COSEWIC Assessment and Status Report

on the

Paxton Lake Benthic and Limnetic Threespine Stickleback Species Pair Gasterosteus aculeatus

in Canada



ENDANGERED 2010

COSEWIC Committee on the Status of Endangered Wildlife in Canada



COSEPAC Comité sur la situation des espèces en péril au Canada COSEWIC status reports are working documents used in assigning the status of wildlife species suspected of being at risk. This report may be cited as follows:

COSEWIC. 2010. COSEWIC assessment and status report on the Paxton Lake Benthic and Limnetic Threespine Stickleback Species Pair *Gasterosteus aculeatus* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xiv + 22 pp. (www.sararegistry.gc.ca/status/status e.cfm).

Previous report(s):

- COSEWIC. 2000. COSEWIC assessment and update status report on Paxton Lake Stickleback Species Pair *Gasterosteus* spp. in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii + 13 pp. (www.sararegistry.gc.ca/status/status_e.cfm).
- Hatfield, T. and J. Ptolemy 1999. Update COSEWIC status report on the Paxton Lake Stickleback Species Pair *Gasterosteus* spp. in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. 1-11 pp.
- Houston, J. 1998. COSEWIC status report on the Texada Island Stickleback Species Pair *Gasterosteus sp.* in Canada. Committee on the status of Endangered Wildlife in Canada. Ottawa. 11 pp.

Production note:

COSEWIC acknowledges Todd Hatfield for writing the provisional status report on the Paxton Lake Sticklebacks, *Gasterosteus aculeatus*, prepared under contract with Environment Canada. The contractor's involvement with the writing of the status report ended with the acceptance of the provisional report. Any modifications to the status report during the subsequent preparation of the 6-month interim and 2-month interim status reports were overseen by Eric Taylor, Freshwater Fishes Specialist Subcommittee Co-chair.

For additional copies contact:

COSEWIC Secretariat c/o Canadian Wildlife Service Environment Canada Ottawa, ON K1A 0H3

Tel.: 819-953-3215 Fax: 819-994-3684 E-mail: COSEWIC/COSEPAC@ec.gc.ca http://www.cosewic.gc.ca

Également disponible en français sous le titre Évaluation et Rapport de situation du COSEPAC sur la paire d'espèces d'épinoches bentiques et limnétiques à trois épines du lac Paxton (*Gasterosteus aculeatus*) au Canada.

Cover illustration/photo:

Paxton Lake Benthic and Limnetic Threespine Stickleback Species Pair — Paxton Lake Limnetic (upper, 65 mm) and Benthic (lower, 75 mm) sticklebacks. The photos are of mature males. Females show similar differences between species in body size and shape (photo by G. Velema, by permission).

©Her Majesty the Queen in Right of Canada, 2010. Catalogue CW69-14/171-1-2010E-PDF ISBN 978-1-100-15970-6



Recycled paper



Assessment Summary – April 2010

Common name

Paxton Lake Limnetic Threespine Stickleback

Scientific name Gasterosteus aculeatus

Status Endangered

Reason for designation

This small freshwater fish is a unique Canadian endemic that is restricted to a single small lake in coastal British Columbia (BC). The wildlife species is highly susceptible to extinction from aquatic invasive species introductions that have been observed to cause rapid extinction of similar species in at least two other lakes. Invasive aquatic species continue to increase in lakes on adjacent Vancouver Island and the lower mainland of BC, and there is, therefore, a reasonable likelihood that invasives could be introduced into the habitat of the species over the next 10 years. This species is also susceptible to habitat loss and degradation from water extraction and land use activities in the surrounding landscape.

Occurrence

British Columbia

Status history

Designated Threatened in April 1998. Status re-examined and confirmed in April 1999. Status re-examined and designated Endangered in May 2000. Status re-examined and confirmed in April 2010.

Assessment Summary – April 2010

Common name

Paxton Lake Benthic Threespine Stickleback

Scientific name

Gasterosteus aculeatus

Status

Endangered

Reason for designation

This small freshwater fish is a unique Canadian endemic that is restricted to a single small lake in coastal British Columbia (BC). The wildlife species is highly susceptible to extinction from aquatic invasive species introductions that have been observed to cause rapid extinction of similar species in at least two other lakes. Invasive aquatic species continue to increase in lakes on adjacent Vancouver Island and the lower mainland of BC, and there is, therefore, a reasonable likelihood that invasives could be introduced into the habitat of the species over the next 10 years. This species is also susceptible to habitat loss and degradation from water extraction and land use activities in the surrounding landscape.

Occurrence

British Columbia

Status history

Designated Threatened in April 1998. Status re-examined and confirmed in April 1999. Status re-examined and designated Endangered in May 2000. Status re-examined and confirmed in April 2010.



Paxton Lake Benthic and Limnetic Threespine Stickleback Species Pair

Gasterosteus aculeatus

Species information

Paxton Lake Benthic and Limnetic Threespine Sticklebacks are sympatric species derived from the Threespine Stickleback, but they have not been formally named. Limnetics primarily exploit plankton, and have traits that are considered adaptations to a zooplankton-consuming lifestyle. Benthics mainly eat benthic invertebrates in the littoral zone, and have a robust body, wide gape and few, short gill rakers, traits considered to be advantageous in benthic feeding. Distributional and molecular genetic data strongly indicate that the pairs have arisen independently, despite similar appearance. Thus, a stickleback species pair from one watershed is genetically and evolutionarily distinct from pairs in other watersheds. Hybridization between Paxton Lake limnetics and benthics occurs naturally in the wild at a low rate.

Distribution

Paxton Lake Benthic and Limnetic Threespine Sticklebacks are restricted to a single lake (Paxton Lake) on Texada Island, southwestern British Columbia.

Habitat

Paxton Lake Benthic and Limnetic Threespine Sticklebacks have similar life histories, but different habitat requirements. In general, Limnetic and Benthic sticklebacks spawn in littoral areas in the spring, feed and grow in pelagic and littoral areas in spring and summer, and overwinter in deep water habitats during the fall and winter.

Biology

Benthic and limnetic sticklebacks are similar to other Threespine Sticklebacks in their overall mode of reproduction. Males construct nests, which they guard and defend, until fry are about a week old. Eggs take up to a week to hatch, depending on temperature, and another three to five days before larvae are free-swimming. Benthics build their nests under cover of macrophytes or other structure; limnetics tend to spawn in open habitats. In the wild, benthics reproduce earlier in the year than limnetics, but there is considerable overlap in their spawning times. There is strong assortative mating, but hybridization occurs naturally in the wild at a low rate.

Limnetics are thought to mature on average as one-year-olds, and rarely live beyond a single breeding season. Reproductive females have multiple clutches in quick succession. Nesting males will mate with several to many females, and are thought to often nest more than once within a single breeding season. Benthics delay sexual maturation and on average begin mating as two-year-olds. They may live up to about five years, and mate in several breeding seasons. Reproductive females have fewer clutches within a breeding season than do limnetics. Like limnetics, males will mate with several to many females, but it is not clear if they nest more than once within a single breeding season.

Population sizes and trends

Only a single study in 2005 has estimated abundance of the Paxton species pair. The estimates were based on standard mark-recapture techniques, and the estimates were considered most accurate for mature benthics. The abundance estimate of about 6,600 mature benthics was considerably lower than the assumed abundance, and has led to additional caution regarding lethal and non-lethal sampling in the lake. Estimates of limnetics were more uncertain, but may approach 90,000.

Threats and limiting factors

Threats to Paxton Lake Benthic and Limnetic Threespine Sticklebacks are varied. Water extractions from Paxton Lake for nearby mining operations caused severe drawdowns in the past. Water use has declined substantially during the last 30 years and this has likely improved stability and productivity of littoral and pelagic habitats. Mining and forest harvest have been extensive in the watershed and continue today. These and other land-based activities have the potential to negatively affect within-lake habitats. The collapse of the species pair in Enos Lake and in experimental ponds into hybrid swarms has highlighted the sensitivity of the pairs to certain types of environmental perturbation. Whereas population modelling indicates the sticklebacks are resilient to environmental perturbations, other observations indicate that continued reproductive isolation depends on environmental factors (water clarity, aquatic plant density, habitat complexity), which to date have been only qualitatively assessed. Yet, it is these other factors that appear to be dominant in maintaining the species pairs as distinct. In this context, the species pairs are not highly adaptable, and are not particularly resilient to environmental disturbance.

Limits to Paxton Lake stickleback abundance are poorly understood, but the main limiting factor is probably food supply—the capability of the lake to produce plankton and benthos—but there are no data to support this view. In any case, the primary factor determining conservation status is that they are endemic to a single lake, not population decline.

Special significance of the species

The significance of Paxton Lake Benthic and Limnetic Threespine Sticklebacks is primarily scientific and as a unique part of Canada's biodiversity. Stickleback species pairs are widely regarded as a scientific treasure because they are among the youngest species on earth: they have likely arisen since the end of the last glaciation, less than 13,000 years ago. They are considered valuable and remarkable research subjects for the study of the origins and persistence of biodiversity.

Existing protection

Paxton Lake Benthic and Limnetic Threespine Sticklebacks are listed as Endangered under Schedule 1 of the *Species at Risk Act*, which results in a number of automatic prohibitions. They were assessed as Endangered by COSEWIC in 2010, and are "red-listed" by the Conservation Data Centre and BC Ministry of Environment. Under the BC Sport Fishing Regulations, it is illegal to fish for, or catch and retain Paxton Lake Benthic and Limnetic Threespine Sticklebacks.

All lands adjacent to Paxton Lake are privately owned. Paxton Lake Benthic and Limnetic Threespine Sticklebacks benefit from the habitat protection provisions of the federal *Fisheries Act* and the provincial *Riparian Areas Regulation*.

TECHNICAL SUMMARY 1 Paxton Lake Limnetic Threespine Stickleback

Gasterosteus aculeatus Paxton Lake Limnetic Threespine Stickleback Endemic to Paxton Lake, British Columbia

épinoche limnétique du lac Paxton

Demographic Information

Generation time	1 yr
Is there a continuing decline in number of mature individuals?	Unknown, but unlikely
(Trend is unknown but may be stable based on repeated trapping over many years; however, abundance was not estimated during these sampling events.)	
Estimated percent of continuing decline in total number of mature individuals within 5 years	Not applicable, decline unlikely
Percent change in total number of mature individuals over the last 10 years.	Unknown
Percent change in total number of mature individuals over the next 10 years.	Unknown
Percent change in total number of mature individuals over any 10 year period, over a time period including both the past and the future.	Unknown
Are the causes of the decline clearly reversible and understood and ceased?	Not applicable
Are there extreme fluctuations in number of mature individuals?	No

Extent and Occupancy Information

< 0.31 km ²
> 0.31 KIII ⁻
0.17 km ²
~ 2 km²
~ 8 km ²
No
1
No

Number of Mature Individuals (in each population)

Population	N Mature Individuals
Estimated from a single mark-recapture study for mature males only (~45,853, 95% CI: 25,806-83,981). Assuming a 1:1 sex ratio, the point estimate can be	~90,000
doubled to obtain a rough estimate for the numbers of mature individuals of both sexes.	

Quantitative Analysis

Probability of extinction in the wild is at least [20% within 20 years or 5 generations, or 10% within 100 years].	Not applicable
Simple PVA calculations were done as part of critical habitat determinations (see Hatfield 2008). Population modelling using an age-structured model indicated that benthic sticklebacks are resilient to population perturbations from environmental stochasticity. In general, the modelling confirmed that high population growth rates allow sticklebacks to recover quickly from short-term, small to moderate environmental perturbations.	

Threats (actual or imminent, to populations or habitats)

Immediate

- Water diversion and draw down
- Habitat loss and degradation from land use practices

Potential

- Introduction of invasive species (although there are presently no invasive species in Paxton Lake, many species are present in nearby areas and the distribution of invasives has increased over the last 10-20 years). Empirical observations indicate that the probability of extinction of species pairs in the presence of invasives is 1.0 (2 of 2 cases).
- Excessive collection for research purposes

Rescue Effect (immigration from outside Canada)

Status of outside population(s)? Not applicable, endemic to one lake	·
Is immigration known or possible?	No
Would immigrants be adapted to survive in Canada?	Not applicable
Is there sufficient habitat for immigrants in Canada?	Not applicable
Is rescue from outside populations likely?	Not applicable

Current Status

	-
COSEWIC: Endangered 201	Λ
	0

Additional Sources of Information: N/A

Status and Reasons for Designation

Status:	Alpha-numeric code:	
Endangered	A3e	

Reasons for designation:

This small freshwater fish is a unique Canadian endemic that is restricted to a single small lake in coastal British Columbia (BC). The wildlife species is highly susceptible to extinction from aquatic invasive species introductions that have been observed to cause rapid extinction of similar species in at least two other lakes. Invasive aquatic species continue to increase in lakes on adjacent Vancouver Island and the lower mainland of BC, and there is, therefore, a reasonable likelihood that invasives could be introduced into the habitat of the species over the next 10 years. This species is also susceptible to habitat loss and degradation from water extraction and land use activities in the surrounding landscape.

Applicability of Criteria

Criterion A:

Meets Endangered A3e - highly susceptible to extinction from exotic species introductions (as has been observed in two other species pair lakes).

Criterion B:

Not applicable. Although EO << $5,000 \text{ km}^2$, IAO << 500 km^2 and there are fewer than 5 locations, there is no evidence of decline or extreme fluctuations in any of the indices relevant to sub-criteria b(i-v) or c(i-iv), respectively.

Criterion C:

Not applicable. Exceeds criteria.

Criterion D:

Meets Threatened D2; exists in a single small lake. Reduction in habitat quality and declines in population size may occur rapidly from exotic species introductions.

Criterion E:

Not done.

TECHNICAL SUMMARY 2 Paxton Lake Benthic Threespine Stickleback

Gasterosteus aculeatus Paxton Lake Benthic Threespine Stickleback Endemic to Paxton Lake, British Columbia

épinoche benthique du lac Paxton

Demographic Information

Generation time	2-3 yrs
Is there a continuing decline in number of mature individuals?	Unknown, but unlikely
(Trend is unknown but may be stable based on repeated trapping over many years; however, abundance was not estimated during these sampling events.)	
Estimated percent of continuing decline in total number of mature individuals within 5 years	Not applicable, decline unlikely
Percent change in total number of mature individuals over the last 10 years.	Unknown
Percent change in total number of mature individuals over the next 10 years.	Unknown
Percent change in total number of mature individuals over any 10 year period, over a time period including both the past and the future.	Unknown
Are the causes of the decline clearly reversible and understood and ceased?	Unknown
Are there extreme fluctuations in number of mature individuals?	No

Extent and Occupancy Information

Estimated extent of occurrence	< 0.31 km ²
(This is an extreme endemic, restricted to a single small lake of 11.2 ha.)	
Area of occupancy	0.17 km ²
Index of Area of Occupancy (IAO)	
1 X 1 km grid	~ 2 km²
2 X 2 km grid	~ 8 km ²
Is the total population severely fragmented?	No
Number of "locations"	1
Is there continuing decline in extent of occurrence?	No
Is there continuing decline in index of area of occupancy?	No
Is there continuing decline in number of populations?	No
Is there continuing decline in number of locations?	No
Is there continuing decline in area, extent or quality of habitat?	No
Are there extreme fluctuations in number of populations?	No
Are there extreme fluctuations in number of locations?	No
Are there extreme fluctuations in extent of occurrence?	No
Are there extreme fluctuations in index of area of occupancy?	No

Number of Mature Individuals (in each population)

Population	N Mature Individuals
Total for males only (single estimate from 2005) is ~3,300 (95% CI: 2,243 –	~6,600
5,305). Assuming a 1:1 sex ratio, the point estimate could be doubled to provide	
a rough estimate of the number of mature individuals of both sexes.	

Quantitative Analysis

Probability of extinction in the wild is at least [20% within 20 years or 5 generations, or 10% within 100 years].	Not applicable
Simple PVA calculations were done as part of critical habitat determinations (see Hatfield 2008). Population modelling using an age-structured model indicated that benthic sticklebacks are resilient to population perturbations from environmental stochasticity. In general, the modelling confirmed that high population growth rates allow sticklebacks to recover quickly from short-term, small to moderate environmental perturbations.	

Threats (actual or imminent, to populations or habitats)

Immediate

- Water diversion and draw down
- Habitat loss and degradation from land use practices

Potential

- Introduction of invasive species (although there are presently no exotic species in Paxton Lake, many species are present in nearby areas and the distribution of invasives has increased over the last 10-20 years). Empirical observations indicate that the probability of extinction of species pairs in the presence of invasives is 1.0 (2 of 2 cases).
- Excessive collection for research purposes

Rescue Effect (immigration from outside Canada)

Status of outside population(s)? Not applicable, endemic	
Is immigration known or possible?	No
Would immigrants be adapted to survive in Canada?	Not Applicable
Is there sufficient habitat for immigrants in Canada?	Not Applicable
Is rescue from outside populations likely?	Not Applicable

Current Status

COSEWIC: Endangered 2010	

Status and Reasons for Designation

Status:	Alpha-numeric code:
Endangered	A3e
Dessen for Designation.	

Reason for Designation:

This small freshwater fish is a unique Canadian endemic that is restricted to a single small lake in coastal British Columbia (BC). The wildlife species is highly susceptible to extinction from aquatic invasive species introductions that have been observed to cause rapid extinction of similar species in at least two other lakes. Invasive aquatic species continue to increase in lakes on adjacent Vancouver Island and the lower mainland of BC, and there is, therefore, a reasonable likelihood that invasives could be introduced into the habitat of the species over the next 10 years. This species is also susceptible to habitat loss and degradation from water extraction and land use activities in the surrounding landscape.

Applicability of Criteria

Criterion A:

Meets Endangered A3e - highly susceptible to extinction from exotic species introductions (as has been observed in two other species pair lakes).

Criterion B:

Not applicable. Although EO << $5,000 \text{ km}^2$, IAO << 500 km^2 and there are fewer than 5 locations, there is no evidence of decline or extreme fluctuations in any of the indices relevant to sub-criteria b(i-v) or c(i-iv), respectively.

Criterion C:

Not applicable. Exceeds criteria.

Criterion D:

Meets Threatened D2; exists in a single small lake. Reduction in habitat quality and declines in population size may occur rapidly from exotic species introductions.

Criterion E:

Not done.

PREFACE

Paxton Lake Benthic and Limnetic Threespine Sticklebacks *Gasterosteus aculeatus* are sympatric, reproductively isolated species that are restricted to a single lake (Paxton Lake) on Texada Island, southwestern British Columbia. The species were designated Threatened in April 1998, a status that was re-examined and confirmed in April 1999. Status was again re-examined in May 2000 and resulted in an Endangered designation. Status was determined based primarily on an extremely restricted distribution and ongoing threats from introduction of exotic species and habitat loss and/or degradation from human disturbance. The species were listed as endangered under *SARA* in 2003.

A recovery strategy, co-led by Fisheries and Oceans Canada – Pacific Region and the British Columbia Ministry of the Environment, was completed in 2007. The recovery strategy lists a series of threats, the greatest of which is introduction of invasive species. Two other species pairs (one in Hadley Lake on Lasqueti Island and another in Enos Lake on Vancouver Island) have been extirpated by invasive species. All of the land surrounding Paxton Lake is privately owned, and there is some potential threat from land use and water use. A recovery action group has been established on Texada Island and the group is monitoring Paxton Lake water quality and undertaking a variety of biological studies. Paxton Lake sticklebacks continue to be intensively studied by researchers interested in ecology, evolution and genetics. In response to perceived high demand for collections of wild fish, the recovery team developed guidelines for limiting impacts from collecting activities. The guidelines are being used to manage collections under *SARA*.

Critical habitat has been proposed for stickleback species pairs and the recommendations subjected to review by the Pacific Scientific Advice Review Committee (PSARC), Fisheries and Oceans Canada, one step in the final approval process. Consequently, although described from a scientific perspective, critical habitat has not yet been legally identified.



COSEWIC HISTORY

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) was created in 1977 as a result of a recommendation at the Federal-Provincial Wildlife Conference held in 1976. It arose from the need for a single, official, scientifically sound, national listing of wildlife species at risk. In 1978, COSEWIC designated its first species and produced its first list of Canadian species at risk. Species designated at meetings of the full committee are added to the list. On June 5, 2003, the *Species at Risk Act* (SARA) was proclaimed. SARA establishes COSEWIC as an advisory body ensuring that species will continue to be assessed under a rigorous and independent scientific process.

COSEWIC MANDATE

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) assesses the national status of wild species, subspecies, varieties, or other designatable units that are considered to be at risk in Canada. Designations are made on native species for the following taxonomic groups: mammals, birds, reptiles, amphibians, fishes, arthropods, molluscs, vascular plants, mosses, and lichens.

COSEWIC MEMBERSHIP

COSEWIC comprises members from each provincial and territorial government wildlife agency, four federal entities (Canadian Wildlife Service, Parks Canada Agency, Department of Fisheries and Oceans, and the Federal Biodiversity Information Partnership, chaired by the Canadian Museum of Nature), three non-government science members and the co-chairs of the species specialist subcommittees and the Aboriginal Traditional Knowledge subcommittee. The Committee meets to consider status reports on candidate species.

DEFINITIONS (2010)

Wildlife Species	A species, subspecies, variety, or geographically or genetically distinct population of animal, plant or other organism, other than a bacterium or virus, that is wild by nature and is either native to Canada or has extended its range into Canada without human intervention and has been present in Canada for at least 50 years.
Extinct (X)	A wildlife species that no longer exists.
Extirpated (XT)	A wildlife species no longer existing in the wild in Canada, but occurring elsewhere.
Endangered (E)	A wildlife species facing imminent extirpation or extinction.
Threatened (T)	A wildlife species likely to become endangered if limiting factors are not reversed.
Special Concern (SC)*	A wildlife species that may become a threatened or an endangered species because of a combination of biological characteristics and identified threats.
Not at Risk (NAR)**	A wildlife species that has been evaluated and found to be not at risk of extinction given the current circumstances.
Data Deficient (DD)***	A category that applies when the available information is insufficient (a) to resolve a species' eligibility for assessment or (b) to permit an assessment of the species' risk of extinction.

- * Formerly described as "Vulnerable" from 1990 to 1999, or "Rare" prior to 1990.
- ** Formerly described as "Not In Any Category", or "No Designation Required."
- *** Formerly described as "Indeterminate" from 1994 to 1999 or "ISIBD" (insufficient scientific information on which to base a designation) prior to 1994. Definition of the (DD) category revised in 2006.



Environnement Canada Service canadien de la faune



The Canadian Wildlife Service, Environment Canada, provides full administrative and financial support to the COSEWIC Secretariat.

COSEWIC Status Report

on the

Paxton Lake Benthic and Limnetic Threespine Stickleback Species Pair Gasterosteus aculeatus

in Canada

2010

TABLE OF CONTENTS

WILDLIFE SPECIES INFORMATION	3
Name and classification	3
Morphological description	3
Spatial population structure and variability	5
Designatable units	
Special significance	6
DISTRIBUTION	7
Global range	7
Canadian range	7
HABITAT	8
Habitat requirements	
Habitat trends	
Habitat protection/Ownership	10
BIOLOGY	
Life cycle and reproduction	10
Physiology	
Dispersal/Migration	
Interspecific interactions	
Adaptability	
POPULATION SIZES AND TRENDS	
Search effort	
Abundance	
Fluctuations and trends	
Rescue effect	-
ABORIGINAL TRADITIONAL KNOWLEDGE	
LIMITING FACTORS AND THREATS	
EXISTING PROTECTION OR OTHER STATUS DESIGNATIONS	
ACKNOWLEDGEMENTS AND AUTHORITIES CONSULTED	-
INFORMATION SOURCES	-
BIOGRAPHICAL SUMMARY OF REPORT WRITER	
COLLECTIONS EXAMINED	22

List of Figures

Figure 1	Paxton Lake Limnetic male (top left) and female (top right) and Benthic	
	male (bottom left) and female mature (bottom right) sticklebacks. The	
	limnetics are about 65 mm total length and the benthics about 75 mm.	
	Photo by G. Velema, UBC, with permission.	4
Figure 2.	Distribution of Paxton Lake sticklebacks in Canada	7

List of Tables

Table 1.	Life history timing for benthic-limnetic stickleback species pairs	10
Table 2.	June 2005 abundance estimates of Paxton Lake limnetics and benthics	14

WILDLIFE SPECIES INFORMATION

Name and classification

Phylum:	Chordata
Class:	Actinopterygii (ray-finned fishes)
Order:	Gasterosteiformes
Family:	Gasterosteidae
Genus:	Gasterosteus
Limnetic Species:	Gasterosteus aculeatus
Benthic Species:	Gasterosteus aculeatus
Common Name	
English:	Paxton Lake Limnetic Threespine Stickleback
	Paxton Lake Benthic Threespine Stickleback
French:	épinoche limnétique du lac Paxton
	épinoche benthique du lac Paxton

Morphological description

The Paxton Lake Benthic and Limnetic Threespine Sticklebacks (Figure 1) are postglacial derivatives of the Threespine Stickleback (*Gasterosteus aculeatus*). The Threespine Stickleback is a small (usually 35-55 mm) fish that is common in coastal marine and freshwater throughout the northern hemisphere (Scott and Crossman 1973; McPhail 2007). The marine form is assumed to be the ancestor of most freshwater forms, and is usually anadromous, meaning it returns to freshwater to reproduce (Schluter and McPhail 1992, 1993; McKinnon and Rundle 2002). The Threespine Stickleback has a laterally compressed body with delicate pectoral and caudal fins. Individuals in most populations are well-armoured with calcified lateral plates, and pelvic and dorsal spines that can be rigidly locked in an erect position (Scott and Crossman 1973; Wooton 1976; Reimchen 1994). Freshwater populations are variable in extent of armour but usually have less than the marine form (Reimchen 1994). Body colour 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).

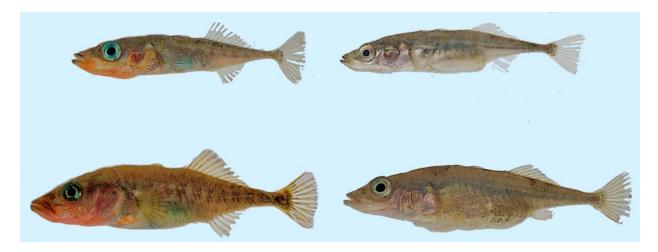


Figure 1 Paxton Lake Limnetic male (top left) and female (top right) and Benthic male (bottom left) and female mature (bottom right) sticklebacks. The limnetics are about 65 mm total length and the Benthics about 75 mm. Photo by G. Velema, UBC, with permission.

Marine sticklebacks are phenotypically similar throughout their range, whereas freshwater sticklebacks are ecologically, behaviourally and morphologically diverse (McPhail 1994). Three sets of genetically and morphologically divergent "pairs" are known from coastal British Columbia (BC, McPhail 1994): parapatric anadromous and stream-resident pairs (i.e., spatial distribution is contiguous and only overlapping in a relatively small area of contact), sympatric limnetic and benthic pairs (i.e., spatial distribution is entirely or mostly overlapping), and parapatric lake and stream pairs. In each case these are referred to as "species pairs" because there is close contact between each member of a pair. Detailed descriptions of solitary freshwater populations, and of each kind of species pair, are provided in McPhail (1994).

Paxton Lake Benthic and Limnetic Threespine Sticklebacks (Figure 1) are one of a handful of sympatric, reproductively isolated species pairs that occur in lakes on islands in a restricted area of the Strait of Georgia, BC (McPhail 1984, 1992; Schluter and McPhail 1992; McPhail 1993, 1994; Gow *et al.* 2008). In each case, limnetics primarily exploit plankton, and have morphological traits such as a fusiform body, narrow mouth and many, long gill rakers, which are traits considered adaptations to a zooplankton-consuming lifestyle (Schluter and McPhail 1992, 1993). Benthics mainly eat benthic invertebrates in the littoral zone, and have a robust body form, wide gape and few, short gill rakers, traits considered to be advantageous in benthic feeding (Schluter and McPhail 1992, 1993). The pattern of morphological and ecological divergence is similar, but not identical, in each of the lakes (Schluter and McPhail 1992; Gow *et al.* 2008), such that limnetics from all species pair lakes look alike, as do all benthics. Most striking are the morphological and ecological similarities among populations of limnetics (and among benthics), but there are also some minor morphological differences (McPhail 1994).

Spatial population structure and variability

A key research question has been whether sympatric stickleback species pairs are the result of a single speciation event or multiple, independent events. The question has been addressed most directly through the examination of microsatellite DNA variation in benthic and limnetic populations from different species pair lakes (Taylor and McPhail 2000). Phylogenetic and genetic distance analyses support the hypothesis that pairs of sympatric species have evolved multiple times. In other words, despite similar appearance among lakes, molecular phylogenies strongly indicate that the pairs are independently derived. Thus, a stickleback species pair from one watershed is genetically and evolutionarily distinct from pairs in other watersheds.

Another focus of research has been the intrinsic and extrinsic barriers to gene flow between limnetics and benthics within lakes. Paxton Lake Benthic and Limnetic Threespine Sticklebacks are each assumed to be a single panmictic population, and there is no *a priori* reason to think there is population structuring within the lake. There appear to be no intrinsic barriers to gene flow between the species: F₁ hybrids between limnetics and benthics are fully fertile and fitness in the laboratory is equivalent to the parental species (McPhail 1992; Hatfield and Schluter 1999), although backcrosses may have slightly lower survival (Hatfield and Schluter 1999). Limnetics and benthics show strong assortative mating in the lab and in the wild (Ridgway and McPhail 1984; Nagel and Schluter 1998; Boughman 2001), and several studies indicate that hybrids are selected against in the wild due to ecologically mediated selection against intermediate trophic morphology (Schluter and McPhail 1993; Schluter 1994, 1995; Hatfield and Schluter 1999).

Hybridization between Paxton Lake limnetics and benthics occurs naturally in the wild, and there appears to be ongoing gene flow between the two species. Based on examination of morphological traits and allozyme frequencies, McPhail (1992) estimated that about 1% of adults in Paxton Lake were hybrids. More recently, with the use of microsatellite markers, Gow *et al.* (2007) found that the proportion of hybrids in the population was somewhat higher. Interestingly, the proportion of hybrids declined through the life cycle from about 7% in juveniles to about 5% of adults, suggesting extrinsic selection against hybrids. Genetic evidence indicates that historical hybridization may have been considerably higher in the Paxton Lake species pair than for the other species pairs (Taylor and McPhail 1999), which is consistent with the high historical perturbations of the lake relative to other species pair lakes.

Designatable units

The Benthic and Limnetic sticklebacks from Paxton Lake warrant designatable unit status within *Gasterosteus aculeatus* because they satisfy the "discrete" and "significance" criteria of COSEWIC (COSEWIC 2009). First, both are genetically distinct from other sticklebacks as evidenced by an assemblage of allozyme, microsatellite, and morphological data (e.g., McPhail 1992; Taylor and McPhail 1999; Taylor and McPhail 2000). In addition, the Paxton Lake pair is only one of three existing cases (occurring in

three different watersheds on two different islands) of sympatric pairs in *Gasterosteus* despite the sampling of hundreds of coastal lakes (McPhail 1994). In addition, all three sets of pairs have evolved independently from one another (Taylor and McPhail 2000). The existence of a sympatric pair in Paxton Lake is, therefore, the result of a unique evolutionary divergence. This unique divergence meets the significance criterion in that it supports the view that Benthic and Limnetic sticklebacks in Paxton Lake exist within a unique ecological and evolutionary setting: divergent populations in sympatry with the associated adaptations (feeding and reproductive) that are crucial to their persistence in sympatry. Also, given that Benthic and Limnetic sticklebacks in Paxton Lake act as distinct biological species (they are genetically, ecologically, morphologically, and behaviourally distinct in sympatry), they merit recognition as two DUs independent from *G. aculeatus* as a whole.

It is appropriate and important that the status of both members of the pair be assessed in the same report for several reasons. First, the significance of the Paxton Lake stickleback pair rests on their distinctions and persistence in sympatry; neither form considered in isolation from the other is particularly unique within *Gasterosteus aculeatus* (although the Paxton Lake Benthic Threespine Stickleback shows greatly reduced pelvic skeleton development which is comparatively rare in sticklebacks, McPhail 1992). Second, interactions between them may contribute to their evolution and persistence. Third, the Limnetic and Benthic sticklebacks share common threats to their habitats, especially breeding habitats, and disturbance to such habitats could lead to increased hybridization between Limnetic and Benthic sticklebacks as has been documented for other sympatric pairs of *Gasterosteus* (Taylor *et al.* 2006).

Special significance

The significance of Paxton Lake Benthic and Limnetic Threespine Sticklebacks is primarily scientific and as a unique component of Canada' biodiversity. 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: evidence suggests that the species pairs have arisen since the end of the last glaciation, a mere 13,000 years ago (Schluter and McPhail 1992; McPhail 1994). The speed with which these distinct fish species evolved has intrigued and excited scientists around the world. They are remarkable research subjects and are being used to understand the biological and physical processes that give rise to the biodiversity we see around us. Newspapers, magazines and scientific journals have published the story of the discovery of these species, and regularly report on the results of ongoing scientific studies.

There is no direct commercial value of Paxton Lake Benthic and Limnetic Threespine Sticklebacks. The species are part of Canada's native fauna, with its own intrinsic value including its contribution to biodiversity, ecology, education and science.

DISTRIBUTION

Global range

Paxton Lake Benthic and Limnetic Threespine Sticklebacks are restricted to a single lake, Paxton Lake, on Texada Island, in the central Strait of Georgia region in southwestern British Columbia (Figure 2).

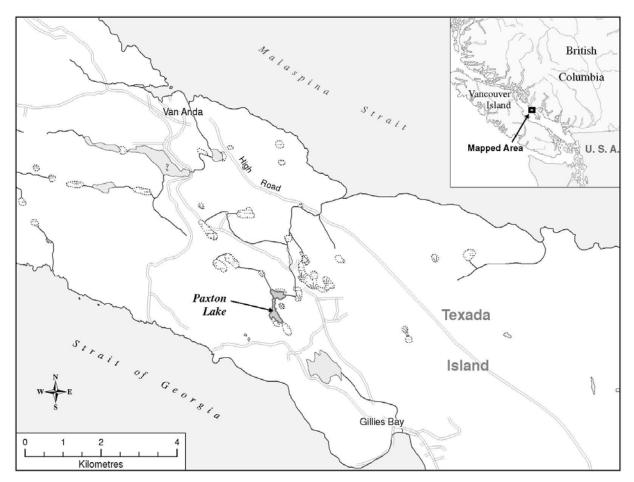


Figure 2. Distribution of Paxton Lake sticklebacks in Canada.

Canadian range

The Paxton Lake Benthic and Limnetic Threespine Sticklebacks are Canadian endemics; they are found in a single lake, Paxton Lake, on Texada Island, British Columbia (Figure 2). The Canadian and global ranges are identical. The extent of occurrence for each species is less than 0.31 km², and the area of occupancy less than 0.17 km². An index of area of occupancy calculated using a 1 km × 1 km overlaid grid was estimated to be less than 2 km², and less than 8 km² using a 2 km × 2 km grid (COSEWIC 2009).

HABITAT

Habitat requirements

Solitary stickleback populations (i.e., those populations for which a single form inhabits a lake) are widely distributed and generally tolerant of significant changes in habitat or water quality. In contrast, stickleback species pairs are highly restricted in their distribution and sensitive to changes in habitat or other environmental factors. As evolutionarily young species that are not yet intrinsically reproductively isolated from one another (i.e., they can produce viable hybrids), environmental changes can disrupt barriers to hybridization and lead to collapse of co-existing species into a hybrid swarm. Therefore, habitat requirements for stickleback species pairs include those same features that limit size or viability of solitary populations (e.g., juvenile rearing area, nesting habitat area), but also those features of the environment that prevent hybridization. In other words, habitat needs for species pairs include features whose alteration or loss will lead to reduction in abundance to an unviable population level, or breakdown of reproductive barriers sufficient to cause collapse into a hybrid swarm. These needs include moderate littoral and pelagic productivity, absence of invasive species, maintenance of natural light transmissivity, and maintenance of natural littoral macrophytes. The latter two are deemed especially important for maintaining mate recognition and are discussed in greater detail in Hatfield (2008).

Paxton Lake Benthic and Limnetic Threespine Sticklebacks have similar life histories, but different habitat requirements (McPhail 1993, 1994). These requirements vary throughout the year, and are described here for each major life stage. In general, Limnetic and Benthic sticklebacks spawn in littoral areas in the spring, feed and grow in pelagic and littoral areas in spring and summer, and overwinter in deep water habitats during the fall and winter.

Spawning habitat

Limnetic and Benthic sticklebacks 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. Benthics build their nests under cover of macrophytes or other structure; limnetics tend to spawn in open habitats (McPhail 1994; Hatfield and Schluter 1996).

Juvenile feeding habitat

Immediately after leaving the protection of paternal care, both limnetic and benthic fry use the littoral zone, where there is abundant food and cover from predators. The extent of habitat partitioning by benthic and limnetic fry is not understood well, but limnetic juveniles are common along steep, rocky, unvegetated littoral shoreline compared to benthic juveniles, which shelter around macrophytes (J. Gow pers. comm. 2008). Eventually, limnetics move offshore to feed in pelagic areas (Schluter 1995).

Adult feeding habitat

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

Overwintering habitat

By late summer, individuals move to deeper 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.

Habitat trends

Trends in habitat quantity and quality can be assessed only qualitatively, because there has been no long-term monitoring of habitat in Paxton Lake. A monitoring program began in June 2006 and measures the following on a monthly basis on Paxton Lake and nearby Priest Lake: surface temperature and pH, temperature and oxygen profiles, Secchi depth, and turbidity. No significant changes have been identified as a result of this monitoring up until the date of writing of this report (Atwood pers. comm. 2009).

Existing water licences permit substantial water extraction from Paxton Lake, though apparently water is not being diverted at present. Records of past water use are not available, so historic trends in water use cannot be determined accurately. Larson (1976) noted that water extractions from Paxton Lake caused severe drawdowns in the past (in excess of 3 m). A small dam at the lake outlet was built to increase storage for water use, which increased the overall lake area by about 1.5 m and flooded nearshore vegetation (Larson 1976). Nevertheless, industrial use of water has declined substantially 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 improved stability and productivity of littoral and pelagic habitats.

Land-based activities still have the potential to negatively affect within-lake habitats. For example, road building or other construction (such as limestone quarry expansion—see **Limiting factors and threats** section) can increase sedimentation via surface water inflows to the Paxton Lake. Mining (surface limestone quarrying) and forest harvest have been extensive in the Paxton Lake watershed, and continue today, but the influences of these land uses on stickleback and their habitats have not been quantified.

Habitat protection/Ownership

All lands adjacent to Paxton Lake are privately owned. At this time there are no habitat protection provisions specifically for the habitat of Paxton Lake Benthic and Limnetic Threespine Sticklebacks, although a local stewardship group has been established specifically to monitor and address threats to stickleback species pairs on Texada Island.

The Recovery Team for Stickleback Species Pairs has identified critical habitat for the species pairs, and a draft report has been reviewed and accepted by the Pacific Scientific Advice Review Committee, Fisheries and Oceans Canada (DFO). The report recommends critical habitat identification of the entire wetted area of Paxton Lake, plus a riparian buffer. The recommendation will be forwarded to DFO and subject to further review for consideration as critical habitat under SARA. In addition, the Paxton Lake watershed in general is afforded some protection from the federal *Fisheries Act* as well as the *BC Forest and Range Practices Act*.

BIOLOGY

Life cycle and reproduction

Benthic and limnetic sticklebacks have similar life histories (McPhail 1993, 1994), and approximate life history timing (Table 1). The observations below are taken from McPhail (1993, 1994) and the authors own personal observations.

Team for Stickleback Species Pairs 2007).	ery

		Jan	Feb	Mar	Apr	Mav	Jun	Iul	Aug	Sep	Oct	Nov	Dec
Species	Life Stage	1234	1234	1234		1 2 3 4	1234	1234		1 2 3 4	1234	1234	1 2 3 4
	Spawning				ХХХ	хххх	х						
	Incubation				хх	хххх	хх						
Limnetic	Juvenile rearing				х	хххх	хххх	хххх	хххх	хх			
	Adult rearing		хх	хххх	хххх	хххх	хххх	хххх	хххх	хх			
	Overwintering	хххх	хх							хх	хххх	хххх	хххх
	Spawning			ХХ	хххх	хх							
	Incubation			х	хххх	ххх							
Benthic	Juvenile rearing				хххх	хххх	хххх	хххх	хххх	хх			
	Adult rearing		хх	хххх	хххх	хххх	хххх	хххх	хххх	хх			
	Overwintering	хххх	хх							хх	хххх	хххх	хххх
		1 2 3 4	1234	1 2 3 4	1 2 3 4	1 2 3 4	1234	1 2 3 4	1 2 3 4	1 2 3 4	1234	1 2 3 4	1 2 3 4
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec

Life history information for both species comes from observations of wild and laboratory-reared populations, but the data are mostly anecdotal. Limnetics are thought to mature on average as one-year-olds, and rarely live beyond a single breeding season. In the lab, reproductive females have multiple clutches in quick succession, and are thought to do the same in the wild. Nesting males will mate with several to many females, and may nest more than once within a single breeding season.

Benthics delay sexual maturation relative to limnetics. Although some individuals likely mate in their first year, many may delay mating until they are two-year-olds. They may live up to about five years, and mate in several breeding seasons. In the lab, reproductive females have fewer clutches within a breeding season than do limnetics, and are thought to do the same in the wild. Nesting males will mate with several to many females, and may nest more than once within a single breeding season.

The sex ratio of both limnetics and benthics is approximately 1:1.

Limnetics and benthics are similar to other Threespine Sticklebacks in their overall mode of reproduction (McPhail 1994). Males construct nests, which they guard and defend, until fry are about a week old. Eggs take up to a week to hatch, depending on temperature, and another three to five days before larvae are free-swimming (McPhail 2007). The nests and contents remain vulnerable to predators of different kinds, including other sticklebacks (Foster 1994). Benthics build their nests under cover of macrophytes or other structure; limnetics tend to spawn in open habitats (McPhail 1994; Hatfield and Schluter 1996).

In the wild, benthics reproduce earlier in the year than limnetics, but there is considerable overlap in their spawning times (Table 1). There is strong assortative mating (Ridgway and McPhail 1984; Nagel and Schluter 1998; Boughman 2001), but as noted above, hybridization occurs naturally in the wild at a low rate.

Immediately after leaving the nest, both limnetic and benthic fry use inshore areas, where there is abundant food and cover from predators. Eventually limnetics move offshore to feed in pelagic areas (Schluter 1995). The timing of this movement is likely dictated by a combination of relative growth rates and predation risk in littoral and pelagic habitats (Schluter 2003). Benthics remain in littoral areas throughout their life.

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). By late summer, individuals begin moving to deeper water habitats where they overwinter.

Physiology

Physiological requirements and tolerances have not been described for Paxton Lake Benthic and Limnetic Threespine Sticklebacks. In general, Threespine Sticklebacks occur in a wide array of environments and they are known to have broad tolerances of many water quality characteristics (e.g., turbidity, water velocity, temperature, depth, pH, alkalinity, calcium and total hardness, salinity, conductivity, etc.). Paxton Lake itself is clear, slightly alkaline, moderately productive, and presumably minimally affected by toxic inputs. Concerns have been expressed (e.g., National Recovery Team for Stickleback Species Pairs 2007; Wood 2007) that deviations from these natural conditions pose a threat to persistence of the species pair, but the concern is usually expressed in connection with reproductive isolation between limnetics and benthics (e.g., mate recognition), rather than physiological tolerance *per se*.

Dispersal/Migration

Paxton Lake Benthic and Limnetic Threespine Sticklebacks do not migrate beyond the limits of Paxton Lake. A few individuals likely become entrained in the outlet stream, but these would be lost to the population and are likely of little consequence to general population dynamics. Within Paxton Lake, there are short-distance, seasonal movements associated with spawning, feeding and overwintering.

Interspecific interactions

Sympatric stickleback species pairs have evolved and persisted in the presence of only one other fish species, Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*; Vamosi 2003). Maintaining a simple ecological community appears to be necessary for persistence of the sympatric pairs, as underscored by the rapid extinction of the Hadley Lake species pair following introduction of Brown Bullhead (*Ameiurus nebulosus*; Hatfield 2001) and the collapse of the Enos Lake pair following the appearance of the American Signal Crayfish (*Pacifastacus leniusculus*; Taylor *et al.* 2006, Rosenfeld *et al.* 2008).

Current predation of sticklebacks in Paxton Lake is likely less than it was historically, since piscivorous Coastal Cutthroat Trout are now rare following damming of the outlet stream. The lake is inhabited by numerous invertebrates that feed on young sticklebacks, and is regularly visited by piscivorous birds (e.g., Heron (*Ardea herodias*), Kingfisher (*Megaceryle alcyon*) and Common Loon (*Gavia immer*)). Their presence, however, is not considered a threat to the sticklebacks.

The greatest interspecific competitors for limnetics are likely benthics, and vice versa. Several studies have demonstrated character displacement between limnetics and benthics, and competition between the two species (Schluter and McPhail 1993; Schluter 1994, 1995).

Adaptability

Paxton Lake has been subjected to considerable human disturbance, including damming of the outlet stream, water extraction for nearby mining, and the introduction of 5,000 of Coho Salmon (*Oncorhynchus kisutch*) in 1968 by government fisheries staff seeking to enhance sportfishing (they did not establish a self-sustaining population in the lake, Larson 1976). The lake's immediate surroundings have been affected by surface and underground mining and forest harvest which may have increased sedimentation and reduced riparian function. Paxton Lake limnetics and benthics have survived these disturbances, although each event has likely influenced stickleback abundance and it is unknown the extent to which limnetics and benthics can be considered "adaptable".

Simple population viability analyses were completed to determine critical habitat needs for benthic sticklebacks (Hatfield 2008). Benthics were selected for these analyses because they mature later, have lower natural abundance, and generally have lower reproductive potential than limnetics; results are therefore more conservative than if limnetics' vital rates had been used in the models. Population modelling using an age-structured model indicated that benthic sticklebacks are resilient to population perturbations from environmental stochasticity. In general, the modelling confirmed that high population growth rates allow sticklebacks to recover quickly from short-term, small to moderate environmental perturbations.

It is fairly straightforward to rear captive populations of Limnetic and Benthic sticklebacks where facilities are available (e.g., Hatfield and Schluter 1996). Both species have been successfully raised in laboratory tanks and experimental ponds at the University of British Columbia (UBC) over multiple generations. But it has been considerably more difficult to rear both species together. For example, in experimental ponds at UBC, limnetics and benthics hybridized at very high levels, which ultimately led to collapse into a hybrid swarm (D. Schluter, pers. comm. 2009).

The collapse of the species pair in Enos Lake and in the UBC experimental ponds has highlighted the sensitivity of the pairs to certain types of environmental perturbation such as the reduction of habitat complexity and variation in turbidity levels. Whereas population modelling indicates the sticklebacks are resilient to environmental perturbations, other observations indicate that continued reproductive isolation is contingent on environmental factors such as maintenance of habitat complexity and light transmission levels, which to date have been only qualitatively assessed. Yet, it is these other factors that appear to be dominant in maintaining the species pairs as distinct (see discussion in Taylor *et al.* 2006). In this context, the species pairs are not highly adaptable, and are not particularly resilient to environmental disturbance, particularly those that influence assortative mating.

POPULATION SIZES AND TRENDS

Search effort

Threespine sticklebacks are common in coastal marine and freshwater throughout the Northern Hemisphere. Physically and reproductively isolated populations exist in numerous low elevation lakes, but sympatric stickleback species pairs occur in only a handful of lakes within a highly confined geographic area in southwestern British Columbia (McPhail 1994). To date, genetic data indicate that each pair is independently derived from a marine ancestor (i.e., the pair in Paxton Lake is different from all other sympatric species pairs, Taylor and McPhail 2000). Biologists have surveyed hundreds of lakes along the BC, Washington and Alaska coasts and found stickleback species pairs in only this area of BC (McPhail 1994). Paxton Lake Benthic and Limnetic Threespine Sticklebacks are considered unique BC endemics.

Abundance

Only a single study has been conducted (Nomura 2005) to estimate abundance of benthics and limnetics in Paxton Lake. Estimates were made separately in June, July and September 2005, using mark-recapture methods, and the modified Peterson estimator. The results for June were considered the most robust ones owing to poor recapture rates in the later samples. Low capture success of limnetics contributed to relatively poor confidence in estimates of limnetic abundance (Table 2).

	Be	nthic		Lin	Both species		
	Reproductive Males	Other ¹	Total	Reproductive Males	Other ¹	Total	Total
N	3,332	29,307	29,380	45,853	8,199	58,800	66,599
lower Cl	2,243	21,360	4,421	25,806	2,593	34,712	53,208
upper Cl	5,305	41,428	39,230	83,981	15,603	102,295	85,483

Table 2. June 2005 abundance estimates of Paxton Lake limnetics and benthics (Nomura 2005).

(¹ The term "other" refers to both females and males that were not in nuptial colour, since they were difficult to differentiate in the field with non-lethal techniques.)

The estimates are based on standard mark-recapture techniques, which have a number of assumptions, such as closed population, sufficient longevity of marks, equal survival of marked and unmarked individuals, and capture success that is unrelated to presence of a mark or prior capture. Specifically in the case of sticklebacks, these estimates apply to individuals that can be caught with Gee (minnow) traps and therefore exclude young of the year (fish less than 1 year old). This method of capture likely underestimates abundance of limnetics, especially limnetic females, which tend to be somewhat trap "shy" and use primarily pelagic habitats where minnow traps are less effective. The estimates for Paxton Lake are considered reasonably good for mature benthics.

The abundance estimate of about 3,300 mature benthic males (Table 2) was somewhat surprising since Paxton Lake sticklebacks have been relatively easy to catch in Gee traps, and there had been a tacit assumption that abundance was higher. This estimate has led to additional caution regarding lethal and non-lethal sampling in the lake, and spurred collecting guidelines that restrict sampling to the southern half of the lake (Recovery Team for Non-Game Freshwater Fish Species in BC 2008).

Fluctuations and trends

There has been no systematic monitoring of abundance in Paxton Lake, so population trends are unknown. However, Paxton Lake Benthic and Limnetic Threespine Sticklebacks have been intensively studied by zoologists at UBC for the last two decades or more (e.g., Schluter and McPhail 1992; McPhail 1994; Taylor and McPhail 1999). Throughout this time both species have remained fairly easy to trap in large numbers in Gee traps.

Rescue effect

The global range of Paxton Lake Benthic and Limnetic Threespine Sticklebacks is entirely within a single lake in Canada, so the concept of rescue effect does not apply to these species.

ABORIGINAL TRADITIONAL KNOWLEDGE

At the time of this writing Aboriginal traditional knowledge (ATK) collection and verification protocols are still being finalized. Consequently, no ATK is presently available

LIMITING FACTORS AND THREATS

Threats to Paxton Lake Benthic and Limnetic Threespine Sticklebacks have been described in the National Recovery Strategy (National Recovery Team for Stickleback Species Pairs 2007). As noted in the Recovery Strategy, the discussion of threats is based primarily on professional opinion, not on quantitative risk assessment. This is because there is an absence of information on the effects of different threats on population vital rates (e.g., hybridization, growth, survival, reproductive success). The threats analysis is nevertheless deemed to be robust.

Invasive species

The primary threat to persistence of stickleback species pairs is spread of invasive species. (The term "invasive species" in this context refers to any species that is translocated, usually by humans, to a location where it does not occur naturally and where it causes harm to native 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 coastal cutthroat trout (Vamosi 2003).

The Hadley Lake species pair quickly became extinct following the introduction of Brown Bullhead (*Ameiurus nebulosus*), which is thought to have preyed on or interfered with nesting stickleback, ultimately leading to complete recruitment failure (Hatfield 2001). The Hadley Lake species pair had a total estimated population size approaching 50,000 (Hatfield 2008). Bullhead were introduced to Hadley Lake in the early 1990s and all stickleback were absent by 1995 (Hatfield 2001). This highlights the vulnerability of the stickleback species pairs and the speed with which a pair can be affected by an introduced species. The Enos Lake species pair has collapsed into a hybrid swarm owing to hybridization (Kraak *et al.* 2001; Taylor *et al.* 2006), and the recent appearance of the American Signal Crayfish has been implicated in causing this example of genomic extinction. The mechanism by which the crayfish affected sticklebacks appears to be through littoral habitat disturbance and alteration (Rosenfeld *et al.* 2008).

The threat of species introductions applies also to a number of other invasive 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. Bradford *et al.* (2008a, b) conducted qualitative risk assessments and concluded that for most regions of BC the probability of becoming widely established once arrived is high or very high, and the likely magnitude of ecological impact in small water bodies is very high. 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*). As discussed above (see Adaptability section), some species that are native to BC, but not naturally found in Paxton Lake (e.g., Coho Salmon) have been introduced to the lake in the past and can increase predation risk on sticklebacks.

Quantifying the threat of invasive species to Benthic and Limnetic Vananda Creek sticklebacks has not been undertaken, but there are a number of indications that the likelihood of introduction is high over a reasonable timeframe (i.e., 10 years or less). Although the species pair lakes are in a rural setting, they are readily accessible to the public. The main road on Texada Island runs adjacent to the eastern shore of Priest Lake and there is a publicly accessible boat launch. Boating and angling activity is light, but there is year-round use of Priest Lake by anglers targeting native Coastal Cutthroat Trout. Source populations for non-native fish species occur in many nearby lakes on the

mainland, Vancouver Island, and other islands in the Strait of Georgia. In fact, from 1980-2000 the distribution of invasive Smallmouth Bass has increased from 19 to 30 lakes and of Pumpkinseed Sunfish from 33 to 41 lakes on Vancouver Island alone (Hatfield and Pollard 2006). From 2000-2010, invasives have continued to spread. For instance, a total of 89 lakes on Vancouver Island now include one or more exotic (and probably invasive) species, Smallmouth Bass are now found in 50 lakes (vs. 30 in 2000), and Pumpkinseed Sunfish are now found in 55 lakes/streams and for the first time Largemouth Bass have been recorded in three lakes (S. Pollard, pers. comm. 2010). In addition, the Hadley Lake pair is located on an even more remote island (Lasqueti Island) and Brown Bullhead became established in that lake leading to the extirpation of the Hadley Lake species pair. There are no significant technical barriers to introducing non-native species should one wish to do so.

Water use

Existing water licences allow annual diversion of water from Paxton Lake of more than twice the volume of the lake, yet inflows are small due to limited catchment area and runoff. Severe drawdowns of Paxton Lake have occurred in the past as part of mining operations (up to 3 m, Larson 1976). Large fluctuations have impacts on littoral productivity and pelagic volume and would be expected to have a direct effect on sticklebacks, limiting both spawning and feeding habitats. The licences that were granted for industrial purposes do not appear to be in use at present, but they remain "active" in that the licences have not been retired.

Land use

There have been numerous land-based development activities within the Paxton watershed: forest harvest, mining and road building (Larson 1976; McPhail 1994). The main concerns from such activities include cumulative impacts on water quality 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. Concerns have also been expressed regarding runoff from nearby limestone quarrying operations, which use fertilizer-based explosives (National Recovery Team for Stickleback Species Pairs 2007). Furthermore, the quarry has encroached to within about 15 m of Paxton Lake in at least one place and long-term plans for the quarry include expansion, yet at present no management plan for such an expansion to prevent impacts (sedimentation, effects on riparian habitat) on Paxton Lake is in place (J. Rosenfeld, pers. comm. 2010).

Collections for research

Stickleback species pairs have been the focus of intense scientific study since the 1980s and there is an increasing demand for wild stock for use in laboratory-based studies and for permits to conduct *in situ* scientific study (The Recovery Team for Non-Game Freshwater Fish Species in BC 2008). Collecting activities have the potential to be a significant source of mortality for adult fish, and constitute a threat to the species

pairs that should be carefully managed. The Recovery Team for Non-Game Freshwater Fish Species in BC (2008) produced guidelines for the collection of stickleback species pairs that recommend limiting the number of individuals removed from Paxton Lake to 200 mature fish of each species and sex (i.e., 200 mature benthic males, 200 mature benthic females, 200 mature limnetic males, 200 mature limnetic females), limiting collecting activities to only half the lake, thorough cleaning of all sampling gear, and prohibitions on the use of hybrids or exotic species in any *in situ* studies.

<u>Other</u>

Impacts may occur from other activities, including illegal bait release from anglers, pollution from recreational boating, introduction of disease, and effects of climate change and pollution. These threats are of concern to the Recovery Team, but are believed to present a lower risk than the threats noted above.

Limits to Paxton Lake stickleback abundance are poorly understood. It is not known whether abundance is limited, singly or in combination, by food production, cover, predation, spawning habitat or other factors. The main limiting factor is probably food supply—the capability of the lake to produce plankton and benthos—but there are no data to support this view. In any case, limnetics and benthics are locally abundant, and not in apparent decline; the primary factor determining conservation status is their extreme endemism, not population decline.

EXISTING PROTECTION OR OTHER STATUS DESIGNATIONS

Paxton Lake Benthic and Limnetic Threespine Sticklebacks are listed as Endangered under Schedule 1 of the *Species at Risk Act* (SARA). Although the species are protected under *SARA*, there has as yet been no final approval of critical habitat for the Paxton Lake species pair and critical habitat, therefore, is not legally identified or protected.

Paxton Lake Benthic and Limnetic Threespine Sticklebacks were assessed as Endangered by COSEWIC in 2010, and are "red-listed" by the Conservation Data Centre and BC Ministry of Environment. Under the BC Sport Fishing Regulations, it is illegal to fish for, or catch and retain Paxton Lake Benthic and Limnetic Threespine Sticklebacks.

Paxton Lake Benthic and Limnetic Threespine Sticklebacks may benefit from the *Fisheries Act*, which provides DFO with powers, authorities, duties and functions for the conservation and protection of fish and fish habitat (as defined in the *Fisheries Act*). The *Fisheries Act* contains provisions that can be applied to regulate flow needs for fish, fish passage, killing of fish by means other than fishing, the pollution of fish-bearing waters, and harm to fish habitat. Environment Canada has been assigned administrative responsibilities for the provisions are administered by DFO.

At this time there are no habitat protection provisions specifically for Paxton Lake Benthic and Limnetic Threespine Sticklebacks. The Recovery Team for Stickleback Species Pairs has, however, identified proposed critical habitat for the species pairs, and a report has been accepted by the Pacific Scientific Advice Review Committee (DFO). The report recommended critical habitat identification of the entire wetted area of Paxton Lake, plus a riparian buffer, and is subject to further approval processes. Consequently, although from a scientific perspective critical habitat has been proposed, it is not yet identified from a legal perspective. In addition, the provincial *Riparian Areas Regulation* provides some protection for riparian areas around the lakes. All lands adjacent to Paxton Lake are privately owned, so the *BC Forest and Range Practices Act*, which has provisions to protect fish habitat from forestry activities, does not apply.

ACKNOWLEDGEMENTS AND AUTHORITIES CONSULTED

The author wishes to acknowledge and thank the Recovery Team for Non-game Freshwater Fish Species in BC for their time and efforts toward conservation of native fish species at risk. Substantial thanks are also due to the many scientists who have worked diligently on the biology of stickleback species pairs and to reviewers of this report.

INFORMATION SOURCES

- Atwood, T. 2009. Coordinator, Texada Stickleback Group, pers. comm. to T. Hatfield, 2009.
- Boughman, J. W. 2001. Divergent sexual selection enhances reproductive isolation in sticklebacks. Nature 411:944-947.
- Bradford, M.J., C.P. Tovey, and L.M. Herborg. 2008a. Biological risk assessment for Yellow perch (Perca flavescens) in British Columbia. Canadian Science Advisory Secretariat (CSAS) Research Document 2008/073. Available online: http://www.dfo-mpo.gc.ca/csas/
- Bradford, M.J., C.P. Tovey, and L.M. Herborg. 2008b. Biological risk assessment for Northern pike (Esox lucius), Pumpkinseed (Lepomis gibbosus), and Walleye (Sander vitreus) in British Columbia. Canadian Science Advisory Secretariat (CSAS) Research Document 2008/074. Available online: <u>http://www.dfompo.gc.ca/csas/</u>
- Canadian Endangered Species Conservation Council (CESCC). 2006. Wild Species 2005: The General Status of Species in Canada. Ottawa: Minister of Public Works and Government Services Canada.
- COSEWIC. 2009. Committee on the Status of Endangered Wildlife in Canada (COSWIC) Operations and Procedures Manual April 2009 CWS, Ottawa.

- 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.
- Gow, J.L., C.L. Peichel and E.B. Taylor. 2007. Ecological selection against hybrids in natural populations of sympatric threespine sticklebacks. Journal of Evolutionary Biology 20: 2173–2180.
- Gow, J.L., S.M. Rogers, M. Jackson, and D. Schluter. 2008. Ecological predictions lead to the discovery of a benthic-limnetic sympatric species pair of threespine stickleback in Little Quarry Lake, British Columbia. Canadian Journal of Zoology 86:564-571.
- Gow, J.L. University of British Columbia Department of Zoology. Email to T. Hatfield, 2008.
- Hatfield, T. 2001. Status of the stickleback species pair, *Gasterosteus aculeatus*, in Hadley Lake, Lasqueti Island, British Columbia. Canadian Field-Naturalist 115:579-583.
- Hatfield, T. 2008. Identification of critical habitat for sympatric stickleback species pairs and the Misty Lake parapatric stickleback species pair. Draft report for review by the Pacific Scientific Advice Review Committee (PSARC), Fisheries and Oceans Canada.
- Hatfield, T. and D. Schluter. 1996. A test for sexual selection on hybrids of two sympatric sticklebacks. Evolution 50:2429-2434.
- Hatfield, T. and D. Schluter. 1999. Ecological speciation in sticklebacks: environmentdependent hybrid fitness. Evolution 53:866-873.
- Hatfield, T. and S. Pollard. 2006. Non-native freshwater fish species in British Columbia. Biology, biotic effects, and potential management actions. Report prepared for Freshwater Fisheries Society of British Columbia, Victoria BC
- 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.
- McKinnon, J.S. and H.D. Rundle. 2002. Speciation in nature: the threespine stickleback model systems. Trends in Ecology & Evolution 17:480-488.
- 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. 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.
- McPhail, J.D. 2007. The freshwater fishes of British Columbia. University of Alberta Press, Edmonton, AB.
- Nagel, L. and D. Schluter. 1998. Body size, natural selection, and speciation in sticklebacks. Evolution 52:209-218.
- National Recovery Team for Stickleback Species Pairs. 2007. Recovery Strategy for Paxton Lake, Enos Lake, and Vananda Creek Stickleback Species Pairs (*Gasterosteus aculeatus*) in Canada. *Species at Risk Act* Recovery Strategy Series, Fisheries and Oceans Canada, Ottawa. v + 31 pp.
- NatureServe. 2009. NatureServe explorer: an online encyclopedia of life. Version 1.8. NatureServe, Arlington VA. Available <u>http://www.natureserve.org/explorer</u>. (Accessed: July 2009).
- Nomura, M. 2005. Population study of Paxton Lake stickleback species pair 2005. unpublished data report.

Recovery Team for Non-Game Freshwater Fish Species in BC. 2008. Guidelines for the collection and in situ scientific study of stickleback species pairs (*Gasterosteus aculeatus*). 3 May 2008. available online: http://www.zoology.ubc.ca/~schluter/stickleback/stickleback_species_pairs/other%

20stickleback%20files/Guidelines%20for%20the%20Collection%20and%20In%20 Situ%20Scientific%20Study%20of%20Stickleback%20Species%20Pairs.pdf

- Reimchen, T.E. 1989. Loss of nuptial color in threespine sticklebacks (*Gasterosteus aculeatus*). Evolution 43:450-460.
- Reimchen, T.E. 1994. Predators and morphological evolution in threespine stickleback. Pages 399-437 in M. A. Bell and S. A. Foster, editors. The evolutionary biology of the threespine stickleback. Oxford University Press, Oxford, UK.
- Ridgway, M.S. and J.D. McPhail. 1984. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): mate choice and reproductive isolation in the Enos Lake species pair. Canadian Journal of Zoology 62: 1813-1818.
- Rosenfeld, J., K. Campbell, E. Leung, and J. Bernhardt. 2008. Effects of alien crayfish on macrophytes and benthic invertebrates in Enos Lake: implications for hybridization of limnetic and benthic stickleback species pairs. Interim Report for BC Forest Science Program Project Y081209.
- Rosenfeld, J.R. BC Ministry of the Environment, Vancouver, BC. Email correspondence to E. Taylor, January, 2010.
- 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.
- Schluter, D. University of British Columbia Department of Zoology. Personal communication to T. Hatfield. 2009.
- Scott, W.B., and E.J. Crossman. 1973. Freshwater fishes of Canada. Bulletin of the Fisheries Research Board of Canada 184.
- Taylor, E.B. and J.D. McPhail. 1999. Evolutionary history of an adaptive radiation in species pairs of threespine sticklebacks (*Gasterosteus aculeatus*). Biological Journal of the Linnean Society 66: 271–299.
- 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.
- Taylor, E.B., J.W. Boughman, M. Groenenboom, M. Sniatynski, D. Schluter and J.L. Gow. 2006. Speciation in reverse: morphological and genetic evidence of the collapse of a three-spined stickleback (*Gasterosteus aculeatus*) species pair. Molecular Ecology 15: 343–355.
- Vamosi, S.M. 2003. The presence of other fish species affects speciation in threespine sticklebacks. Evolutionary Ecology Research 5:717-730.
- Wood, P.M. 2007. Core area scenarios for Vananda Creek Wildlife Habitat Area. report for BC Ministry of Forests and Range.
- Wooton, R.J. 1976. The biology of the sticklebacks. Academic Press, London, UK.

BIOGRAPHICAL SUMMARY OF REPORT WRITER

Todd Hatfield is a consulting biologist, based in Victoria, British Columbia. In 1995, he completed a Ph.D. at UBC, focusing on the evolutionary ecology of Paxton Lake Benthic and Limnetic Threespine Sticklebacks. His consulting work focuses on applying scientific methods and decision-making techniques to the resolution of natural resource management issues and environmental conflicts. He works extensively on species at risk and water management issues. Since 2003, he has coordinated the Recovery Team for Non-game Freshwater Fish Species in BC.

COLLECTIONS EXAMINED

No museum collections were examined for this report.