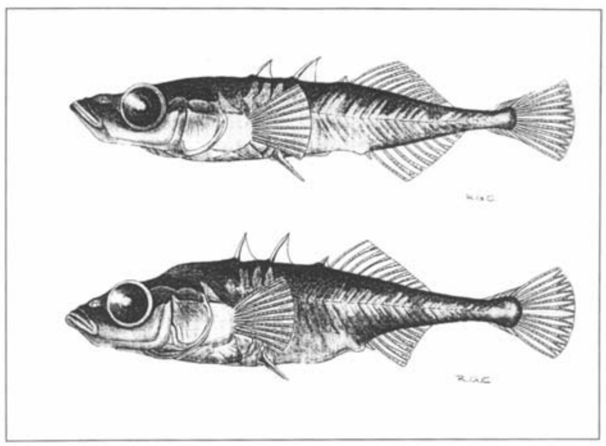
COSEWIC
Assessment and Update Status Report

on the

Enos Lake Stickleback Species Pair
Gasterosteus spp.

Limnetic Enos Lake Stickleback
Benthic Enos Lake Stickleback

in Canada



ENDANGERED
2002

COSEWIC
COMMITTEE ON THE STATUS OF
ENDANGERED WILDLIFE
IN CANADA

COSEPAC
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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:

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Previous report:

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Également disponible en français sous le titre Évaluation et Rapport du COSEPAC sur la situation de l'épinoche benthique du lac Enos (*Gasterosteus* spp.) et l'épinoche limnétique du lac Enos (*Gasterosteus* spp.) au Canada – Mise à jour.

Cover illustration:
Enos Lake stickleback — Limnetic (upper) and benthic (lower) forms of the Enos Lake Stickleback species pair, *Gasterosteus* spp. Drawings courtesy Westlands Resources Group, Vancouver, B.C.

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COSEWIC
Assessment Summary

Assessment summary — November 2002

Common name
Benthic Enos Lake stickleback

Scientific name
Gasterosteus spp.

Status
Endangered

Reason for designation
These fish are restricted to a single, small lake on Vancouver Island and are experiencing severe decline in numbers due to deteriorating habitat quality and the introduction of exotics.

Occurrence
British Columbia

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

Assessment summary — November 2002

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COSEWIC
Executive Summary

Enos Lake Stickleback Species Pair
Gasterosteus spp.

Species Information

Sticklebacks in Enos Lake independently evolved into limnetic and benthic populations. Populations in four other lakes near Georgia Strait similarly possess limnetic/benthic species pairs. Those in Hadley Lake have already become extinct. Historically, Enos benthic and limnetics typically exhibited <1-2% hybridization. During 1999 or 2000, hybridization rates reached 12%. Unpublished data of University of British Columbia researchers suggest hybridization could have approached 20%. Limnetics are more slender and have longer gill rakers adapted for capturing plankton than have bottom feeding benthics. Gene loci and associated allozyme frequencies distinguish these populations and suggest distinct Evolutionary Significant Units. Although other *Gasterosteus* populations may share similar morphology and feeding strategies, none have trophic or reproductive isolating mechanisms allowing such close sympatry as those described in this report. Instances of hybridization were deduced in large part on morphological traits that are found in limnetic/benthic species pairs. Allozyme frequencies and mitochondrial DNA demonstrate genetic differences between limnetic and benthic populations. D. Schluter, University of British Columbia, provided much of the significant information. Some genetic analyses on Enos stickleback hybridization were not available or complete at the time of writing this report.

Distribution

Enos limnetic and benthic sticklebacks occur only in Enos Lake, a small water body near Nanoose Bay on Vancouver Island. Other limnetic/benthic populations occur on other islands of the nearby Strait of Georgia; however, they evolved independently from marine sticklebacks and do not represent immigrants from other limnetic/benthic lake populations. Other morphological types of *Gasterosteus* occur in the interconnected outlet stream and swampland downstream; however, they were isolated from the lake by a dam built in 1958, or earlier, and could have had closer contact in the past. *Gasterosteus aculeatus* also occur in small ponds along nearby ridges and would normally be isolated from Enos Lake except when perturbations (i.e., housing developments or rain storms) divert temporary drainages into Enos Lake.

Habitat

During the warmer productive months, limnetics feed on plankton in mid-water above the deeper portions of the lake. Benthics frequent areas nearer the shoreline or bottom and feed on benthic organisms. An anoxic hypolimnion at deeper depths excludes fish from deeper water during the warmer summer months. During cooler winter months and the breeding season, both forms orient closer to bottom and littoral habitats.

Biology

Both limnetics and benthics have essentially the same life cycle as other freshwater *Gasterosteus aculeatus.* Major exceptions are that the small sized limnetics are adapted to capturing planktonic prey and the larger benthics utilize food resources nearer the bottom and shoreline. Limnetics mature faster, breed earlier and do not live as long. Each population chooses different shoreline habitats when breeding. The biggest difference from most other *Gasterosteus* populations is the development of trophic and reproductive isolating mechanisms that have maintained their historic genetic integrity in sympatry.

Population Sizes and Trends

Previous population estimates ranged up to 100,000 with recent hybridization being in the order of 1 or 2%. However, such numbers become less relevant if hybridization rates rise exponentially due to deteriorating environments. Estimates of hybridization based on morphometric studies were 10 to 20% in 2001-2002, and are likely to increase if present habitat changes are not compensated or reversed. Although previous researchers estimated higher population numbers, limnetic sticklebacks are proportionately fewer due to the reduced area of limnetic habitat. An anoxic hypolimnion forces fish to inhabit surface waters during the summer. Population size becomes irrelevant if numbers are being exponentially reduced in the face of hybridization.

Limiting Factors and Threats

The Enos species pair occurs only in one lake. Historically, each population adapted to different resources and reproductive behaviours through strong competition and natural selection disfavoring hybrid survival. Current hybridization is likely due to habitat changes which are detrimental to the limnetic/benthics, thus creating more space for hybrids to survive. Introduced crayfish (*Pacifastacus leniusculus*) have increased dramatically and may have altered habitat. Sticklebacks are vulnerable to the introductions of exotic species such as catfish (*Amiurus nebulosus*), which have already eliminated the Hadley Lake species pair. Real estate and golf course development potentially threaten the Enos Lake populations. Control of lake level with a small dam requires careful regulation so as not to raise water too quickly during the spring when sticklebacks breed in very shallow water. Wave wash from dam-raised water might erode banks and cloud water and thus impair visual cues that sticklebacks behaviorally respond to during reproduction. The future for the survival of Enos limnetic and benthic sticklebacks depends on land-use negotiations to moderate impacts from urban development, and in particular restricted use of Enos Lake in the face of renewals of water licences with clauses that expired on December 31, 2001 and have since been renewed.

Special Significance

The Enos Lake species pair is the first known sympatric species pair of *Gasterosteus*. They represent a major example of evolutionary processes and have received extensive scientific interest and represent textbook examples of how species evolve.

Existing Protection

There is little specific protection beyond existing environmental and water quality regulations. Though the law restricts the transport of native fishes British Columbia, exotic fish species are still illegally transported in that province. Local water, environmental and fishery authorities are well versed in the issues of Enos Lake, as is the landowner. Given the urgency of the Enos Lake situation, provincial fisheries authorities within the BC Ministry of Water, Lands and Parks, as well as Fisheries and Oceans Canada, sponsored a workshop during 2002 on conservation and restoration of stickleback species pairs in British Columbia.

COSEWIC MANDATE

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) determines the national status of wild species, subspecies, varieties, and nationally significant populations that are considered to be at risk in Canada. Designations are made on all native species for the following taxonomic groups: mammals, birds, reptiles, amphibians, fish, lepidopterans, molluscs, vascular plants, lichens, and mosses.

COSEWIC MEMBERSHIP

COSEWIC comprises representatives from each provincial and territorial government wildlife agency, four federal agencies (Canadian Wildlife Service, Parks Canada Agency, Department of Fisheries and Oceans, and the Federal Biosystematic Partnership), three nonjurisdictional members and the co-chairs of the species specialist groups. The committee meets to consider status reports on candidate species.

DEFINITIONS

Species	Any indigenous species, subspecies, variety, or geographically defined population of wild fauna and flora.
Extinct (X)	A species that no longer exists.
Extirpated (XT)	A species no longer existing in the wild in Canada, but occurring elsewhere.
Endangered (E)	A species facing imminent extirpation or extinction.
Threatened (T)	A species likely to become endangered if limiting factors are not reversed.
Special Concern (SC)*	A species of special concern because of characteristics that make it particularly sensitive to human activities or natural events.
Not at Risk (NAR)**	A species that has been evaluated and found to be not at risk.
Data Deficient (DD)***	A species for which there is insufficient scientific information to support status designation.

* 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.

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.

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Canada

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

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2002

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SPECIES INFORMATION

Name and Classification

Phylum:	Chordata chordates
Class:	Actinopterygii rayed fishes
Order:	Gasterosteiformes gasterosteiform fishes
Family:	Gasterosteidae sticklebacks
Genus:	*Gasterosteus* threespine sticklebacks
Species A	sp. – "L" limnetic population
Species B	sp. – "B" benthic population
Common names:	Enos Lake limnetic stickleback
	Enos Lake benthic stickleback
Both populations	Enos Lake sticklebacks - épinoches du lac Enos
Hybrids:	sp.– "L x B" Enos Lake limnetic x benthic sticklebacks

*Note: "Limnetic" refers to sticklebacks inhabiting open, mid-water habitats; "benthic" refers to those frequenting near bottom habitats. See Table 1 for list of differentiating features.

Enos Lake sticklebacks (Figs. 1, 2 and 3) have not been assigned scientific names by COSEWIC, BC Conservation Data Centre (i.e., Cannings and Ptolemy 1998) or other authorities. Divergent morphology between benthic and limnetic sticklebacks evolved independently in five coastal lakes of British Columbia. They provide separate examples of parallel evolution converging toward similar morphology and life styles within each lake. Application of traditional scientific nomenclature for populations in each lake is impractical. Limnetics and benthics occur in Enos, Hadley, Paxton, Emily and Balkwill lakes as limnetic/benthic species pairs adapted to similar ecological niches, each pair behaving as independent Evolutionary Significant Units and having different mitochondrial DNA and/or allozyme frequencies.

Description

McPhail (1984) separated Enos limnetics and benthics on the basis of allele frequencies at three loci (*Mdh-3*, *Ck* and *Pgm*) and stated that the *Mdh-3* locus was polymorphic in limnetic sticklebacks and fixed in benthics (see Table 1). He suggested that each morph maintained itself as a discrete entity, that there is no evidence of significant gene flow between them, and that they are distinct biological species. Ridgway and McPhail (1984) emphasized the fact that *Mdh-3* frequencies indicated some gene flow and hybridization in limnetics, but frequencies were fixed at 100% in benthics, implying no hybridization. Gene frequencies differ at two polymorphic loci for Enos Lake and four of five loci for Paxton Lake limnetic and benthic populations (*see* Kraak et al. 2001). Taylor and McPhail (1999) state that mtDNA haplotype frequencies exist between limnetics and benthics in Enos, Priest and Emily lakes, but not in Paxton Lake.

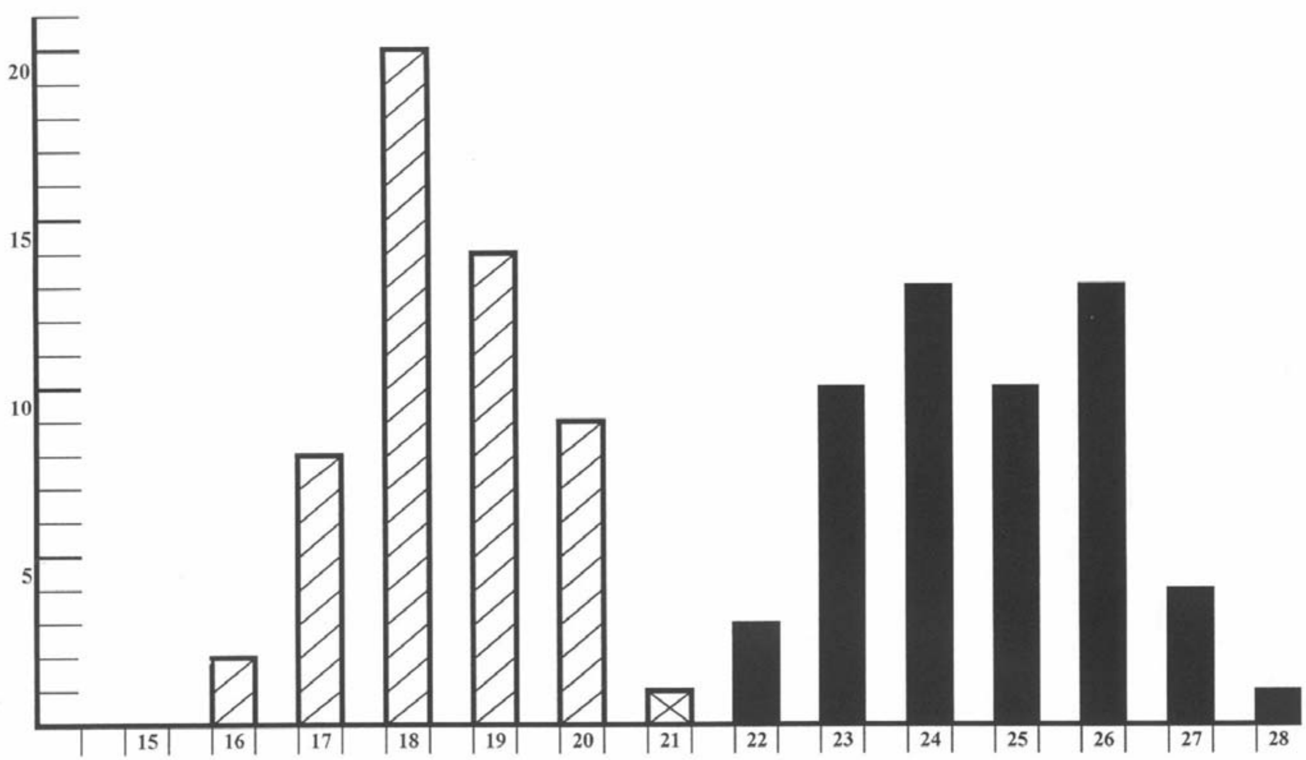

Figure 1. Distribution of gill raker numbers in Enos Lake sticklebacks (McPhail 1984, as redrawn from Kraak, et al. 2001). Vertical axis indicates number of specimens; horizontal axis, number of gill rakers; dark bars, limnetic sticklebacks; cross-slashed bars, benthics**;** bar with “X” in centre, intermediate specimen**.**

Table 1. Diagnostic features separating limnetic from benthic sticklebacks in Enos Lake (McPhail 1984). Numbers in parentheses indicate standard deviation.

Characteristic	Electromorph	Limnetic	Benthic
Dorsal spine no.:		Mean = 2.70 (0.46)	Mean = 3.03 (0.33)
Anal pterygiophore no.:		Mean = 11.0 (0.56)	Mean = 9.45 (0.76)
Gill raker number:		Mean = 25.9 (1.49)	Mean = 18.5 (1.09)
Electrophoretic loci:			
Ck	100	0.036	0.940
"	85	0.964	0.060
Mdh-3	100	0.822	1.000
"	55	0.178	0.000
Mdh-1	100	1.00	1.00
"	82	0.000	0.000
Pgi-1	100	1.00	1.00
"	105	0.00	0.00
Pgi-2	100	o.944	0.920
"	147	0.056	0.080
Pgm	100	0.558	0.573
"	103	0.010	0.403
"	93	0.000	0.000
"	90	0.432	0.024
"	80	0.000	0.000
Reproductive colour:		Males with red throats and blue backs	males black
Feeding habitat:		Females obligatory plankton feeders; Males, usually plankton feeding	Feeds on benthic organisms
Habitat		Much of the year in mid-water	Normally near bottom

Table 2. Comparison of physical dimensions of five lakes possessing limnetic and benthic species pairs of *Gasterosteus*.

Lake	Area	Elevation	Volume	Length	Width	Depth
Enos (2001)#	17.6 ha.	46 to 48 m		1400 m	200 m	max. = 11m
Balkwill*	11.5 ha.	approx. 80 m	584 acre ft+	948 m	199 m.	mean = 6.28 m; max = 14.3 m
Emily		40 m				
Priest*	44.1 ha	approx. 80 m	1849 acre ft+	1590 m	367 m	mean = 5.4 m; max. = 16.5 m
Paxton*	27.6 ha	61 m	554 acre ft+	764 m	irregular	mean = 20.3 ft; max. = 13.1 m
Hadley				700 m approx.	irregular	max. = 15+ m

#data from either Brown (2000) or McPhail (1984, 1985)
*data from BC Fish and Wildlife maps illustrated by Schluter's Univ. BC Web Page (2001)
+acre ft = official measure for water storage in BC registry for water use

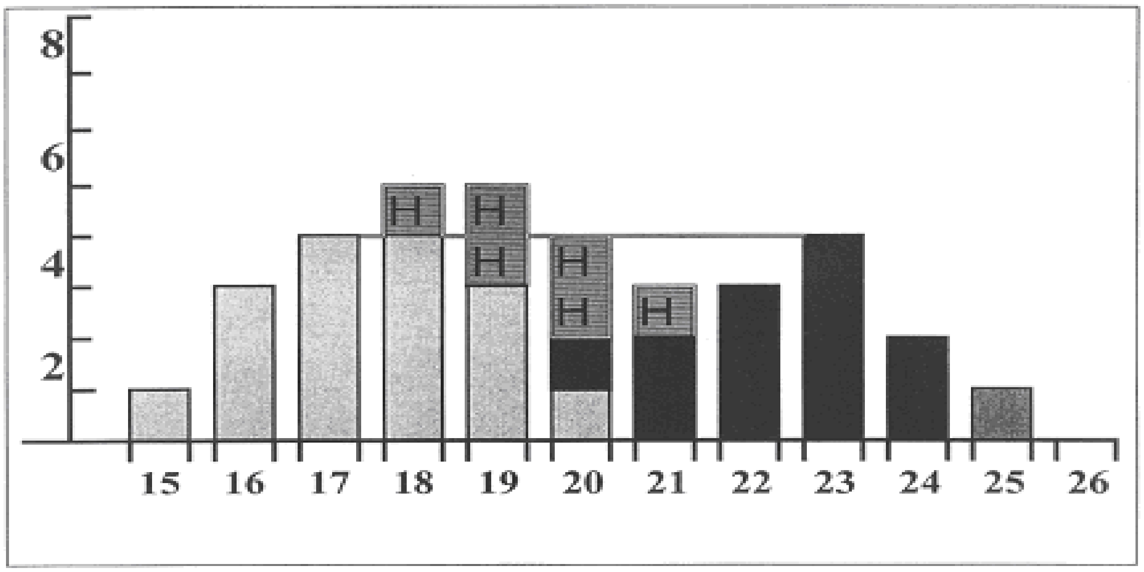

Figure 2. Distribution of gill raker numbers in Enos Lake sticklebacks (redrawn from Kraak, et al. 2001). Cross-slashed bars = benthics; black bars = limnetics; gray bars = hybrids. Stippled background indicates approximate distribution of hybrids as shown to writer a year later (Schluter pers. comm. 2001); note decreased bimodality of data, minimizing uniqueness of benthic and limnetic populations. Based on Schluter's observation and data, there appears to be the beginning of a hybrid swarm requiring confirmation and immediate contingent restorative planning for the population.

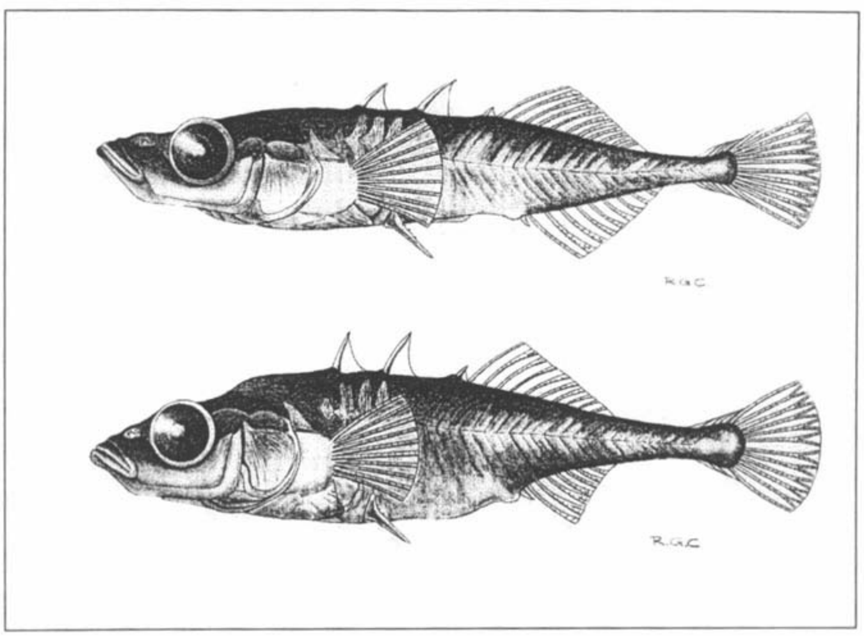

Figure 3. *Gasterosteus* species pair from Enos Lake: "Limnetic" above; "Benthic" below.

Hatfield (1997) verified McPhail's (1984) observation of limnetics having longer and more numerous gill rakers, more lateral plates, longer pelvic fin spines and smaller (slender) bodies. Benthics apparently have shorter jaws and smaller eyes and are adapted morphologically and behaviorally for feeding on macrobenthos in littoral habitats, whereas limnetics are adapted for planktivory in the limnetic zone of lakes (*see* Kraak et al. 2001). Schluter (2000) traced the presumed evolution of *Gasterosteus* species pairs and repeats McPhail's observation that each species pair was formed by a process of double invasion and character displacement after Pleistocene Glaciation. A key part of Enos evolutionary history was that an intermediate form resulting after the first invasion of a marine ancestor was displaced toward a more benthic lifestyle at the time when a second invasion of marine sticklebacks occurred. The second invader did not evolve an intermediate phenotype like that attained the first time, but instead retained a shape closer to that of the marine ancestor. Recent changes to Enos Lake have disrupted this 10,000 + years of evolutionary divergence, as evidenced by the present interbreeding population. Sediment cores for Enos Lake indicate sand prior to 12,840 years before present (ybp); clay and marine shell in deposits between 12,840 and 11,624 ybp (Brown 2000). Subsequent strata did not show marine deposits to support postulation of a second *Gasterosteus* invasion (McPhail 1984), although sticklebacks could have accessed Enos Lake, if sea levels were high enough to overcome waterfall barriers downstream and allow upstream dispersal into Enos Lake. Westland Resource Group (1998) noted molecular genetic analyses demonstrating genetically distinct units between different species pairs of stickleback (see Withler and McPhail, 1985; Orti et al. 1994; and Taylor et al. 1997). See McPhail (1984) regarding genetic differentiation between benthics and limnetics.

Figure 1 and Table 1 numerically compare characters differentiating benthic and limnetic sticklebacks (McPhail 1984). Historically, hybridization in Enos lake was less than 1% (McPhail 1984: Ridgway and McPhail 1984). In 1999, a breakdown of ecological and reproductive isolating mechanisms occurred between limnetic and benthic sticklebacks in Enos Lake (Fig. 2). Amongst 49 fish, 6 (12%) were hybrids (Kraak et al. 2001). Amongst males, 16 were benthics, 13 limnetics, and 6 (17%) were hybrids (Figure 2). The shaded area behind these bars approximates unpublished results suggested during the writer's conversation with Schluter (D. Schluter, Department of Zoology and Centre for Biodiveristy Research, University of British Columbia, Vancouver, B.C.; 2001 personal communication) in which hybrids may actually comprise from 15 to 20% of samples. Unfortunately Schluter's data are not yet published. These results also raise concern for possible genetic swamping of the historic genome. This factors suggest need for planning the population's restoration and stimulated a workshop sponsored by the Biodiversity Branch, BC Ministry Water, Lands and Air Protection and Fisheries and Oceans Canada (Rankin and Bicego 2002 draft report); the conclusions were not published.

Swamp habitats along the seasonal outlet stream below Enos Lake support another morph of *Gasterosteus* (Fig. 4). Their relationship to benthics and limnetics is unknown; however, they probably represent the regular, ubiquitous sticklebacks typical of most freshwaters in nearby coastal regions. Although this morph is not presently known from the lake itself, the significance of past genetic introgression into lake-populations is likely minimal, but unknown. Historically there must have been gene flow between lake, stream and swamp. Each Enos morph must have coexisted at various times with this ubiquitous potential immigrant and resisted genetic introgression if populations accessed the lake. Competitive niche partition appears to have historically allowed limnetics and benthics to persist without significant interbreeding.

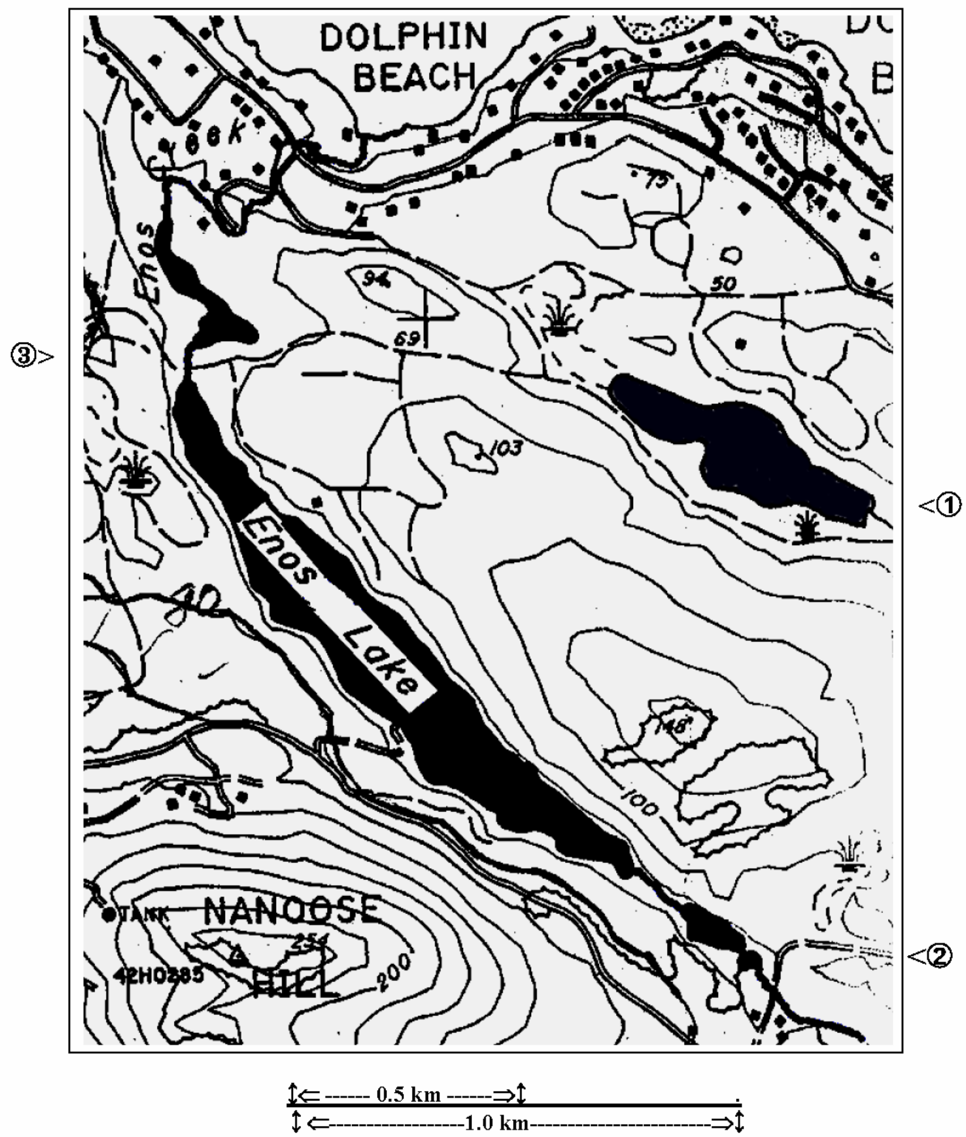

Figure 4. Contour map of lands surrounding Enos Lake. Lakes and tributaries in black ink. Dolphin Lake (left of “1”). Elevation contours at 25m intervals indicated by thin (solid) black lines. Road crossing intermittent creek draining into Enos Lake (opposite “2”, lowest right corner). Black squares (“■“) indicate housing. Existing golf course contacts western-most end of Dolphin Lake. Dashed lines near lake indicate footpaths and potential roads. Area of swamps occurs along creek to right of “3”, immediately north of Enos Lake. Dam occurs at outlet, right of “3”.

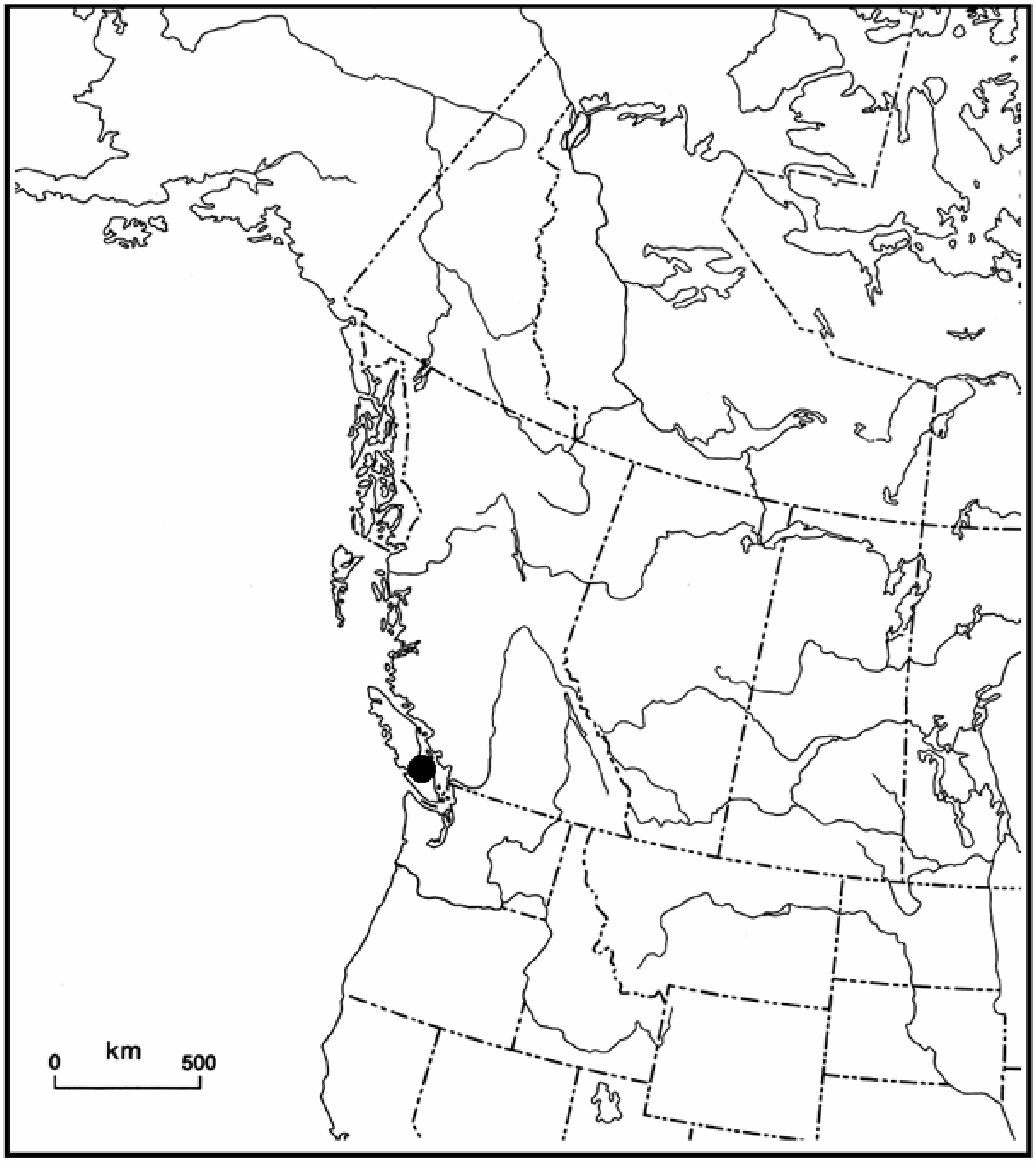

Figure 5. Large black “DOT” indicates approximate location of Enos Lake on Vancouver Island**.**

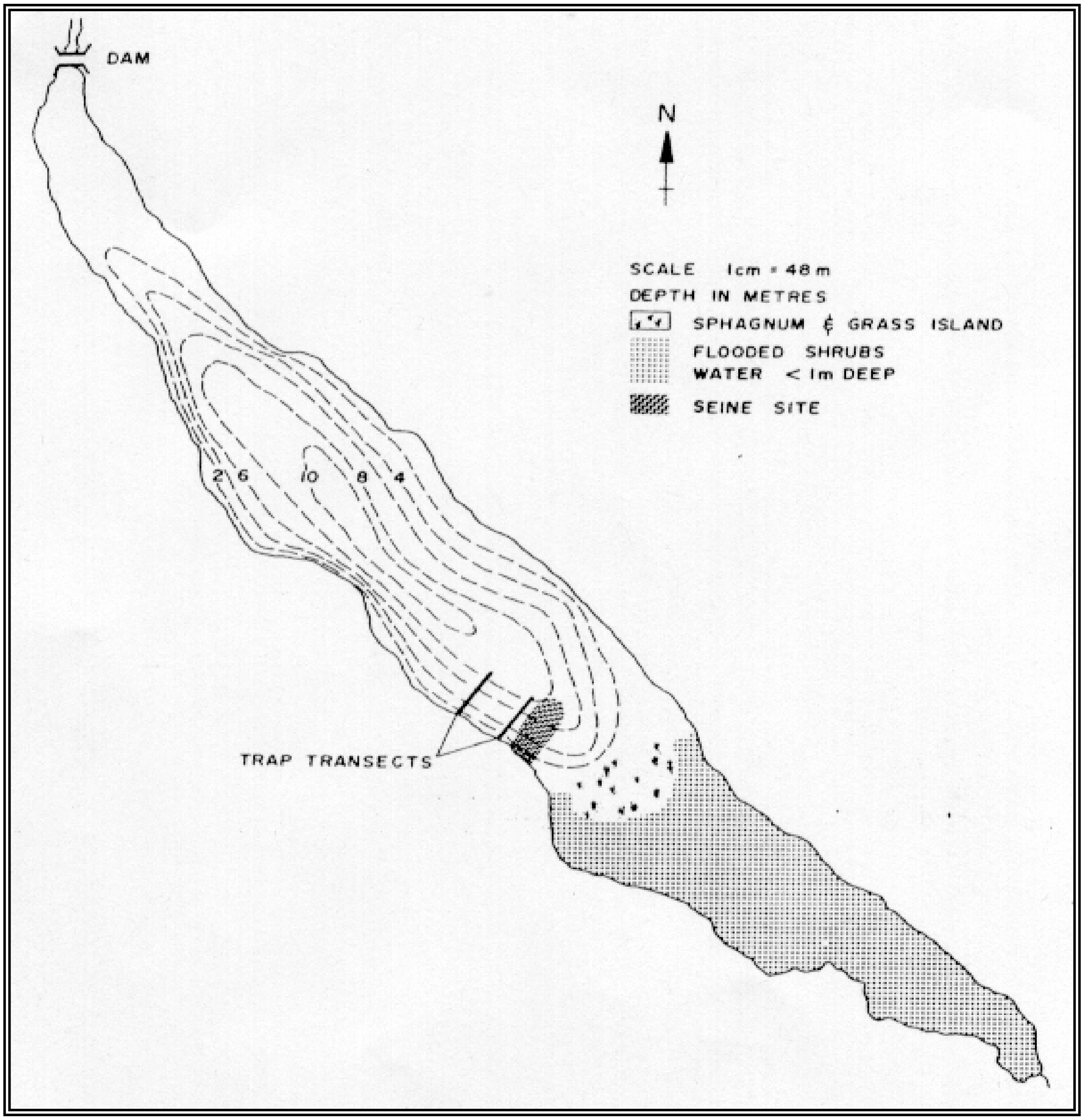

Figure 6. Map of Enos Lake from McPhail (1984, 1985) showing depth contours, shallow swamp and brush at south end (large shaded area), zone of sphagnum moss indicated by dotted area. Transects from McPhail's survey indicated with small area of seining shown next to transects Dam is indicated at north end of lake.

DISTRIBUTION

The Enos Lake species pair of sticklebacks is confined to Enos Lake (Figs. 4, 5 and 6), situated north of Nanoose Bay on Vancouver Island (McPhail 1984). Though similar in life history, they are independent of other lake dwelling species pairs of *Gasterosteus* because of separate evolutionary origins. They are the only known limnetic/benthic species pair on Vancouver Island. Other independently derived populations include Paxton, Priest, Balkwill, Emily and Hadley lakes on Lasqueti and Texada islands in the Strait of Georgia (McPhail 1984).

The northern two thirds of Enos Lake have deeper water, where the focus of limnetic vs. benthic studies has concentrated, and where evolutionary processes may have arisen and competitive natural selection been more intense (see Figs. 6 and 7 regarding water depth). Seasonal use of the southern third of the lake is not well documented, although limnetics are likely absent (published documents do not note all sites of capture within the lake). Prior to a one-meter rise of water from the dam built in the 1950s, or earlier, (McPhail 1984), the shallower, southern portions would have been more exposed and not representative of that found today. Rates of natural sedimentation suggest the area of shoreline and limnetic habitat would have been deeper much more extensive at the time the populations first invaded Enos Lake (*see* Brown 2000).

Sticklebacks were observed stranded in small pools below the outlet during a very dry summer in September 2001. Whether these downstream populations could move freely, in and out of the lake before dam construction, is unknown. Neither population is known to be in contact with other populations along ridges above the lake where drainages normally flow away from Enos Lake, although land reconfiguration for new roads or housing could redirect flow toward Enos Lake. Beaver dams are reputed to have flooded the lower portions of Enos Creek in the past, and could have been a factor in spreading sticklebacks upstream. McPhail (1984) previously confirmed that waterfalls in the downstream portions of Enos Creek block upstream passage of sticklebacks from the ocean.

HABITAT

Habitat Requirements

Previous studies indicated that the limnetic population inhabits limnetic habitat in the lake during the productive summer months during which there is a high degree of microhabitat partitioning with benthic sticklebacks (Kraak et al. 2001). Each morph occupies the littoral zone to breed in spring where there is a high degree of habitat partitioning as they build and defend nests. Although no other fish species occur naturally in Enos Lake, local residents are reported to have introduced cutthroat trout (*Oncorhynchus clarki*) previously stranded in other nearby waterways. There is a lack of natural spawning habitat for trout in Enos Lake and therefore trout populations are not expected to be a serious problem for sticklebacks. Table 3 compares the physical dimensions of five lakes possessing limnetic with benthic species pairs.

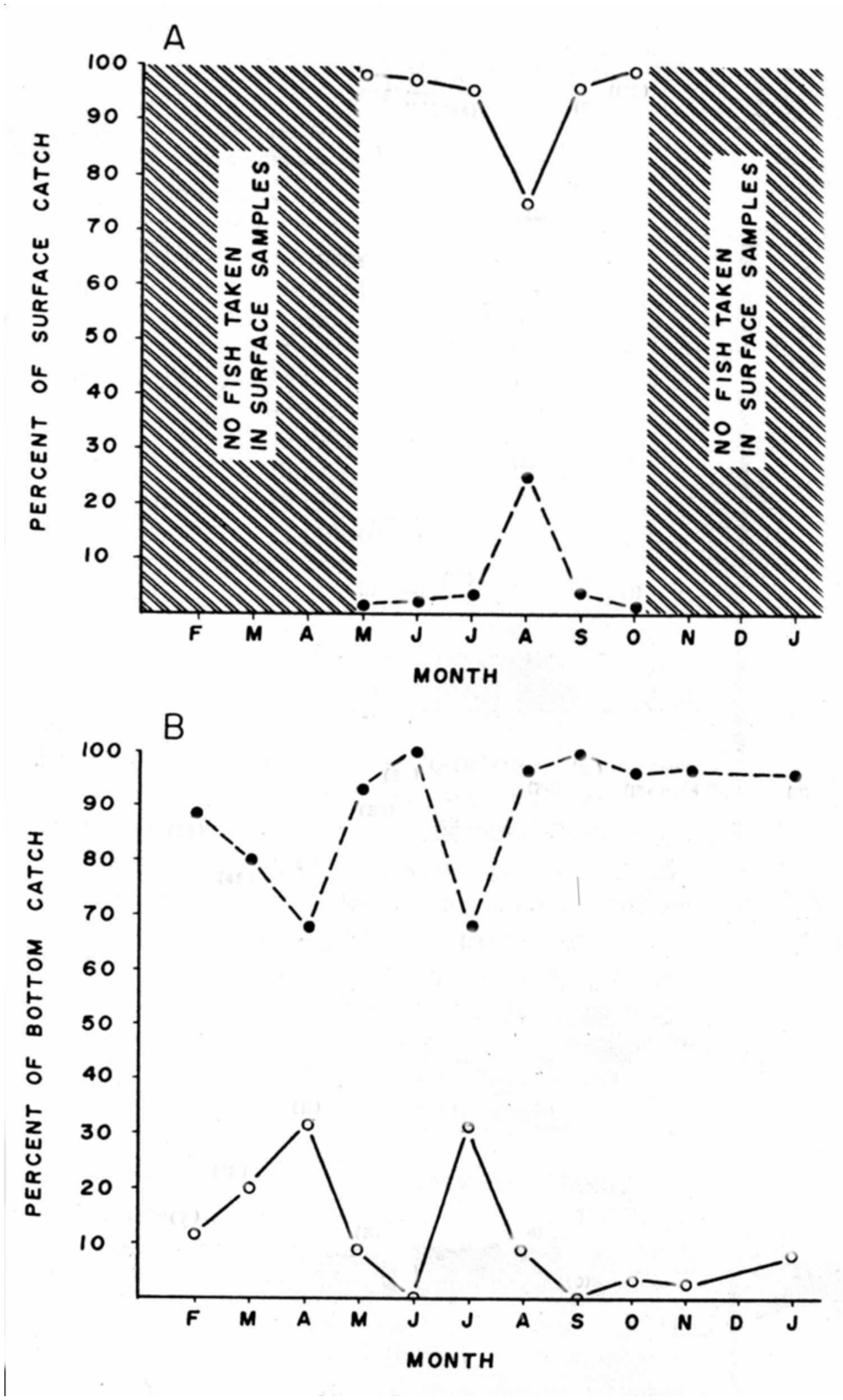

Figure 7. **A**. Proportion of Enos Lake sticklebacks at surface during summer: solid circles = benthics (i.e., 10%); open circles = limnetics (i.e. 90%). **B**. Proportion of Enos Lake sticklebacks in bottom benthic habitat: solid circles = benthics (i.e., 90%); open circles = limnetics (i.e., 10%). Modified from Bentzen et al. (1984).

Table 3. Frequency of food items found in stomachs of 20 limnetic and 30 benthic *Gasterosteus* Lavin and McPhail (1986).		
	OPEN WATER (limnetics - N = 20)	**LITTORAL (benthics - N = 30)**
Chironomids	12	128
Chaoborus	-	1
Megaloptera (larvae)	-	1
Ephemoroptera	4	5
Unidentified insect larvae	4	4
Gasterosteus eggs	28	99
Unidentified eggs	-	10
Ostracods	20	433
Hydrarina	-	1
Nematodes	-	5
Simulidae (adult)	-	8
Unidentified insect	6	3
Cladocera	26	-
Calanoid copepods	68	-

Enos Lake is a small coastal lake at 48-m elevation above sea level after damming (McPhail 1984, 1985, 1988). Topographic maps show elevations as low as 47 m (the lake's original level before dam construction). Maximum depth is 11 m with an area of 17.6 hectares and no permanent drainage flowing into the lake (Fig. 6). An outlet drains the lake toward the northwest in the rainy season (McPhail 1985, 1988.).

Trends

Brown (2000) provides data on sedimentation rates indicating the rate of eutrophication and filling of Enos Lake. Approximately 10 m of bottom sediment indicate the lake is approximately half filled after 12,000 years of sedimentation since the Pleistocene. Habitat has likely changed since the two stickleback invasions noted by McPhail (1984). The present rate of filling over the last 1,200 years is double that in the first 10,800 years since the Pleistocene and (Brown 2000) suggests lake habitat could be eliminated within 6,000 years [the writer speculates that urbanization will likely quadruple this filling rate]. During the lake's history, ecological conditions were undoubtedly more oligotrophic with a much larger surface area than at present. Given eutrophication processes and the annual anoxic hypolimnion in summer, use of deepwater habitat by Enos Lake sticklebacks may be much more limited than in the distant past.

Recently, changes toward greater water turbidity have been noted and Schluter (pers. comm. 2001) believes this trend interferes with female visual selection of coloured conspecific males for breeding [see Boughman's (2001) discussion in section on reproduction]. Schluter (pers. comm. 2001) as well as McPhail (J.D. McPhail, Department of Zoology, University of British Columbia, Vancouver, B.C.; personal communication, 2001) indicated crayfish (*Pacifastacus leniusculus*) were recently introduced into Enos Lake. The species now occurs in significant numbers. Earlier studies have not noted the crayfish in the lake. Premek (1998) suggests this is the only known crayfish species in British Columbia and it may naturally occur in the lower Fraser Valley. However, he reports little evidence that they previously inhabited Vancouver Island although they are now well established in southern portions of the island. Assuming crayfish distribution is similar to most primary freshwater fish species, they have presumably been historically absent, and introduced to the region. Crayfish introductions in Europe and elsewhere have led to wide scale habitat destruction and introduction of exotic species are of concern in other areas of North America (*see* Lodge et al. 2000a,b).

The density of crayfish has changed the bottom of the lake, but it is not known if the appearance of crayfish is the only cause of the increased turbidity which is not due to logging or construction. McPhail (1984) states that the lake is highly productive and from June to August there are repeated algae blooms. However, the issue of algae blooms provides a different issue regarding light penetration, thus the effect on colour perception and the penetration of the light spectrum would be different.

John Baldwin (Water Management Officer, BC Ministry Water Land Air Protection, Nanaimo, B.C.; personal communication, 2001) reported that beaver dams have caused up to a 2-m rise of waters and resulted in the flooding of houses in residential areas around the lake. Effects of flooding, if any on the swamp and lake are not documented. Local authorities apparently destroy such dams whenever they are observed in Enos Creek, but whether such structures historically affected the lake is not known. It is difficult to define historical boundaries of Enos Lake where available maps illustrate the southwestern end as extensive swamp. A small dam at the outlet was authorized prior to December 31, 1958. The northwestern half is deeper, reaching 11-m depths in the area in which the limnetic sticklebacks occur (Fig. 6). Rock fill now stretches across the outlet to provide a dirt road and trail separating lake from creek and marshland. Historically, these stream and lake populations probably met and interacted to some extent before dam construction. Now, the property owner has water rights to block a culvert through the dam and increase the water level of the lake (Fig. 6). During an unusually dry summer (August and September 2001), there was little water in the downstream marshy area; however, hundreds, if not thousands of sticklebacks could be dip-netted from small drying pools of less than 10 to 20 cm deep. Dead (cedar?) trees occurred where swampland was still moist and perhaps where beaver dams could have historically affected water levels by backing water into Enos Lake habitat. Natural water levels are threatened by increases in water withdrawal due to irrigation of a golf course and a request for an expanded water licence (2001) to irrigate a second golf course; however, the landowner has expressed interest regarding environmental impacts and a willingness to discuss issues. Proposed modification of the dam could raise lake-waters to 49 m (= 2m above the lake's original elevation).

In Sept. 2001 Peden observed high fill (or dam) across the narrows at the north end of Enos Lake, along with culvert and grate to filter out woody debris. This structure served as a potential road access for logging. It presently functions as part of a nature trail associated with the development, but could potentially become a road adding additional stress to the local environment if the municipal community plan for the Nanoose area comes into effect (Nanoose Bay Regional Community Plan. Web site 07/10/2001).

The drop in water level below the culvert is presently 0.5 m and effectively blocks movement of *Gasterosteus* between the downstream marshland and the lake in the dry season. Most *Gasterosteus* studies have concentrated on populations in and adjacent to the deeper portions of Enos Lake. The relationships between the lake and swamp or marsh populations require clarity as to whether the swamp or marsh populations were historically isolated from the lake as they are today, or if they were once part of a freely interconnected benthic population between lake shore and marsh. In either case, the swamp/stream inhabiting populations are probably typical of most nearby streams of Vancouver Island, without the same life history adaptations that limnetic and benthic sticklebacks have had in Enos Lake.

Protection/Ownership

See Section on Existing Protection.

BIOLOGY

General

In general, species pairs of *Gasterosteus* on Texada and Lasqueti islands evolved toward the same lifestyle as Enos populations. Attributes described for Texada, Balkwill, Emily and Priest Lakes (Westland 1998) parallel patterns of life history found in Enos Lake populations.

<u>Limnetics</u>

Westland (1998) states that as for other stickleback species pairs, limnetic males prefer unvegetated, open locations. 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. Because preferred spawning habitat is not uniformly distributed, nesting males are clumped in their distribution. Eggs take approximately 7 – 10 days to hatch. During this time males fan the eggs by thrusts of their pectoral fins. Male sticklebacks vigorously defend their nests and continue to protect the young for about a week. By late summer, limnetics become large enough to escape predators. At this time they school up and forage for plankton in the open water.

If water levels drop more than 1 m during spawning then the limnetics may be forced to spawn in the same areas used by the benthics. This could partially account for increased hybridization, but the influence of increased turbidity cannot be ruled out because of the colour perception issue.

Benthics

Westland (1998) observed that benthics in Paxton and Enos Lakes lived longer and reproduced less often than limnetics. Benthics did not seem to become sexually mature after one year, and appeared to live well beyond two years, perhaps as long as seven years. There is little or no sexual dimorphism in benthics, and if present, it tends to be in the opposite direction from that of limnetics, reproductive males tending to be smaller on average than gravid females. In the lab, females produce only one or two clutches per season, regardless of food availability. Females had a similar life history in the wild. Westland further found that benthics prefer densely vegetated nesting locations, usually among beds of *Chara*. Their nests were highly concealed and difficult to find in the field. They tended to nest in water of greater depth than limnetics, although usually less than 2 m depth. Benthics were reported by Westland (1998) to be similar to limnetics in all aspects of parental care and development. About a week after they hatch, the young dispersed into the littoral vegetation where they feed. Juvenile benthics continued to feed in the shallow littoral zone under cover of or within close proximity to vegetation cover.

Reproduction

Enos Lake populations have the generalized reproductive behaviors typical of sticklebacks, with males defending nests in the littoral zone, and females being courted by males and choosing which male to breed with. While using the littoral zone for breeding, limnetic and benthic populations exhibited a high degree of habitat partitioning. Schluter (in Kraak et al. 2001) states that females choose males based in part on the adaptive morphological traits that distinguish the species, especially size but probably also shape. By inference, coloration of males is important, Boughman (2001) provided evidence that *Gasterosteus* live in different light environments. She showed that female perceptual sensitivity to red light varies with the extent of redshift in the light environment, and contributes to divergent preferences. Male nuptial colour varies with environment and is tuned to female perceptual sensitivity. McPhail (1984) notes the nuptial colour of breeding male benthics is black whereas that for breeding male limnetics is typical of *Gasterosteus aculeatus* with red throats and blue backs. The extent of divergence amongst populations in both male signal colour and female preference for red is correlated with the extent of reproductive isolation in these recently diverged species. She further concluded that sexual selection generated by sensory drive contributes to speciation. Given claims of changes in water clarity in Enos Lake, Boughman's observations provide a plausible explanation for the recent increased incidence of hybridization.

Movement/Dispersal

Limnetics

As suggested by their name, limnetic sticklebacks congregated in the surface portions of the lake to forage between May and October but disappear from surface waters in winter months with many dispersing toward benthic habitat in winter. Some also move into the shallowest depths of the lake during spring and early summer to breed. They presumably do not survive in the anoxic hypolimnion of summer (Figures 6 and 7). Recent drier summers and withdrawal of water during the summer months for domestic and commercial uses could be exacerbating the layer and further reducing available habitat. It is not known if the anoxic hypolimnion is stable or if the lake turns over in the fall. Such mixing could lead to fish kills. Small numbers were also found in bottom habitats throughout the year (Bentzen et al. 1984). Males use the shallower littoral zone for the purposes of reproduction and holding nesting sites.

Benthics

Benthics congregate nearer the lake bottom, particularly in the littoral areas. They outnumber limnetics in the benthic areas of the lake through the year, although perhaps avoiding the anoxic hypolimnion in August (Bentzen et al. 1984).

Nutrition and Interspecific Interaction

Diets from limnetic and benthic stickleback populations in the Cowichan River system were recorded by Lavin and McPhail (1986) and may be representative of food items used by limnetics and benthics in Enos Lake. Data for May emphasizes preponderance of Cladocera and calanoid copepods taken by limnetics (Table 3)

Because there are no other fish species within Enos Lake, other than introduced cutthroat trout without available spawning habitat, non-fish taxa are then significant as food, competitors or predators. The potential impact of presumed introductions of crayfish are discussed elsewhere.

Behaviour/Adaptability

Although sticklebacks are highly adaptable to estuary, river, stream, lake or pond habitats, their localized morphological adaptations such as those in Enos Lake are habitat and site-specific. In Enos Lake, adaptations evolving during the last 10,000 years became site-specific, but are now breaking down. Their genetic integrity will be lost if trends toward hybridization swamp both genomes adapted to mid-water and bottom (littoral) foraging.

Hybrid Fitness

Previous research has shown that hybrids are not ecologically and/or reproductively as fit as are the benthic/limnetic parents from which they arose. In the case of Paxton Lake sticklebacks, Hatfield and Schluter's (1999) experiments found that hybrids may prove to be fit under laboratory conditions, but not in their natural habitat. Hybrids transplanted into natural habitat grew at 73% of the growth rate of benthics and at 76% of the rate that limnetics grew in the wild; a result attributed to reduced foraging efficiency. This reduced growth of hybrids is attributed to their competitive inefficiency of foraging within the historically natural habitat of benthics and limnetics. Recent habitat changes in Enos appear to have favoured better survival conditions for hybrids. The full extent of these changes requires better documentation. One reason could be habitat changes, such as predation on eggs or larvae by crayfish at stickleback nesting sites, thus reducing the total numbers of sticklebacks and thus reducing competition for available prey or nesting sites, thus opening opportunity for hybrids to survive.

Vamosi and Schluter (1999) similarly compared reproductive success in Paxton Lake and in the laboratory, and found greater mating success between conspecifics than back-crosses of hybrids. However, they caution that successful mate choices tend to be between similar-sized fish, and caution in the interpretation of results is required.

POPULATION SIZES AND TRENDS

Earlier reports suggested a total of 100,000 of each form in Enos Lake (McPhail 1985, 1988). Bentzen et al. (1984) collected 3,885 benthics and 281 limnetics in the their sampling of the northern area of the lake, suggesting that benthics may outnumber limnetics. The southern third of Enos Lake is shown on maps as flooded marsh that might support benthics at various seasons of the year, and would certainly provide benthics more usable habitat within the lake. It is the specialized limnetic genome that is most at risk because of their proportionally smaller area of habitat compared to larger areas of shallow benthic habitat around the periphery of the lake. There appears to be no data addressing the homogeneity of southernmost populations and whether limnetics stray from the area of deeper water which supports them.

Under present circumstances, total population size is meaningless, without accurately knowing the ratio between sticklebacks possessing the indigenous genotypes and those that are hybrids.

Using mark-recapture techniques, Matthews et al. (2001) calculated levels of limnetics to be in the range of 12,000 to 94,000 (mean = 22,000, $p = 0.05$) and benthics between 30,000 and 47,000 (mean = 37,000, $p = 0.04 - 0.05$); however, numbers of hybrids were not estimated. They did note that the high variability in the limnetic estimate was related to the low catchability of limnetics during the study period. Limnetics are harder to catch in the open water region of the lake.

LIMITING FACTORS

In the last 2 years, increased rates of hybridization were discovered and thought to be a major potential threat to the survival of limnetic and benthic sticklebacks in Enos Lake. The causes for increased hybridization are not yet verified and much of the following is speculative.

Change in water clarity was proposed as a likely factor that possibly impedes mate selection of conspecific females to males by misdirecting them to the courtship display of heterospecific males (Schluter pers. comm.). Given the red coloration of breeding male limnetics McPhail (1984), visual acuity for red colour of males may be hindered with receptive female limnetics accepting courtship of darker colored benthic males instead. Introduced crayfish compete for habitat and their digging into lake-bottom tends to cloud the water and could be cause for misdirected selection by females for courting males (Schluter pers. comm.). Crayfish may consume stickleback spawn or larvae on nests, a mortality factor for which limnetics and benthics have no experience, or evolved defensive mechanisms.

Perhaps there was a shift in abundance of planktonic prey items making limnetics less fit. The effect of water draw down for the golf course on population abundance also requires study. Because Enos Lake is relatively shallow, lower water levels may offer increasingly limited habitat for limnetics.

Because Enos Lake has been filling with sediment since Pleistocene Glaciation, continual reduction of limnetic habitat can be expected. Optimal habitat favoring limnetic sticklebacks requires definition before restorations, as does the level of resource competition required to reduce hybrid fitness.

Previous reports discounted access of other stickleback populations from other water bodies that could affect genetic dynamics of resident populations; yet, such access should not be discounted during periods of floods or other catastrophic events. Before the dam was built in the 1950s, small juveniles from the stream could have easily had access into the lake, especially if beavers had built dams at the right locations. Public access facilitates potential introductions of exotic species to the lake proper, especially a paved road to Fairwinds, where roadside swamp water might have temporary seasonal flow into the upstream (southwestern) end of Enos Lake. The introduction of an exotic species could have disastrous consequences. The loss of the Hadley Lake species pair due to the introduction of catfish provides a most relevant example, although the date of catfish introductions and who the culprits were are undocumented.

Issues of water clarity require better documentation as to what parts of the light spectrum are filtered out, and whether this affects stickleback reproductive behavior. There should be more quantification for abundance of food items compared to that of previous years. Issues of crayfish require more background data to quantify their impact on stickleback habitat. If crayfish are similarly intolerant of marine water as are primary freshwater fish, crayfish could not have inhabited Vancouver Island without human assistance. Their role in the hybridization of Enos Lake sticklebacks needs to be substantiated.

SPECIAL SIGNIFICANCE

Within British Columbia, Enos Lake sticklebacks provide a classic textbook case for recent evolutionary processes (McPhail 1984). The Enos Lake species pair, is the first described of five known stickleback species pairs, each member having separate niche partitioning and reproductive isolation within the same lake.

The genus *Gasterosteus* provides evolutionary textbook examples of speciation ranging from local differentiation to fully differentiated sympatric species. Examples include: populational variants (i.e. unarmored sticklebacks on Queen Charlotte Islands, Moodie and Reimchen 1973); parapatric populations (i.e. marine and freshwater forms breeding in adjacent sections of streams, see Hagen 1966); giant melanistic forms in lakes, Moodie 1984); and full sympatric species (i.e. *G. aculeatus* Linneaus and *G. wheatlandi* Putnam). However, the Enos Lake species pair is the closest example to full sympatric speciation, albeit, two marine invasions of ancestral marine sticklebacks led to reinforcement of isolating mechanisms (Bentzen et al. 1984). Ecologically, Enos Lake populations fit definitions of biological species (McPhail 1984). However, scientific species names have not been provided because of the systematic complexity of gasterosteid populations in general.

EXISTING PROTECTION

In the past, Enos Lake sticklebacks were naturally protected when the surrounding area was isolated within a military reserve without public access. After ownership was transferred to the private sector for land development, eligibility for protection such as the BC Forest Practices Code for Crown lands didn't apply. Presently Enos Lake sticklebacks are classed as threatened (COSEWIC 1988). The British Columbia Conservation Data Centre recognizes the population as G-1, S-1. Dovetail Consulting Inc. recently facilitated a workshop cosponsored by the BC Ministry of Water Lands and Air Protection and Fisheries and Oceans Canada concerning restoration of *Gasterosteus* species pairs in respect to many of the perceived threats indicated in this report (Rankin and Bicego 2002). Under the National Accord for the Protection of Species at Risk (1996) and the soon to be proclaimed federal Species at Risk Act, recovery plans will be required.

SUMMARY

COSEWIC previously recognized the stickleback pair in Enos Lake as threatened (McPhail 1985. 1988). The population size of the limnetic form may be lower than that for benthic sticklebacks, because of proportionally less limnetic habitat compared to that for benthics, making limnetics increasingly susceptible to extinction. Further surveys are required to determine if that is the case. However, there is less habitat available to the limnetics and that has been impacted by the increased turbidity which is apparently leading to a breakdown in isolating mechanisms. The recent increase in hybridization implies that their genetic integrity will soon be greatly altered and compromised. Enos Lake represents one of five BC lakes where species pairs evolved, each lake independently supporting parallel post-Pleistocene evolution. Each is not evolutionarily synonymous with the other.

Changes in water quality and the introduction of an apparently exotic crayfish were cited by Schluter (pers. comm) as being possible causes. As there are no known indigenous species of crayfish on Vancouver Island, *Pacifastatus leniusculus* is presumed to be the species in Enos Lake (Premek 1998). Schluter also suggested habitat disturbance by crayfish may have altered water colour and interfered with female selection for males during reproduction. Within Enos Lake, morphological and genetic factors differentiating benthic and limnetic populations may be lost due to introgression, to eventually produce a genetically homogeneous population.

TECHNICAL SUMMARY

***Gasterosteus* spp**
Enos Lake Sticklebacks, *Épinoche du lac Enos*

DISTRIBUTION:	
Extent of occurrence:	Benthics = 0.176 km^2 Limnetics = 0.009 km^2
Area of occupancy:	Benthics = 0.14 km^2 Limnetics = 0.007 km^2
Habitat trend:	Decreasing
POPULATION INFORMATION	
Total Numbers in Canadian populations:	Benthics 30-47,000 (mean = 37,000) Limnetics 12-94,000 (mean = 22,000)
Number of Populations within Canada:	Benthics 1 Limnetics 1
Generation Time:	Benthics >1 year Limnetics <1 year
Population trend:	Apparent decline due to hybridization
Rate of decline:	Not estimated (the proportion of hybrids increased by more than 12% in the last year).
Is population fragmented?	No
Does the species undergo fluctuations?	Unknown

Threats
Immediate threat of extinction from introgressive hybridization resulting from habitat alteration and the possible introduction of additional exotics.

RESCUE POTENTIAL
These fish are endemic to Lake Enos. There is no rescue potential.

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BIOGRAPHICAL SUMMARY OF CONTRACTOR

Alex E. Peden received his Master of Science degree from the University of British Columbia in 1964 and Doctorate at the University of Texas at Austin in 1970. After receiving a postdoctoral appointment at the National Museum of Canada, he was appointed Curator of Marine Biology at the British Columbia Provincial Museum in 1971. He participated in ichthyological collection and/or fisheries work in southeastern USA, Mexico, Northwest Territories, Alaska, Bering Sea and waters adjacent to British Columbia. Alex also had the dubious distinction of describing two new species of Texan fishes (Poeciliidae) only to see them become extinct and is personally concerned of possibly similar demise with Enos Lake sticklebacks. He devoted much of his career in documenting the diversity of fish species of the Canadian West Coast, and contributed

COSEWIC status reports of western Canadian fish species since 1980. Previously, Peden authored status reports on species such as speckled dace, Umatilla dace, leopard dace, shorthead sculpin and mottled sculpin. Peden documented the first occurrences of more than 60 marine fish species inhabiting marine waters off British Columbia.

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COLLECTIONS EXAMINED

Samples are housed at the University of British Columbia and Royal BC Museum, however most studies on Enos Lake sticklebacks have used live fish for experimental studies or other non-collection objectives.