at risk when water quality degrades beyond specific thresholds for oxygen, temperature, pH, or pollutants. The current provincial water quality standards for the protection of aquatic life are appropriate guidelines for basic parameters of water quality in lakes with stickleback species pairs (see <http://srmwww.gov.bc.ca/risc/pubs/aquatic/interp/index.htm>). However, some aspects of water quality in species pair lakes must be maintained in a much narrower range than that required for short-term individual survival (see light transmission and nutrient status).

Light transmission – Aspects of water chemistry that affect light transmission could be a component of a critical habitat definition for stickleback species pairs, because changes may disrupt mate recognition and therefore reproductive isolation (Boughman 2001). At present, the relationships between various water quality factors and mating preferences are not sufficiently precise to allow their inclusion in a detailed definition of critical habitat. However, due to their importance we suggest in the interim that factors affecting light transmission be maintained within the natural range of conditions present in species pair lakes.

Nutrients and productivity – The evolution and maintenance of stickleback species pairs is believed to have been possible only under certain levels of benthic and pelagic invertebrate production, which facilitated exclusive adaptations to either a pelagic (zooplankton) or littoral (benthic invertebrate) food resource. Changes to nutrient status that alter the relative productivity of zooplankton and benthos could therefore alter the adaptive environment for stickleback species pairs (Schluter 1995; Vamosi et al. 2000), leading to demographic collapse, or excessive hybridization. The precise relation between nutrient status and maintenance of stickleback species pairs is not known at present, so it is suggested here that a critical habitat definition could include nutrient levels that are within the natural range for these lakes.

6.3. Schedule of Studies Needed to Identify Critical Habitat

The following information is needed to identify the range of conditions typical of species pair lakes, and the aspects of habitat that need to be maintained to permit long-term persistence of species pairs.

1. Identify and fill information gaps (life-history and habitat use) that prevent objective definition of critical habitat. (2006-2008)
2. Determine acceptable minimum population levels for limnetics and benthics that will ensure species persistence. (2006-2008)
3. Develop water quality guidelines for species pair lakes. (2006-2007)
4. Map the present extent of littoral habitat and extent of macrophytes. (2006-2008)
5. Determine crayfish effects on stickleback recruitment and critical habitat. (2006-2008)
6. Define acceptable levels of water fluctuations/drawdowns that will permit species pair persistence, based on extent of littoral habitat at different water levels, historic data, and a comparison between conditions in species pair lakes and single-species lakes. (2006-2008)
7. Develop acceptable ranges of invertebrate production in the benthos and pelagic that will permit species pair persistence, by comparison between species pair lakes and single-species lakes. (2006-2008)

RECOVERY

7. RECOVERY GOAL

The goal of this recovery strategy is to secure the long-term viability of all extant populations of stickleback species pairs. It is likely that these species will always remain at some risk due to their extremely limited distributions.

8. RECOVERY OBJECTIVES

Short-term (over the next five years):

1. Maintain self-sustaining populations of stickleback species pairs in Paxton Lake and the Vananda Creek watershed.
2. Establish captive populations of the Enos Lake species pair.

Long-term (over the next 20 years):

1. Maintain self-sustaining populations of stickleback species pairs in Paxton Lake and the Vananda Creek watershed.
2. Establish or recover a viable population of the Enos Lake species pair, preferably in Enos Lake.
3. Re-establish a stickleback species pair in Hadley Lake from an extant population by restoring Hadley Lake habitat and introducing a species pair from an extant population on Texada Island.

9. STRATEGIES TO ADDRESS THREATS

Strategies identified by the Recovery Team to achieve recovery goals and objectives fall into three broad, complementary categories: stewardship, protection¹, and research. These strategies are stated as follows.

1. Foster awareness of stickleback species pairs (including their unique importance in evolutionary studies, which is recognized internationally), their conservation status and threats to their persistence through direct education and involvement of stakeholders in recovery implementation.
2. Maintain, and where possible enhance, the ecological integrity of species pair lakes, in particular the habitat features that permit persistence as species pairs.
3. Increase scientific understanding of stickleback species pairs, the threats to their persistence, and the mechanisms involved in specific threats.

The general approach recommended for undertaking these strategies includes:

- establishing and supporting stewardship initiatives,
- undertaking specific research activities to clarify threats,
- delineation and protection of key habitats,
- participation in the development and implementation of an exotic species management plan,
- minimizing impacts from land and water use, and
- designing and implementing sound monitoring programs.

A description of the recommended strategies and approaches is presented in Table 3.

¹ Protection can be achieved through a variety of mechanisms including: voluntary stewardship agreements, conservation covenants, sale by willing vendors on private lands, land use designations, and protected areas

Table 3. Prioritized strategies and recommended approaches for the recovery of stickleback species pairs.

Priority ²	Strategy	Approaches	Performance Measure ³
Necessary	Establish and support Recovery Implementation Groups (RIGs) or alternative working groups for Texada Island and Enos Lake.	<ol style="list-style-type: none"> 1. Invite stakeholders and interested parties to participate in one or more RIGs. (Due to the geographic separation of species pair lakes it will likely be necessary to establish more than one stewardship group.) 2. Encourage local governments (e.g., regional districts) to have membership or representation on RIGs to facilitate Action Plan communication and implementation. 3. Establish the RIG leadership (chair, facilitator, etc.), develop terms of reference, and obtain necessary funding to support RIG activities. 4. Develop and implement an Action Plan, which is to be guided by the Recovery Strategy. 	<p>Has a RIG or working group been established for each stickleback species pair?</p> <p>Are the RIGs adequately supported with funding and technical expertise?</p> <p>Has an Action Plan been developed?</p> <p>Are the RIGs achieving the goals outlined in the Recovery Strategy?</p>
Necessary	Establish and support a "Research Action Group" to undertake specific research activities and provide detailed technical advice.	Invite relevant researchers to participate in a Research Action Group, set terms of reference, and obtain necessary funding.	<p>Has a Research Action Group been established?</p> <p>Is it supported with adequate funding and technical expertise?</p> <p>Is it meeting the research needs identified in the Recovery Strategy?</p>

² Priority has been assigned based on professional judgement into one of three groups, from highest to lowest: necessary, primary, secondary.

³ Performance measures plot the progress toward meeting the stated objectives. The performance measures are presented here as questions, the answers to which can be plotted in time to monitor progress.

Priority²	Strategy	Approaches	Performance Measure³
Necessary	Develop and implement an ongoing long-term monitoring program.	<p>RIGs and Research Action Group to develop a monitoring program to assess population response to management activities or threats. Monitoring may include:</p> <ul style="list-style-type: none"> • trends in abundance of each species, • trends in habitat quantity and quality, • trends in hybridization rates within species pairs' lakes, • exotic species distribution and range expansion, • water quality, • land use, and • water use. <p>RIGs will need to secure long term funding to ensure implementation of an effective monitoring program. Monitoring priorities will need to be set within the constraints of available budget.</p>	<p>Have monitoring programs been implemented? How long has a monitoring program been in place? Is it effective? Is funding secure for the long term?</p>
Necessary	Support development and implementation of an exotic species management plan with direct links to stewardship groups.	<p>RIGs to work with government agencies to:</p> <ol style="list-style-type: none"> 1. develop and implement a comprehensive exotic species management plan. 2. develop an emergency action plan to implement in case an exotic species is introduced into a species pair lake. 	<p>Has an effective exotic species management plan been developed and implemented? Has an emergency action plan been developed and approved? Are there resources available to carry it out?</p>

Priority ²	Strategy	Approaches	Performance Measure ³
Necessary	Determine the feasibility of restoring habitat in Enos and Hadley Lakes and introducing species pairs.	<p>Conduct a feasibility study to assess the social and technical issues regarding re-establishing species pairs in Hadley and Enos Lakes. Feasibility may be determined by assessing the following issues:</p> <ol style="list-style-type: none"> 1. Determine whether introduced crayfish are responsible for hybridization of stickleback species pairs in Enos Lake. 2. Investigate the available methods for extirpating exotic species in Enos and Hadley Lakes. 3. Investigate the ecological requirements for species pairs re-introductions. 4. Assess social and economic benefits and costs of different scenarios for re-establishing species pairs. 5. Introduction of sticklebacks to Enos Lake would preferably come from the captive breeding program for the Enos species pair (see additional strategies and approaches below). Introduction of sticklebacks to Hadley Lake would preferably come from one of the extant pairs on Texada Island. 	<p>Has a defensible decision been reached to re-establish a species pair in Enos Lake and/or Hadley Lake? Has the role of crayfish in hybridization been unambiguously determined? Is extirpation of exotics feasible and desirable? Have factors permitting reintroduction of species pairs been unambiguously identified?</p>
Primary	Conduct studies to identify critical habitat for the stickleback species pairs.	Undertake necessary research to define critical habitat and to delineate it in the wild. See Section 6.3 for a list of necessary research activities.	Has critical habitat been defined for stickleback species pairs?
Primary	Establish water quality objectives for all species pair lakes.	<ol style="list-style-type: none"> 1. Current provincial water quality standards for the protection of aquatic life are appropriate guidelines for basic parameters of water quality in lakes with stickleback species pairs (see http://srmwww.gov.bc.ca/risc/pubs/aquatic/interp/index.htm). 2. Species-specific water quality objectives may need to be established, particularly with respect to light transmission and nutrient status. 3. Communicate objectives to appropriate authorities and stakeholders. 	Have water quality objectives been established and communicated to relevant regulators and stakeholders?

Priority ²	Strategy	Approaches	Performance Measure ³
Primary	Develop a comprehensive water management plan for each basin.	RIGs will reduce risk to species pairs by working with Water Stewardship Division (Ministry Of Environment) and water licence holders to: <ol style="list-style-type: none"> 1. review existing licences 2. review existing water uses 3. secure unallocated water for conservation purposes 4. use a planning process involving stakeholders to establish objectives for present and future water management (e.g., criteria for acceptable levels of water drawdown) 	Has a water management plan been completed and implemented?
Primary	If re-introduction is feasible, establish a captive breeding program for the Enos Lake species pair.	<ol style="list-style-type: none"> 1. Capture relic non-hybrid broodstock from Enos Lake, and establish captive populations of both species at UBC. 2. Invite Research Action Group to review protocols for breeding design (e.g., to prevent loss of genetic variance and minimize adaptation to artificial environments), and obtain necessary funding to support research and population maintenance. 	Have captive populations been established for the Enos Lake species pair? Is the captive population thriving? Have genetic goals been established for the breeding program and are they being achieved?
Primary	Develop and implement an information and education plan that includes the following elements: <ol style="list-style-type: none"> 1. Public education material regarding the threat of exotic species 2. Presentation materials for public schools 3. Educational signage for appropriate placement 	RIGs to work with government agencies and educators to develop <ol style="list-style-type: none"> 1. educational material (e.g., an educational brochure) to explain potential ecological impacts of introducing organisms to new environments. 2. educational material for use in public schools, particularly schools in the vicinity of the species pairs' lakes. For example, a "Wild BC" module could be prepared and may be widely used. 3. educational signage for placement at specific locations (e.g., Powell River - Texada Island ferry terminals, at the lakeside of specific lakes, etc.). Obtain funding for sign construction and maintenance. 	<ol style="list-style-type: none"> 1. Have educational materials been produced? Has public perception and awareness been affected? 2. How many classes have received educational presentations? Has public perception and awareness been affected? 3. How many educational signs have been erected? Has public perception and awareness been affected?

Priority ²	Strategy	Approaches	Performance Measure ³
Secondary	Determine the potential impacts of recreational fishing in species pair lakes and develop mitigation measures as required.	<p>Work with provincial agencies and the Freshwater Fisheries Society to develop guidelines or regulatory proposals including:</p> <ul style="list-style-type: none"> ▪ no enhancement of recreational fishing through stocking. ▪ no fishing on lakes where sport species are not indigenous. ▪ no bait where sport fisheries are allowed. <p>Consult on the rationale for the approach with stakeholders and consider additional measures that either limit impacts or support existing fisheries.</p>	Are the minimal regulatory changes implemented?
Secondary	Investigate potential water quality implications from use of explosives for mining activities within species pairs' watersheds.	Review and summarize current or planned mining activities and reassess this threat. If relevant, RIGs to review relevant literature and conduct water quality testing. RIGs to work with Research Action Group as necessary on technical issues. Communicate results for consideration during future review of the Recovery Strategy. Obtain necessary funding to support review, sampling and analysis.	<p>Has a literature review been conducted and communicated to the Recovery Team?</p> <p>Have water quality samples been taken of runoff from mining sites?</p> <p>Have the samples been analyzed and results effectively communicated?</p>
Secondary	Determine potential impacts of gas operated motor boats on water quality in the species pair lakes and develop mitigation measures as required, and discourage impacts from lakeshore development and recreational use.	RIGs to work with local government and stakeholders to establish designations of no motor or electric motor only on species pair lakes. Note: Canadian Coast Guard is the regulator.	Are gas powered boat motors allowed on species pairs' lakes?
Secondary	Jointly develop land management strategies for crown and private lands.	<p>Develop criteria for assessing effects of land developments (including forest harvest) on stickleback, develop guidelines for good stewardship, establish Wildlife Habitat Areas (WHAs) where appropriate, and establish species pair watersheds as Special Development Areas.</p> <ol style="list-style-type: none"> 1. For crown lands, establish one or more Wildlife Habitat Areas to minimize cumulative long-term habitat impacts. 2. For private lands, work with land owners to encourage good stewardship. 	Have forest harvest and land management criteria been developed? Have WHAs been established? Is forest harvest and land development meeting the criteria?

Priority²	Strategy	Approaches	Performance Measure³
Secondary	Develop sound protocols for scientific investigations (e.g., limit use of hybrids in <i>in situ</i> experiments, limit number of fish collected each year, etc.)	Research Action Group to work with government agencies to set boundaries for experimental work in species pair lakes. Note: SARA permits are required to legally collect and undertake research on listed stickleback species.	Have scientific investigation protocols been set and communicated? Have they been implemented?

10. ANTICIPATED CONFLICTS OR CHALLENGES

Stickleback species pairs are currently of little or no economic value, and this is unlikely to change. By contrast there are other public, private and commercial interests in watersheds in which the species pairs reside. These interests include mining, forestry, water extraction for industrial and residential use, roads, pipelines, residential property development, and low-level (at present) recreational use for fishing, boating, and swimming. It is important to understand that many of the threats to species pairs can be reduced but not eliminated.

11. RECOVERY FEASIBILITY

As part of the SARA process, the competent minister must determine the feasibility of recovery for species at risk. To help standardize these determinations, current draft policy (Government of Canada 2005) poses four questions, which are to be addressed in each recovery strategy. These questions are posed and answered here.

1. Are individuals capable of reproduction currently available to improve the population growth rate or population abundance?

Yes. Stickleback species pairs naturally have a very restricted distribution. The species pairs on Texada Island are self-supporting with healthy abundance levels and are not in apparent decline (but will continue to be at risk due to their limited geographic range). The Enos Lake species pair has collapsed to a hybrid swarm, but a self-supporting population of Enos Lake limnetics exists in Murdo-Fraser in North Vancouver, and efforts to establish a self-supporting population of Enos Lake benthics are underway and appear to be successful. The Hadley Lake species pair is extinct and recovery of these two species is therefore not feasible

2. Is sufficient suitable habitat available to support the species or could it be made available through habitat management or restoration?

Yes. Sufficient suitable habitat exists on Texada Island to support Paxton Lake and Vananda Creek species pairs in their natural habitats. Feasibility of restoring habitats in Hadley Lake is dependent on extirpation of brown bullhead and may require the removal of crayfish in Enos Lake, both of which were introduced to the lakes. Feasibility of habitat restoration and re-introduction of stickleback species pairs to these lakes is currently under study.

3. Can significant threats to the species or its habitat be avoided or mitigated through recovery actions?

Yes. Controlling threats to the species pairs is feasible, but rests more on social than technical considerations. For example, the primary threat is from the introduction of exotic species. Exotic fish species are spread by unauthorized introductions, and would be best prevented by educating the public about the risks associated with intentionally spreading organisms. Such a program is expected to be beneficial, but its efficacy is nevertheless likely to be less than 100%. Most other threats, such as those from excessive water use, can be managed with existing regulations, but will require consultation with stakeholders.

4. Do the necessary recovery techniques exist and are they demonstrated to be effective?

Yes. Special recovery techniques are not required for recovery of stickleback species pairs on Texada Island. What is required is effective management of current and future threats, which is believed to be entirely feasible. It should be noted however that stickleback species pairs will likely always be very restricted in their distribution even if they are successfully introduced to fishless lakes in the region. As a result, they are likely to remain at some risk. Recovery efforts for species pairs as a group are best concentrated on controlling threats, and if possible re-introducing the pairs to their original habitats (i.e., Hadley Lake and Enos Lake).

The feasibility of re-introducing the pairs to their original habitats depends on two main technical factors: removing exotic species, and introducing (or re-introducing) species to a lake with no stickleback. Both have significant technical challenges. Overcoming these challenges will require additional research, which is currently underway (see Section [13](#)).

Based on the assessment above, recovery of the stickleback species pairs is determined to be both technically and biologically feasible.

12. RECOMMENDED APPROACH / SCALE FOR RECOVERY

The recovery strategy for stickleback species pairs recommends the use of a modified single species approach (rather than an ecosystem approach) because the ecology of the species pairs is common across watersheds and the threats to each species pair are similar. Introduction of exotic species and effects of water management and land-based development are seen as the main threats to extant wild populations.

There are few apparent opportunities to combine recovery efforts for stickleback species pairs with existing management plans, actions, or policies. One of the greatest opportunities for conservation of stickleback species pairs would be to participate in the development and execution of a regional exotic species management plan.

13. KNOWLEDGE GAPS

We know a great deal about the evolution of the species pairs, but remarkably little about their basic ecology, particularly during early life stages. If the species pairs are to be re-introduced to Hadley and Enos Lakes (or introduced to other lakes) as part of the recovery process, there are good reasons to develop a greater understanding of the basic ecology of the species and their native lakes.

The following are a series of topics that highlight knowledge gaps affecting management of the species pairs. Additional topics will require work if critical habitat is to be well-defined (see Section [6.3](#)).

Basic Biology

- Define critical habitat for species pairs, and how it can be protected
- Habitat use during early life stages
- Age structure of populations
- Abundance trends (among seasons and years) of limnetics and benthics within each lake
- Habitat factors required to maintain species segregation
- Hybridization trends within each lake
- Hybridization rates in undisturbed conditions
- Hybridization thresholds in relation to species pair collapse

Threat Clarification

- Regional trends in the spread of exotic species
- Relative severity of exotic species introductions (e.g., should some exotic species be targeted for special attention?)
- Effects of changes in water quality on stickleback species pairs
- Relationship between water use and risk to stickleback
- Assess the types and extent of land use activities that can be safely permitted within these watersheds

Rebuilding Techniques

- Exotic species (e.g., brown bullhead and crayfish) removal techniques
- Understand the ecological preconditions for maintenance of the species pairs and why pairs collapsed in experimental ponds

Effectiveness of Stewardship

- Understand the effectiveness of stewardship initiatives (e.g., education programs, signage, angler education)

14. POTENTIAL MANAGEMENT IMPACTS FOR OTHER SPECIES

Management actions implemented to mitigate threats to species pairs are unlikely to negatively affect other indigenous species since other species that are known to co-exist with species pairs are widely distributed.

15. ACTIONS ALREADY COMPLETED AND/OR UNDERWAY

A variety of recovery actions have been completed or initiated.

1. A “Research Action Group” was established in 2003, made up primarily of researchers from UBC.
2. A wide variety of scientific investigations have been completed or continue to occur:
 - a. monitoring of the status of species pairs (this was done in an *ad hoc* manner in the past, but has recently become somewhat more formalized)
 - b. laboratory husbandry techniques are now well worked out.
 - c. translocation to experimental ponds (early experiments in experimental ponds have indicated some of the difficulties associated with translocation)
 - d. genetics research (microsatellite work continues to be conducted)
 - e. ecological and evolutionary research (feeding efficiency experiments, behaviour, mate choice, morphometrics)
 - f. scientific documents and publications (there is a long list of primary research publications, primarily completed by researchers at UBC)
3. Prior to the collapse of the Enos Lake stickleback species pair, a population of Enos Lake limnetics was established by adding wild fish in 1988 and 1999 (under permit from the Fisheries Branch of the British Columbia Ministry of Environment, Lands and Parks) to a pond in Murdo-Frazer Park in North Vancouver. A viable population was confirmed in spring 2002 (D. Schluter, unpublished data).
4. A program was initiated in 2003 to establish broodstock for future recovery of the Enos Lake species, by capturing putative “pure” benthics and breeding them in the lab. Genetic and morphological testing is underway to confirm identity of individuals used as breeding stock.

5. Public awareness and education (e.g., publication of a Stickleback Species Pair brochure in the Wildlife in British Columbia at Risk series; "Evolution in Action," a program for Knowledge Network)

16. STATEMENT OF WHEN ACTION PLANS WILL BE COMPLETED

Within two years of posting the final recovery strategy, one or more action plans will be developed. The plans will include descriptions of programs, plus a timeline of programs with estimated budgets, and will encompass a timeframe of at least five years.

17. REFERENCES CITED

Bell, M.A., and S.A. Foster. 1994. editors. The evolutionary biology of the threespine stickleback. Oxford University Press, Oxford, UK.

Bentzen, P., and J.D. McPhail. 1984. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): specialization for alternative trophic niches in the Enos Lake species pair. Canadian Journal of Zoology 62:2280-2286.

Boughman, J.W. 2001. Divergent sexual selection enhances reproductive isolation in sticklebacks. Nature 411: 944-947.

Campbell, R.W., N.K. Dawe, I. McTaggart-Cowan, J.M. Cooper, G.W. Kaiser and M.C.E. McNall. 1990. The birds of British Columbia. Volume I. Nonpasserines. Royal British Columbia Museum and Canadian Wildlife Service, Victoria, British Columbia.

Chilibeck, B., G. Chislett, and G. Norris. 1992. Land development guidelines for the protection of aquatic habitat. Fisheries and Oceans Canada.

Foster, S.A. 1994. Evolution of the reproductive behaviour of threespine stickleback. Pages 381-398 in M.A. Bell and S.A. Foster, editors. The evolutionary biology of the threespine stickleback. Oxford University Press, Oxford, UK.

Foster, S.A., J.A. Baker, and M.A. Bell. 2003. The case for conserving threespine stickleback populations: protecting an adaptive radiation. Fisheries 28(5):10-18.

Government of Canada. 2005. Species at Risk Act Policy. Draft policy on the feasibility of recovery. January 06, 2005

Hatfield, T. 2001a. Status of the stickleback species pair, *Gasterosteus* spp., in Hadley Lake, Lasqueti Island, British Columbia. Canadian Field-Naturalist 115:579-583.

Hatfield, T. 2001b. Status of the stickleback species pair, *Gasterosteus* spp., in the Vananda Creek watershed of Texada Island, British Columbia. Canadian Field-Naturalist 115:584-590.

Hatfield, T. 2003. Threats to stickleback species pairs. report prepared for the National Recovery Team for Stickleback Species Pairs. Unpublished Manuscript

Hatfield, T. 2006. Critical habitat for stickleback species pairs in British Columbia. Report prepared for BC Ministry of Environment, Victoria BC.

- Hatfield, T. and D. Schluter. 1996. A test for sexual selection on hybrids of two sympatric sticklebacks. *Evolution* 50: 2429-2434.
- Hatfield, T., and J. Ptolemy. 2001. Status of the stickleback species pair, *Gasterosteus* spp., in Paxton Lake, Texada Island, British Columbia. *Canadian Field-Naturalist* 115:591-596.
- Kliwer, E.V. 1970. Gill raker variation and diet in lake whitefish, *Coregonus clupeaformis*, in northern Manitoba. Pp. 147-165 in C. C. Lindsey and C. S. Woods (eds.), *Biology of coregonid fishes*. University of Manitoba Press, Winnipeg, Canada.
- Kraak, S.B.M., B. Mundwiler, and P.J.B. Hart. 2001. Increased number of hybrids between benthic and limnetic three-spined sticklebacks in Enos Lake, Canada; the collapse of a species pair? *Journal of Fish Biology* 58:1458-1464.
- Larson, G.L. 1976. Social behavior and feeding ability of two phenotypes of *Gasterosteus aculeatus* in relation to their spatial and trophic segregation in a temperate lake. *Canadian Journal of Zoology* 54:107-121.
- Lavin, P.A., and J.D. McPhail. 1985. The evolution of freshwater diversity in threespine stickleback (*Gasterosteus aculeatus*): site-specific differentiation of trophic morphology. *Canadian Journal of Zoology* 63: 2632-2638.
- Lavin, P.A., and J.D. McPhail. 1986. Adaptive divergence of trophic phenotype among freshwater populations of the threespine stickleback (*Gasterosteus aculeatus*). *Canadian Journal of Fisheries and Aquatic Sciences* 43: 2455-2463.
- Lavin, P.A., and J.D. McPhail. 1987. Morphological divergence and the organization of trophic characters among lacustrine populations of the threespine stickleback (*Gasterosteus aculeatus*). *Canadian Journal of Fisheries and Aquatic Sciences* 44: 1820-1829.
- Magnuson, J.J. and J.G. Heitz. 1971. Gill raker apparatus and food selectivity among mackerels, tunas, and dolphins. *Fisheries Bulletin* 69:361-370.
- Matthews, B., P. Ramsay and K. Tienhaara. 2000. The Endangered Species Recovery Planning Matrix . Undergraduate Honours Thesis. University of British Columbia. available at <http://www.science.ubc.ca/envsc/theses.html>
- McPhail, J.D. 1969. Predation and the evolution of a stickleback (*Gasterosteus*). *Journal of the Fisheries Research Board of Canada* 26: 3183-3208.
- McPhail, J.D. 1984. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): morphological and genetic evidence for a species pair in Enos Lake, British Columbia. *Canadian Journal of Zoology* 62: 1402-1408.
- McPhail, J.D. 1989. Status of the Enos Lake stickleback species pair, *Gasterosteus* spp. *Canadian Field-Naturalist* 103:216-219.
- McPhail, J.D. 1992. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): evidence for a species-pair in Paxton Lake, Texada Island, British Columbia. *Canadian Journal of Zoology* 70: 361-369.

McPhail, J.D. 1993. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): origin of the species pairs. *Canadian Journal of Zoology* 71:515-523.

McPhail, J.D. 1994. Speciation and the evolution of reproductive isolation in the sticklebacks (*Gasterosteus*) of southwestern British Columbia. Pages 399-437 in M. A. Bell and S. A. Foster, editors. *The evolutionary biology of the threespine stickleback*. Oxford University Press, Oxford, UK.

Nagel, L. and D. Schluter. 1998. Body size, natural selection, and speciation in sticklebacks. *Evolution* 52: 209-218.

National Recovery Working Group. 2003. Working Draft Recovery Handbook. April 2003. Recovery of Nationally Endangered Wildlife, Ottawa, Ontario. 40+ pp. plus appendices.

Nomura, M. 2005. Population study of Paxton Lake stickleback species pair – 2005. unpublished data report.

Province of British Columbia. Water quality guidelines for the protection of aquatic life. Available at: <http://srmwww.gov.bc.ca/risc/pubs/aquatic/interp/index.htm>

Reimchen, T.E. 1989. Loss of nuptial color in threespine sticklebacks (*Gasterosteus aculeatus*). *Evolution* 43: 450-460.

Reimchen, T.E. 1992. Injuries on stickleback from attacks by a toothed predator (*Oncorhynchus*) and some implications for the evolution of lateral plates. *Evolution* 46: 1224-1230.

Rowland, W.J. 1989. The effects of body size, aggression and nuptial coloration on competition for territories in male threespine sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour* 37: 282-289.

Sanderson, S.L., J.J. Cech, and M.R. Patterson. 1991. Fluid dynamics in suspension-feeding blackfish. *Science* 251: 1346-1348.

Schluter, D. 1994. Experimental evidence that competition promotes divergence in adaptive radiation. *Science* 266: 798-801.

Schluter, D. 1995. Adaptive radiation in sticklebacks: trade-offs in feeding performance and growth. *Ecology* 76: 82-90.

Schluter, D. 2003. Frequency dependent natural selection during character displacement in sticklebacks. *Evolution* 57: 1142–1150.

Schluter, D., and J.D. McPhail. 1992. Ecological character displacement and speciation in sticklebacks. *The American Naturalist* 140:85-108.

Schluter, D. and J.D. McPhail. 1993. Character displacement and replicate adaptive radiation. *Trends in Ecology and Evolution* 8: 197-200.

Seehausen, O., J.J.M. van Alphen and F. Witte. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* 277: 1808-1811.

Stockner, J.G., E. Rydin, and P. Hyenstrand. 2000. Cultural oligotrophication: causes and consequences for fisheries resources. *Fisheries* 25(5):7-14.

Taylor, E.B., and J.D. McPhail. 1999. Evolutionary history of an adaptive radiation in species pairs of threespine sticklebacks (*Gasterosteus*): insights from mitochondrial DNA. *Biological Journal of the Linnean Society* 66:271-291.

Taylor, E.B. and J.D. McPhail. 2000. Historical contingency and ecological determinism interact to prime speciation in sticklebacks, *Gasterosteus*. *Proceedings of the Royal Society of London, Series B* 267: 2375-2384.

Vamosi, S.M. 2003. The presence of other fish species affects speciation in threespine sticklebacks. *Evolutionary Ecology Research* 5: 717–730.

Vamosi, S.M., T. Hatfield, and D. Schluter. 2000. A test of ecological selection against young-of-the-year hybrids of sympatric sticklebacks. *Journal of Fish Biology* 57: 109-121.

Wetzel, R.G. 2001. *Limnology. Lake and river ecosystems*, 3rd Edition. Academic Press, San Diego.

Wood, P., J. Oosenbrug, and S. Young. 2003. Vananda Creek Stickleback Species Pair Managing Identified Wildlife Account (draft).

Wootton, R.J. 1976. *The biology of the sticklebacks*. Academic Press, London, UK.

18. APPENDIX I- RECORD OF COOPERATION AND CONSULTATION

The stickleback species pairs are listed on Schedule 1 of the *Species at Risk Act* (SARA), and as an aquatic species are under federal jurisdiction and managed by Fisheries and Oceans Canada (DFO): 200 - 401 Burrard Street, Vancouver, BC.

To assist in the development of an initial draft of this Recovery Strategy, as well as those for other listed freshwater fishes in British Columbia, DFO in cooperation with the Province of BC assembled a group of experts from various levels of government, academia, consultants, and non-governmental organizations to form the Pacific Region Non-Game Freshwater Fish Recovery Team. This team, co-chaired by DFO and the Province of BC, is responsible for drafting recovery strategies for Pacific Region freshwater fish species listed under SARA, including the stickleback species pairs. The recovery planning process for the stickleback species pairs was initiated through a stakeholder workshop in Nanaimo in March 2002. In addition, local stakeholders have subsequently established Recovery Implementation Groups for the Texada Island and Enos Lake species pairs.

Consultation on the draft Recovery Strategy was provided through a series of multi-stakeholder Community Dialogue Sessions and First Nations information exchanges in BC communities, as part of DFO Pacific Region's Fall Consultation Program. A consultation weblink was sent to 198 First Nations, Tribal Councils and Aboriginal Fisheries Commissions, as well as other stakeholders, and notices announcing the Community Dialogue Sessions were placed in 74 newspapers. Specific presentation and discussion sessions on the proposed Recovery Strategy for Stickleback Species Pairs were held in Sechelt in September 2005, and Nanaimo in November 2005, with no attendees at the Nanaimo session.

Additional input on the draft Recovery Strategy was sought through a discussion guide and feedback form available on the internet (October – December 2005). One response was received from a local resort developer. Input from the Province of BC was received through recovery team participation. An external peer review was conducted by Dr. Joe Nelson of the University of Alberta. All feedback received was considered in the finalization of the Recovery Strategy.

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