Vananda Creek Limnetic Stickleback

Gasterosteus species 16

Vananda Creek Benthic Stickleback

Gasterosteus species 17

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Species Information

Taxonomy

The two Vananda Creek stickleback species occur *in situ* as a pair of closely-related species and therefore are described together in this account. They are known as the Vananda Creek Limnetic Stickleback (*Gasterosteus* species 16) and the Vananda Creek Benthic Stickleback (*Gasterosteus* species 17).[1]

The threespine sticklebacks (*Gasterosteus* spp.) are found only in the northern hemisphere. They are a species complex consisting of numerous reproductively isolated populations distributed along the coastal areas of the north Atlantic and north Pacific oceans, both in marine and adjacent freshwater environments (Bell and Foster 1994a). The amount of phenotypic variation among freshwater populations, and their rapid rate of evolution from marine forms have offered evolutionary biologists tremendous insight into the mechanisms of adaptive radiation and speciation. The recently evolved (post-Pleistocene) populations of North American freshwater sticklebacks have been of particular interest. Among these populations, Lavin and McPhail (1985) have documented a tendency: in large, deep lakes, limnetic plankton-feeding forms have evolved; and, in small, shallow lakes, littoral benthic-foraging forms have evolved (see also Hatfield and Schluter 1999).

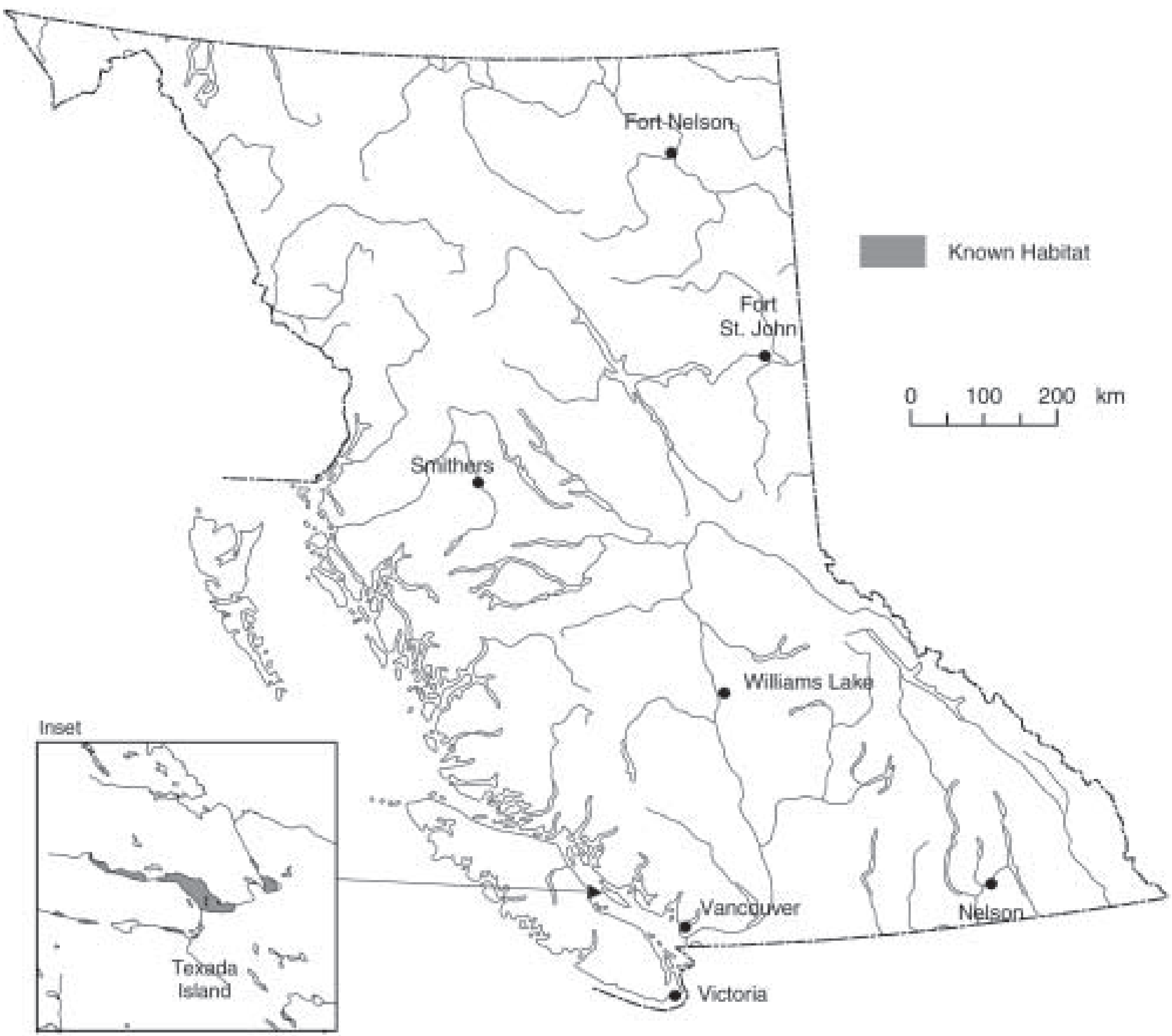
However, among all stickleback populations in the world, only in six small lakes in British Columbia have sympatric limnetic and benthic forms evolved (McPhail 1994, p. 418): the Enos Lake Limnetic and Benthic sticklebacks (McPhail 1984, 1989); the Paxton Lake Limnetic and Benthic sticklebacks (McPhail 1992); the Hadley Lake Limnetic and Benthic sticklebacks (McPhail 1994); and, in Emily, Priest, and Spectacle lakes on Van Anda Creek, what are now known as the Vananda Creek Limnetic and Benthic sticklebacks (McPhail 1994; Hatfield 2001b).

Even more surprising than the phenomenon of sympatric, reproductively isolated species is the realization that these four pairs of species evolved in parallel (Rundle et al. 2000; Schluter 2000). A recent review of the concept of evolutionarily significant units suggests that some gene flow between or among reproductively isolated populations within species complexes may be necessary for long-term viability (Crandall et al. 2000). However, there is little question among stickleback researchers that the pairs of sticklebacks in British Columbia are not simply evolutionary significant units (Foster et al. 2003), but are biological species in themselves (Hatfield 2001b, p. 586). They are also among the world's best examples of rapid adaptive radiation and parallel evolution (Bell and Foster 2003). Not surprisingly, therefore, these pairs of sticklebacks are the subject of intense interest and research among evolutionary biologists (cf. Schluter and McPhail

1 The two species described in this account were named after Van Anda Creek. Until recently, the spelling for this creek was "Vananda" (i.e., one word) as was the town of the same name. The spellings of the town and the creek have now been changed to "Van Anda" (i.e., two words). The common names for the two stickleback species, however, still use the one-word spelling: Vananda.

Vananda Creek Limnetic and Benthic Sticklebacks

(Gasterosteus sp. 16 and 17)



Note: This map represents a broad view of the distribution of habitat used by this species. The map is based on current knowledge of the species' distribution. This species may or may not occur in all areas indicated.

1992; Bell and Foster 1994b; Nagel and Schluter 1998; Rundle et al. 2000; Kraak et al. 2001).

The Hadley Lake pair is now extinct (Hatfield 2001a). This species account describes the Vananda Creek pair of sticklebacks.

Description

McPhail (1984, 1989, 1992, 1994), Hatfield (2001b), and Hatfield and Ptolemy (2001) have described the three remaining pairs of stickleback species in British Columbia. In general terms, they are small, silvery-green to black fish, <70 mm in length, with a laterally compressed body form. They have calcified lateral plates and retractable dorsal and pelvic spines.

The limnetic sticklebacks are smaller but more thoroughly armoured than the benthic sticklebacks. They are pelagic, zooplankton-feeding fish, and their relatively high numbers of gill rakers are presumed to be a plankton-feeding adaptation (Bentzen and McPhail 1984).

By contrast, the benthic sticklebacks are bottom-foraging fish with a larger and relatively stockier or chunky body form. They have conspicuously wide, short jaws, which are also presumed to be a feeding adaptation (Bentzen and McPhail 1984).

There is genetic evidence that the Enos Lake, Paxton Lake, and Vananda Creek pairs represent separate gene pools (McPhail 1984, 1992; Taylor and McPhail 1999).

Distribution

Global

The Vananda Creek Stickleback species occur only on Texada Island, British Columbia.

British Columbia

In British Columbia, these two species occur only in Emily, Priest, and Spectacle lakes in the Van Anda Creek watershed on Texada Island. There is no evidence to suggest that any sticklebacks in the fourth lake in the Van Anda Creek watershed, Kirk Lake, have evolved into a species pair.

Forest region and district

Coast: Sunshine Coast

Ecoprovince and ecosection

GED: SOG

Biogeoclimatic unit

CWH: xm

Elevation

The surface elevation of Emily Lake is approximately 40 m, while that of both Priest and Spectacle lakes is approximately 80 m (Hatfield 1998).

Life History

Diet and foraging behaviour

The Vananda Creek limnetics form loose schools in the open-water portions of the lakes where they feed on zooplankton (e.g., copepods and insect larvae) (Hatfield 2001b).

Vananda Creek benthics forage near the shallower lake edges, or in somewhat deeper water, for prey such as clams, dragonfly nymphs, and snails. As benthics grow larger, they pursue larger prey (Hatfield 2001b).

Juvenile sticklebacks remain in the littoral regions of the lakes where they pick invertebrates off vegetation. While nesting in the littoral zone, the males of both species—limnetics and benthics—often prey on benthos (Hatfield 2001b).

Reproduction

The Vananda Creek limnetics mature after 1 year and rarely live beyond 2 years; whereas the benthics seem to mature older and live longer, possibly as long as seven years. Breeding season is from April to June in B.C. populations, and is initiated when the males develop reddish throats and fore-bellies, and construct tubular nests (Foster 1994). Although courtship is a complex ritual, mate selection by the females is largely influenced by visual cues, particularly the red colouration on the males (Bakker and Rowland 1995; Baube et al. 1995). Immediately after a female lays her eggs in a nest, the male fertilizes them.

Males may mate with several females over a 1–4 day period before switching to a parental-care phase. In this phase, the male protects the eggs and fry from predators and also fans them, thereby providing them with sufficient oxygen (Foster 1994).

Females, by contrast, do not tend the young and continue to produce multiple clutches. Typical fecundity for a limnetic female is between 30 and 40 eggs per clutch or approximately 50 or 60 eggs for a really large female. Limnetic females produce several clutches a year in quick succession if food availability is high. Benthic females often carry more than 150 eggs and can carry up to 200 eggs. They produce only one or two clutches a season, regardless of food availability.

Home range/Site fidelity

The two species are restricted to the three small lakes—Emily, Priest, and Spectacle—on the Van Anda Creek mainstem. The two species remain in the lacustrine environment year round.

The males will defend a territory during the nest construction, mating, and parental care phases of the breeding process. The size of the defended territory is usually related to the size of the individual male.

An individual male may repeat the cycle of phases several times during a single breeding season. As a nest is generally severely damaged during the release of the fry, a male repeating the cycle will of necessity build a new nest (T. Hatfield, pers. comm.).

Movement and dispersal

When sufficiently large, the juveniles disperse from the littoral zones along the shorelines to open-water (limnetics) or deeper-water (benthics) portions of the lakes. For the limnetics, dispersal occurs towards late summer, when they become larger and swift enough to escape predators and their spines are of sufficient size to act as a deterrent (B.C. MELP 1999). This distance can be a matter of a few tens of metres, or perhaps upwards of a few hundred metres. Benthics continue to forage along the shallow margins of the lake for larger and larger prey as they grow, then move to deeper water to overwinter.

Habitat

Important habitats and habitat features

Breeding

From April to June, both species move from the more open-water or deeper-water portions of the lakes to the shallower, vegetated littoral zones to breed. Males of both species construct their nests in these shallow, vegetated littoral zones (McPhail 1994; Vamosi and Schluter 1999). The specific habitats in which limnetics and benthics choose to build their nests differ slightly (McPhail 1994). Hatfield (2001b) has noted that limnetic males choose slightly more open nesting sites (i.e., those sites with less aquatic vegetation) on gravel or rock substrates, or on submerged logs, and at water depths of no more than 1 m. Benthic males, by contrast, choose sites with aquatic vegetation, and in slightly deeper water, but rarely deeper than 2 m. These breeding microhabitats are highly sensitive, as discussed under "Threats" below.

Foraging

As the names of the two species imply, one feeds in the open-water, limnetic portions of the lakes near the surface, while the other feeds along the shallow margins of the lake either on the bottom (benthos) or by picking invertebrates off plants. It is precisely this difference in behaviour that is believed to have led to the reproductive isolation of these species, despite the fact that they inhabit the same lakes (Schluter 1993, 1995).

Conservation and Management

Status

The Vananda Creek Limnetic and the Vananda Creek Benthic Stickleback are on the provincial *Red List* in British Columbia. In Canada, both species are designated as *Endangered* (COSEWIC 2002).

Summary of ABI status in BC and adjacent jurisdictions (NatureServe Explorer 2002)

BC	Canada	Global
S1	N1	G1

Trends

Population trends

Total population sizes and trends are unknown. However, Hatfield (2001b) reported that the populations were abundant in all three lakes.

Habitat trends

The aquatic habitats of Priest, Spectacle, and possibly Emily lakes have been impacted for some time by the dam located at the outlet of Priest Lake (Priest and Spectacle by the impoundment and the regulation of water levels; Emily by any regulation of the flow regime downstream of the dam). Records indicate that the current dam is a concrete structure, 1.8 m in height. A review of the water licence data suggests that major changes to the associated waterworks occurred around 1956, and a significant change in the storage capacity of the reservoir occurred around 1973 (J.G. Norris, pers. comm.).

The aquatic habitats of the three lakes can be impacted by sedimentation derived from erosion events on the lands within the watershed surrounding the lakes. The lands in the Van Anda Creek drainage have a long history of disturbances including forest harvesting. The authors are not aware of any references that document the exact timing, extent, or type of logging in this drainage in the past. While it was a not uncommon practice in the late 1800's to log with what are now known as "high-grading" practices (i.e., removing only the biggest trees), "a majority of stands are second growth…with no mention of vets in the polygon label" on the forest cover maps. "Given the activity around Van Anda around the turn of the century, and the active underground mining in the area, a lot of timber would have been required" (B. Kukulies, pers. comm.). The amount of soil disturbance created at the time is not known.

Approximately 60% of the Priest Lake Community Watershed is on Crown land, which is under the administration of the Ministry of Forests. The Ministry of Forests has approved a forest development plan including provisions for forest harvesting (A20507 Blocks 701P, 702P, 703P, and 704P; and A20489 Block 904P) in the Priest Lake Community Watershed (B.C. MOF 2001).

Threats

Population threats

These species are found in Emily, Priest, and Spectacle lakes—all in the Van Anda Creek drainage, Texada Island—and nowhere else in the world. Van Anda Creek itself flows from Spectacle Lake at the upper end of the drainage basin directly into Priest Lake and then into Emily Lake. Van Anda Creek also flows from Emily Lake to tidewater.

An unauthorized introduction of catfish (*Ameiurus nebulosis*) into Hadley Lake, on Lasqueti Island, occurred in the 1990s, and the limnetic and benthic stickleback species that formerly lived in the lake have now been assessed by COSEWIC (2002) as being extinct. Direct predation by the catfish is strongly implicated. If catfish, or any other species that preys on sticklebacks, were to be introduced into Emily, Priest, or Spectacle lakes, the Vananda Creek pair of sticklebacks might easily be driven to extinction.

Signal crayfish (*Pacifastacus leniusculus*) have been introduced into Garden Bay Lake on the Sechelt Peninsula with "devastating" effects on the allopatric stickleback population in that lake (S.A. Foster, pers. comm.). These crayfish, also introduced into Enos Lake on Vancouver Island, appear to have disrupted the habitat of that lake's pair of stickleback species. Although crayfish may directly prey upon stickleback eggs (S.A. Foster, pers. comm.), the major impacts appear to be through habitat-disruptive mechanisms, three of which have been hypothesized (D. Schluter, pers. comm.). First, the crayfish stir up bottom sediments, creating turbid water. In Enos Lake, the crayfish are so numerous that their collective ability to create turbid water conditions is real. Second, the crayfish consume large quantities of vegetative matter in the littoral zone of Enos Lake. A lack of vegetative matter could interfere with the breeding microhabitat requirements of the two stickleback species, thereby leading to a breakdown in assortative mating. Finally, the comparatively large male benthics in Enos Lake might not be growing to their former large size due to a lack of suitable benthos to feed upon, or due to a lack of suitable benthic feeding sites, given the heavy macrophytic feeding habits of the introduced crayfish. Because size of the male sticklebacks is one of the visual cues that female sticklebacks use in their selection of mates, the recently-smaller benthic males could now be confused for limnetic males in the assortative mating process. This too might lead to hybridization and a subsequent collapse of the species pair.

An introduction of crayfish into the Van Anda Creek watershed is therefore considered to be a threat to the Vananda Creek species pair, given the similarity of habitats, especially the breeding microhabitats, between Enos Lake and Emily, Priest, and Spectacle lakes.

Coastal cutthroat trout (*Oncorhynchus clarki*) feed on sticklebacks, and they do reside in Emily, Priest, and Spectacle lakes. So far, they seem to coexist with the sticklebacks, at least at current population levels. However, any increase in the number of cutthroat trout in the lakes, for example through a stocking program, could upset the current balance between the stickleback and trout populations.

Habitat threats

The Vananda stickleback species pairs are potentially more sensitive to changes in habitat and water quality than normal populations of sitcklebacks. Relatively minor changes in environmental conditions could result in the limnetic and benthic species hybridized and collapsing into a hybrid swarm. The limnetic and benthic species are maintained as true species with limited gene flow by reproductive isolating mechanisms including strong assortative mating, low hybrid survival relative to the parent species, and relatively high growth and survival of the limnetic and benthic morphologies in their respective habitats. Changes in water quality that affect transparency (e.g., increases in turbidity or dissolved organic carbon) may interfere with females discriminating between males of either species, and an increase in hybridization frequency by as little as 3% (D. Schluter, pers. comm.) is sufficient to cause the two species to collapse into a hybrid swarm. Changes in the relative productivity of benthic relative to limnetic prey (zooplankton) associated with changes in water quality (nutrients or suspended solids) may also affect relative growth rates of either species or their hybrids. A decrease in benthic invertebrate production associated with environmental disturbances may lead to decreased growth (and therefore fitness) of benthic juveniles relative to hybrids, thereby selecting against the benthic species rather than hybrids. Decreased growth of benthics could also prevent them from growing large enough to be discriminated as benthic males by breeding limnetic females.

Recent changes in water and/or microhabitat characteristics in Enos Lake appear to have precipitated an increase in hybridization between this lake's limnetic and benthic species with a consequential loss of reproductive potential and the likelihood of collapse of both species (Kraak et al. 2001). Turbidity (very fine suspended solids) in the water is strongly implicated.

For a pair of cichlid species (family Cichlidae) in Lake Victoria in Africa, turbidity is the likely cause of the breakdown of assortative mating. In these species, as in the sympatric stickleback pairs in British Columbia, one of the assortative mating cues is the red colouration of the males; a slight difference in colour allows the females to distinguish between males of the two sympatric species. With turbidity, the females appear less able to distinguish between males of the two species (Seehausen et al. 1997).

In recent laboratory experiments using Enos Lake limnetic and benthic sticklebacks, Boughman (2001) observed that, in relatively clear water, blue and red are "high-contrast signal colours" (p. 944), meaning that females can use the slightly more red or slightly more blue colouration on the males to distinguish between limnetic and benthic males. In turbid water, this visual cue is masked or lost because the light that does penetrate the turbid water is "redshifted" (i.e., the ambient light in the water fails to illuminate the slight colour difference between the limnetic and benthic males). As a result, it has been suggested that females may mate with males of the other species (Kraak et al. 2001; D. Schluter, pers. comm.).

Thus, turbidity in the water would appear to be a significant threat to all sympatric stickleback pairs, including the Vananda Creek pair. Turbidity during the breeding season (April through June) would seem to cause a breakdown in the assortative mating between the two species, leading to the collapse of both species by way of hybridization. In addition, the risk to sympatric stickleback pairs, including the Vananda Creek pair, from sediment delivery is significantly higher because of the very short lifespan of the species. Due to the relatively fast turnover of generations, the degree of hybridization or recruitment failure that could occur in the first and/or second breeding period affected by a sediment event could seriously and irreversibly harm the species (T. Hatfield, pers. comm.). However, the degree and duration of the turbidity events that would precipitate such a collapse of these species is currently unknown.

Forest management practices have the potential to result in increased turbidity and sedimentation. Risks to sticklebacks from increased turbidity associated with suspension of very fine sediments is a serious concern, since this may potentially interfere with both mate recognition and zooplankton productivity. Changes in productivity of the benthos and zooplankton may affect viability of the species pairs and their hybrids (see above discussion). Very fine suspended solids are usually associated with erosion from soils with a high clay content, or runoff from logging roads.

Typically, release of suspended sediments into fish-bearing water bodies occurs as a result of altered hydrology or runoff over exposed soils or logging roads. Soils may be exposed during road building, forest harvest, and clearing for building sites. There is broad scientific literature indicating negative behavioural and physiological consequences from high deposition of sediment. The risk to species pairs from sedimentation is, at present, difficult to gauge, but remains a concern.

Forest management may result in other habitat disturbances or alterations. For example, riparian and littoral habitat can be affected by harvest and side-casting from roads. Riparian logging and littoral modifications are of minor intensity at present, but such impacts may increase in the future.

In addition, forestry may have cumulative effects on turbidity, water chemistry, or dissolved organic carbon that may influence water clarity or cause eutrophication.

An active placer mining operation near Priest Lake poses a threat of sediment delivery to one or more of Emily, Priest, and Spectacle lakes, but reports conflict about the amount of aggregate sorting now occurring at this mine. However, any soil disturbance, such as during forest road development or forest harvesting activities but also including natural disturbances, in the forested lands surrounding Emily, Priest, and Spectacle lakes could precipitate an erosion event, which could lead to subsequent sediment delivery into the lakes.

Water levels in Priest and Spectacle lakes are regulated by a dam at the outlet of Priest Lake. This has resulted in an increased surface elevation for Priest Lake and the back-flooding of the section of Van Anda Creek that joins Priest and Spectacle lakes. There are potential consequences resulting from the dam and water management decisions with regard to the regulation of flows and lake level:

- an elevated lake level may result in less suitable littoral habitats and erosion of riparian soils;
- the exposure of littoral areas during periods of drawdown may result in sediment generation during rainfall events;
- any changes in lake level elevation during spawning periods may affect reproductive success; and
- the dam may reduce the opportunity for gene flow with Emily Lake or may enhance gene flow between Priest and Spectacle lakes.

None of these potential issues have been evaluated in the Vananda Creek populations (T. Down, pers. comm.).

Legal Protection and Habitat Conservation

The two Vananda Creek sticklebacks are not legally recognized under the provincial *Wildlife Act*, but are protected by the provincial *Fish Protection Act*, and the habitat provisions of the federal *Fisheries Act*. The *Fish Protection Act* provides the legislative authority for water managers to consider impacts on fish and fish habitats before approving new water licences or amendments to existing licences, or issuing approvals for works in and about streams. However, the *Fish Protection Act* cannot be used to supercede activities authorized under the provincial *Forest Act*, or where the Forest Practices Code or its successor, the *Forest and Range Practices Act*, applies (see Section 7(7), *Fish Protection Act*).

Section 35(1) of the federal *Fisheries Act* prohibits activities that may result "in the harmful alteration, disruption, or destruction of fish habitat." Similarly, Section 36(3) of the Act prohibits the deposition of a "deleterious substance of any type" into waters frequented by fish.

Also of note is the fish habitat policy of the federal Department of Fisheries and Oceans, which includes a goal of "… no net loss of the productive capacity of fish habitat", which is designed to maintain the maximum natural fisheries capacity of streams (Chilibeck et al. 1992).

There are no provincial or federal protected areas in the Van Anda Creek watershed.

Provisions enabled under the Forest Practices Code or its successor, the *Forest and Range Practices Act*, that may help maintain habitat for this species include: ungulate winter range areas; old growth management areas; riparian management areas; community watersheds; coarse woody debris retention, visual quality objectives; and the wildlife habitat feature designation. All of these, except community watersheds, have the ability to protect relatively small portions of streamside vegetation (i.e., a few hundred hectares) along a stream and/or lake shoreline; community watersheds have the potential to protect an entire population of a stream and/or lake resident form.

A major portion of the Van Anda Creek drainage is designated as the Priest Lake Community Watershed, with Priest Lake being the water source for the community of Van Anda. The Code and FRPA do allow forest harvesting in a community watershed, provided that a watershed assessment has been conducted and that the recommendations from the assessment are being followed. A Coastal Watershed Assessment Procedure (CWAP) has been completed for the Priest Lake Community Watershed (Clarke and BaBakaiff 2000; Clarke and Gemeinhardt 2001).

Recovery planning for these species is underway.

Identified Wildlife Provisions

Wildlife habitat area

Goal

Prevent site-specific or cumulative forestry impacts to aquatic habitat or water quality that may lead to hybridization and introgression of stickleback species pairs or population decline in occupied lakes.

Feature

Establish a WHA at known sites (Spectacle Lake, Priest Lake, Emily Lake).

Size

The WHA should include the Crown land portion of the height-of-land watershed upstream of the outlet of Emily Lake, which would include the Crown land portion of the Priest Lake Community Watershed (which includes Priest and Spectacle lakes). This is necessary at least as an interim measure until a recovery strategy and action plans for the Threespine Stickleback species pairs are completed. Work on the recovery strategy is underway and scheduled for completion in 2003.

As the Priest Lake Community Watershed measures 1131 ha (Clarke and Babakaiff 2000), it is estimated that the overall Emily Lake height-of-land watershed would be approximately 1250 ha. With the Crown land portion of the Community Watershed estimated at 60% (B. Kukulies, pers. comm.), and assuming a similar land ownership for the area surrounding Emily Lake, the overall WHA would be expected to be approximately 750 ha. However, the overall height-of-land watershed includes the surface areas of the four lakes (Emily 7.1 ha; Priest 43.7 ha; Spectacle 10.6 ha; and Kirk ±8 ha), the surface areas of the stream channels joining the lakes, and other areas not contributing to the harvestable forest land base (e.g., marshes).

Design

The WHA should include a core area and management zone. The core area should be established around the three occupied lakes and all streams flowing into these lakes. The size of the core area will vary depending on the risk of sedimentation to the lakes but may be between 30–90 m (both sides of streams). The management zone should include the Crown forest lands that drain into these lakes, up to the height of land. It is recognized that these recommendations are more conservative than standard riparian management practices. However, given the international significance of these species and the consequences of an error in judgement (global and irreversible extirpation), it is reasonable to argue for more conservative riparian setbacks and harvesting practices to reduce the risk of potential impacts.

General wildlife measures

Goals

1. Minimize soil disturbance and prevent erosion and sediment delivery to the lakes.
2. Minimize road access.

Measures

Access

- Do not develop new roads in core areas. Construction and maintenance of existing roads must be done in a manner, and at times, that prevent or preclude sediment delivery to any water feature.

Harvesting and silviculture

- Do not harvest or salvage in the core area.
- Plan harvesting of management zone to meet goals of the general wildlife measure
- Conduct silvicultural activities in a manner that prevents or precludes sediment delivery to any water feature.

Pesticides

- Do not use pesticides.

Recreation

- Do not develop trails, recreation sites, facilities, or structures in the core area. In the management zone, restrict recreational developments to those designed to mitigate impacts from recreational activities.

Additional Management Considerations

The management of water levels within Priest and Spectacle lakes should consider the life history requirements of sticklebacks. In particular, significant changes, up or down, in the surface level elevations of the lakes during the breeding season may affect reproductive success. Further, to prevent erosion and sediment delivery to the lakes, riparian soils should not be flooded. In addition, the exposure of littoral habitat should be minimized at all times of the year, but especially during the typical rainy season.

Measures must be taken to prevent the introduction into these lakes of any exotic species that might prey on the sticklebacks, or otherwise disrupt their life history and habitat requirements. Similarly, no measures should be taken that might enhance the "native" cutthroat trout population.

Information Needs

1. The exact extent to which existing and potential sources of soil erosion could result in sediment delivery to one or more of the three lakes. Existing sources include private forest lands surrounding the three lakes, private residential lands surrounding the three lakes, and an active placer mining operation near Priest Lake.
2. The relationship between degrees of turbidity in the species' resident lakes and the resulting rates of hybridization.
3. The effects of crayfish on the breeding and foraging habitats of threespine sticklebacks.

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