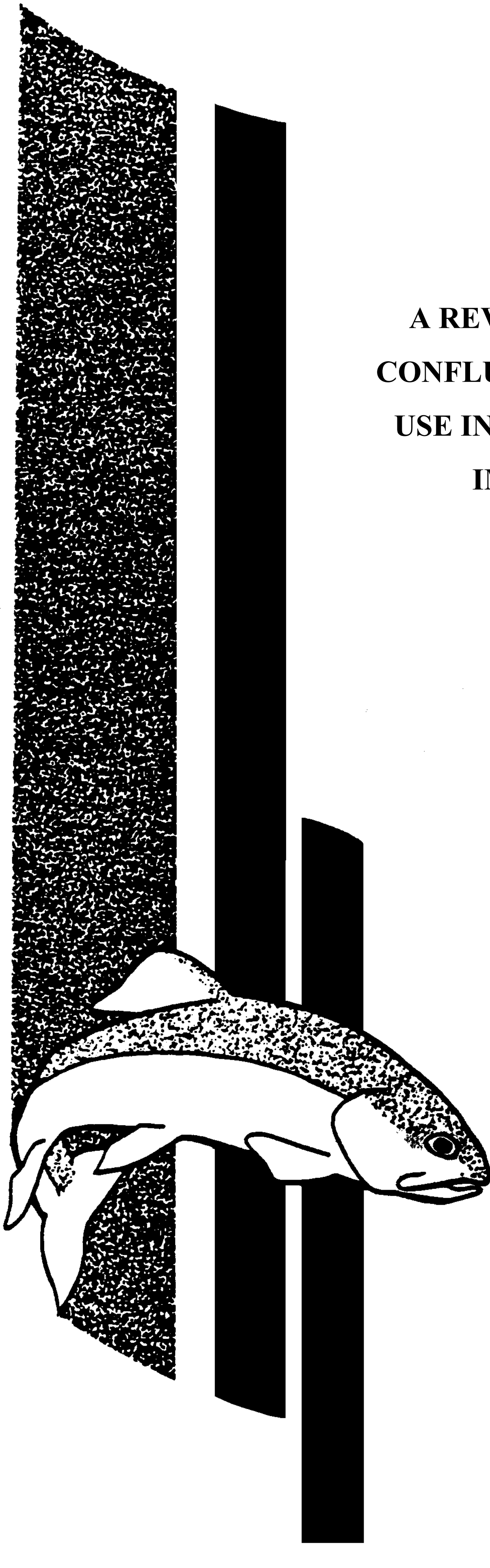
Appendix 67

A Review of Bull Trout Life-History and Habitat Use in Relation to Compensation and Improvement Opportunities



A REVIEW OF BULL TROUT (SALVELINUS CONFLUENTUS) LIFE-HISTORY AND HABITAT USE IN RELATION TO COMPENSATION AND IMPROVEMENT OPPORTUNITIES

by

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Abstract

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The bull trout *(Salvelinus confluentus)* is a char endemic to western North America. It has had a confused taxonomic history, and its specific distinction from the Dolly Varden *(Salvelinus malma)* is still in doubt. In the areas where the two nominal species overlap there is evidence of hybridization and even introgression. This taxonomic problem has management implications, and will only be solved by studies in the areas of geographic overlap.

The bull trout spawns in the fall (September to October) in flowing water. The threshold spawning temperature is around 9°C. Courtship and spawning behaviour are similar to other char. The female chooses the deposition site and digs the redd. The degree of sexual dimorphism varies among populations, but in most populations males develop bright spawning colours and a kype, while females are less colorful. The eggs are about 5-6 mm in diameter and optimal incubation temperature ranges from 2 to 4°C. In the wild, fry emerge approximately 220 days after egg deposition. Newly emerged fry are secretive and hide in the gravel along stream edges, and in side channels. Juveniles are found mainly in pools, but also in riffles and runs. They maintain focal sites near the bottom and are strongly associated with instream cover, especially overhead cover. Juveniles feed primarily on aquatic insects taken from the bottom or from drift. As they grow, their diet shifts to fish, and most adults (except for stream residents) are piscivores.

Like many char, the bull trout occurs as a number of life-history forms. The stream-resident form lives out its life in small headwater streams. It is often dwarfed and reaches sexual maturity at a small size, and sometimes at an early age. The fluvial form lives as an adult in large rivers but spawns in small tributary streams. It often attains a large size, reaches sexual maturity at about five, and undergoes long migrations between mainstem rivers and small tributary spawning streams. The lacustrine-adfluvial form has a similar life-history. It spawns in tributary streams but lives as an adult in lakes. It grows to a large size, usually reaches sexual maturity in about its fifth year, and often makes long migrations between lakes and spawning streams. A fourth possible life-history type is anadromy. The evidence for the existence of anadromous bull trout is still slim, but in the Puget Sound-Strait of Georgia region they probably occur. There has been no formal attempt to document the life-history of anadromous bull trout. The evidence for homing in migratory bull trout is equivocal, and some populations probably home with great fidelity while others show a high rate of straying.

The genetic structuring of bull trout populations suggest that many populations have been through genetic "bottlenecks". Genetic variability within populations is low, but genetic differences among populations often are marked. This, along with striking inter-population differences in nuptial colouration and sexual dimorphism, suggest the existence of distinct stocks.

Adult and juvenile densities are often low, and the species is sensitive to environmental degradation and over-fishing. Human activities that create migration barriers, increase siltation, and increase variation in natural temperature and flow regimes within streams, are particularly harmful. Bull trout do not do well in competition with introduced salmonids, and there is evidence that introduced lake trout have replaced bull trout in a number of lakes.

Bull trout are declining in numbers throughout their range, especially at the southern edges of their distribution where a number of populations have become extinct. Unfortunately, opportunities for enhancement are limited, and the major hope for restoring bull trout numbers lies with regulation (e.g., closures, gear restrictions and harvest limits) and public education.

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1.0 INTRODUCTION

The bull trout *(Salvelinus confluentus)* is an endemic western North American char. Most of the species' original distribution (Fig. 1) was to the west of the Continental Divide, and extended from northern California (the McCloud River) and a few upper Snake tributaries in Nevada, throughout most of Oregon (from the Willamette system east), Washington, Idaho, inter-mountain Montana, British Columbia, and the southeastern headwaters of the Yukon system (Lindsey et al. 1981). In addition, the species was native to east-flowing rivers in the Rocky Mountain foothills of northern Montana (Brown 1971) and Alberta (Nelson and Paetz 1992). In British Columbia and Washington, the bull trout is an interior species found predominately in areas east of the Coast Mountains (Cascades).

In recent years the bull trout's range has contracted, especially along its southern edges. Apparently, bull trout are now extinct in the McCloud River of California (Rode 1988) and, in the Willamette system in Oregon, the species has disappeared from at least three major tributaries (Goetz 1989). Its status in the Bruneau River, Nevada, where it was reported by Miller and Morton (1952) is unclear, but it is probably extinct. In Washington (Brown 1992) and Alberta (Carl 1985) there is evidence for precipitous declines in a number of populations. In British Columbia the major declines appear to be in the Columbia system and in the lower Fraser Valley (Hagen and Baxter 1992; Hagen 1993a, b; Gordon Haas, University of British Columbia, Vancouver, personal communication; Al Stobbart, Department of Fisheries and Oceans, Pitt River Hatchery, personal communication), along with other systems where overfishing has occurred. This loss of peripheral southern populations, and evidence of declines elsewhere, has led to a general concern about the status of bull trout and this, in turn, has resulted in an petition to list bull trout under the US Endangered Species Act. Under this act, the US Fish and Wildlife Service (Department of the Interior), is required to examine the available evidence and, within 90 days, determine whether a status review is warranted. This 90 day examination was positive (Federal Register, May 17, 1993) and a status review was completed in 1994. The review recommended that bull trout be listed in the conterminous United States, but that the information on population trends in Canada and Alaska is insufficient to warrant listing throughout the species entire range (Federal Register, June 10, 1994). One problem the status review did not grapple with is the bull trout's confused taxonomic history, especially with regard to its relationship to the Dolly Varden *(Salvelinus malma).*

The bull trout was originally described from the Puyallup River, southern Puget Sound, in 1858 (Suckley 1858); however, for over one hundred years it was treated as either a subspecies, or a variant, of the Dolly Varden. In 1978, the bull trout was resurrected from synonymy and redescribed as a distinct species (Cavender 1978) but, even now, its taxonomic status and relationships are not clear. There is a growing body of information (chromosomal, morphological, and molecular) that indicates the Arctic char *(Salvelinus alpinus)* is the closest relative of the Dolly Varden, and that the bull trout represents a lineage distinct from the Dolly Varden-Arctic char lineage (Cavender 1980; Cavender and Kimura 1989; Grewe et al. 1989; Phillips et al. 1989; Haas and McPhail 1991; Phillips and Pleyte 1991). A serious problem with this conclusion is the geographic origin of the data. With one exception, Haas and McPhail (1991), it is based on studies of allopatric populations of bull trout and Dolly Varden; however, the critical test of a species is whether two forms can coexist without significant gene exchange (Mayr 1963). For example, the coastal and westslope cutthroat trout (*Oncorhynchus clarki clarki* and *0. clarki lewisi*), have interior and coastal distributions much like those of bull trout and Dolly Varden; also the level of morphological differentiation between the two cutthroat trout is similar to that found between the two char. There is, however, no natural area of overlap in the geographic distributions of the two cutthroat trout. Consequently, their ability to coexist is untestable. Thus, their taxonomic status becomes a matter of judgement and, in this case, the weight of taxonomic opinion favours subspecific status for the two cutthroat trout (Benkhe 1992; Allendorf and Leary 1988).

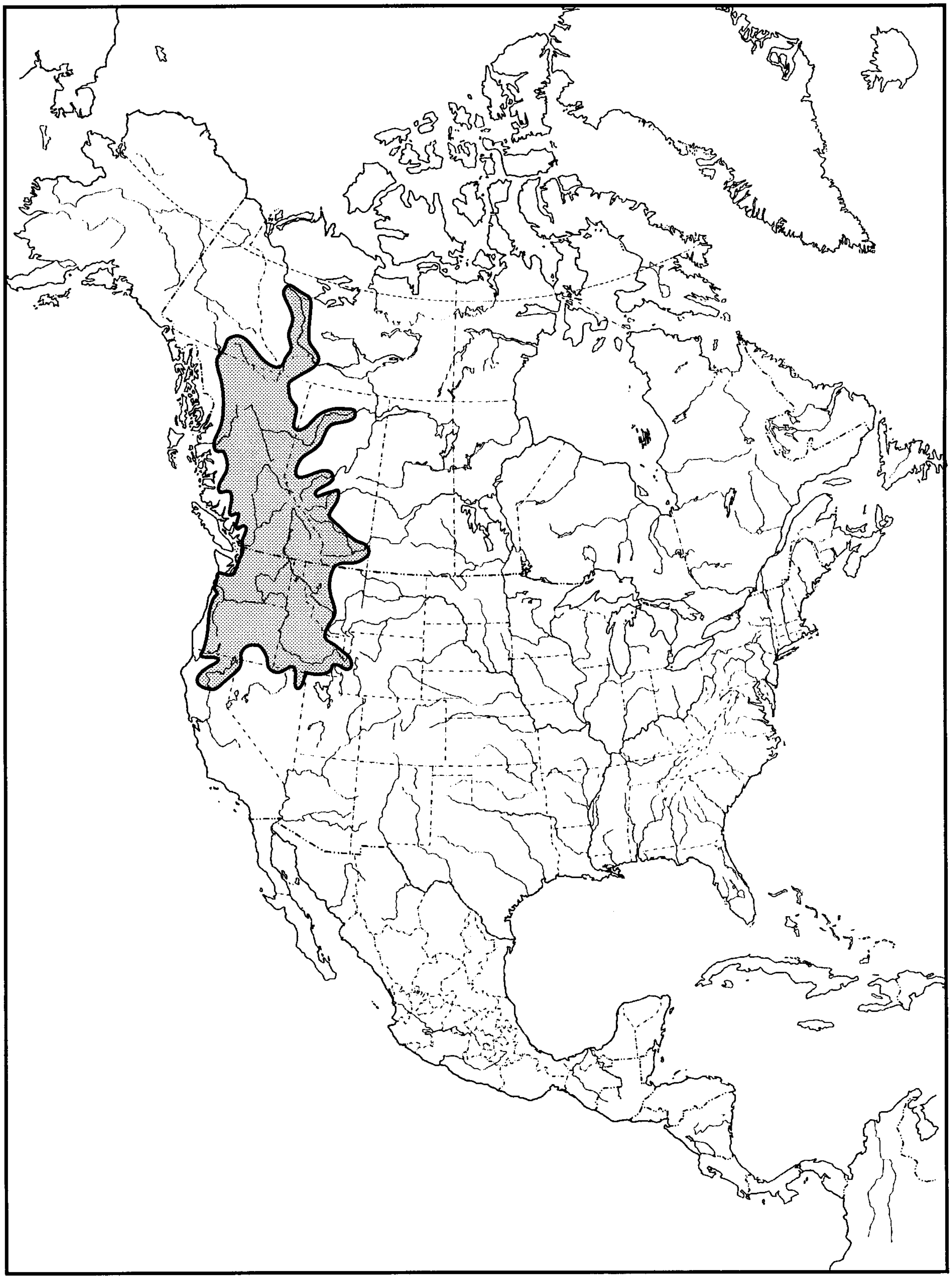

Fig. 1. Approximate original distribution of bull trout *Salvelinus confluentus*.

Therefore the presence of an area of overlap is a critical difference between the bull trout-Dolly Varden situation and the two subspecies of cutthroat trout. Although the bull trout is primarily an interior species, and the Dolly Varden is a coastal species, in some areas the two forms come in contact. Indeed, it is their ability to coexist, apparently without extensive hybridization, that is the most compelling argument for their status as separate species (Cavender 1978; Haas and McPhail 1991; Baxter et al. in prep.). Their geographic ranges overlap where the Interior Plateau abuts against the Coast Mountains in northern and west-central British Columbia, and in the lower Fraser Valley, as well as in the Puget Sound and Olympic Peninsula regions of western Washington (Fig. 2). It is what happens in these areas of range overlap (sympatry) that is crucial to understanding the relationship between bull trout and Dolly Varden.

Unfortunately, until recently research has focused on bull trout outside the area of overlap and, consequently, the picture in areas of sympatry is not clear. Although the data are sketchy, in northern and west-central British Columbia, Dolly Varden and bull trout appear to occur in the same river systems without extensive hybridization (Haas and McPhail 1991). In such areas, there are often clear ecological differences between the two char: the bull trout are usually the adfluvial form (adults in lakes but spawning in tributary streams), and Dolly Varden are permanent stream residents (Bustard and Royea 1995; McPhail personal observations). In contrast, in the more southern areas of overlap (e.g., the lower Fraser Valley and Skagit River) the situation is confused. At some sites both char are present, while at other sites only one or the other of the char is present, and at other sites there is morphological evidence of hybridization (Brown 1992; McPhail personal observations). In addition, in these areas, molecular markers (both mitochondrial and nuclear) that are diagnostic for each of the species in allopatry (Grewe et al. 1989; Phillips and Pleyte 1991) turn up in the "wrong" morphological species (McPhail and Taylor 1995).

Such observations imply that in areas of contact, bull trout and Dolly Varden can, and do, exchange genes. This brings the specific status of the bull trout into doubt. Indeed, the two char show all of the attributes of classical subspecies (Bailey et al. 1954): clear morphological differences that are stable over most of their largely allopatric distributions, a small (relative to their allopatric distributions) area of overlap, and clear evidence of gene exchange within the area of overlap. In such cases, however, evidence of hybridization is not sufficient evidence of gene exchange. The critical issue is the fate of hybrids. Are hybrids between Dolly Varden and bull trout sterile, or can they backcross? Are they ecologically fit, or are they selected against because their intermediate morphology places them at an ecological disadvantage relative to "pure" Dolly Varden and bull trout? These are questions that need answers before a rational decision can be made on the taxonomic status of bull trout, and they are questions that can only be answered in the areas where the ranges of the two char overlap.

In the two regions of British Columbia that are the focus of this review (the Columbia-Kootenay system and the Peace-Liard system) the taxonomic status of bull trout is of little concern. Only bull trout occur in the Columbia-Kootenay system, but in the Peace system (Thutade Lake tributaries) and the southwestern headwaters of the Liard there are both bull trout and Dolly Varden (Lindsey 1956; Haas and McPhail 1991; McPhail and Carveth 1992; Baxter et al. in prep.). Presumably, Dolly Varden colonized these regions by way of headwater captures of coastal drainages (the Skeena and Stikine rivers). As in other areas of overlap, there is morphological evidence for hybridization (UBC Fish Collection), and in the Thutade system both morphological and molecular evidence of gene flow (Baxter et al. in prep.) Both the lower Liard and lower Peace contain only bull trout, but it is not clear how far downstream in the Mackenzie system bull trout extend. There are records of char from many streams that rise in the Mackenzie and Richardson mountains (Hatfield et al. 1972) but no specimens are available for examination; however, a biologist experienced with bull trout, Arctic char and Dolly Varden (Peter McCart, Fisheries Consultant, Calgary, personal communication) reports bull trout downstream as far as the confluence of the Great Bear and Mackenzie rivers. In the upper Columbia and upper Kootenay systems, bull trout are widely distributed; however, in British Columbia they are curiously absent from western Columbia tributaries (e.g., Kettle, Okanagan and Similkameen rivers; McPhail and Carveth 1992).

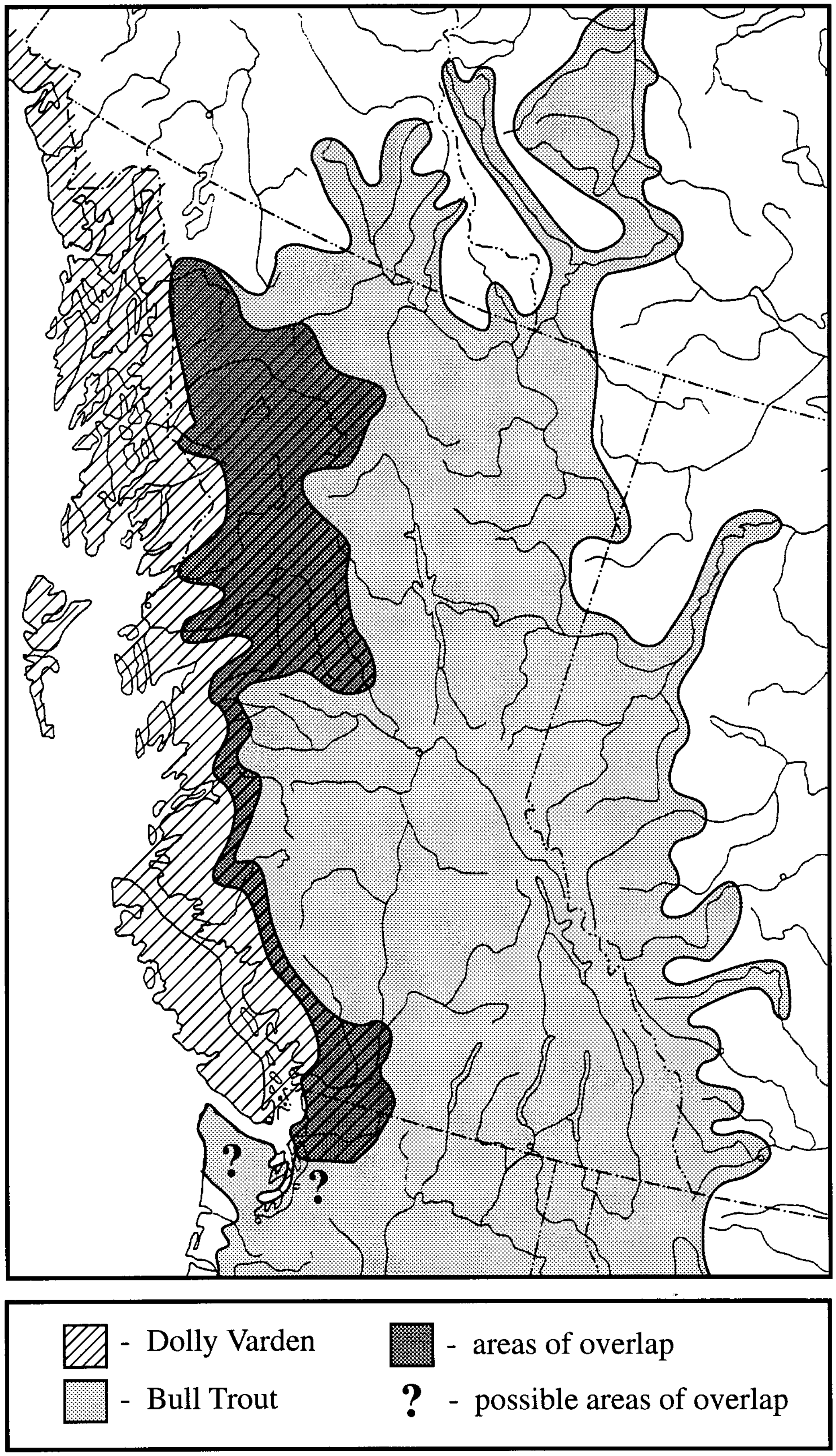

Fig. 2. Approximate British Columbia distribution of bull trout (Salvelinus confluentus) and Dolly Varden (Salvelinus malma) showing areas of overlap.

2.0 BULL TROUT LITERATURE

Most of the literature that specifically refers to bull trout is relatively recent. Before the bull trout was re-described in 1978, government agencies in both the US and Canada showed little interest in the species, and many anglers, at least in British Columbia, did not regard bull trout as a "real" sport fish. All this changed with the appreciation that bull trout were in decline, especially in the United States, and that they might qualify for protected status under the 1973 Endangered Species Act. After 1978, interest in the species on both sides of the border started to grow. In an early report on bull trout biology in the Arrow Lakes (McPhail and Murray 1979), the only paper cited from the primary literature (peer reviewed journals) that dealt with the life-history and ecology of bull trout was Cavender's re-description of the species (Cavender 1978). Through the 1980s, however, the literature on bull trout grew rapidly. Forty-one biologists attended the Flathead River basin bull trout conference (MacDonald 1985), and by 1989 a literature review of the biology of bull trout (Goetz 1989) listed 92 citations containing information on bull trout. In the 1990s the literature continues to grow at an accelerating rate, and conferences on bull trout have become commonplace events (e.g., the Gearhart Mountain Workshop, 1992; the Calgary Bull Trout Conference, 1994).

Unfortunately, much of the recent bull trout literature is in the so called "grey" literature. This "grey" literature consists of consultants reports, government reports, and unpublished theses. It often contains original and useful information, but accessing the "grey" literature is a vexing problem. Usually these reports are only cursorily reviewed and have limited distributions: they are rarely deposited in major libraries, and almost never appear in standard abstracts. Consequently, there is no efficient way to find this material and, as a result, it is often over-looked. Unfortunately, in British Columbia, and in the surrounding provinces and states, most of the recent information on bull trout life-history, ecology and management is buried in this "grey" literature.

3.0 BIOLOGY OF RELEVANT LIFE HISTORY STAGES

3.1 Spawning

3.1.1 Areas and habitat characteristics

As far as is known, all bull trout populations spawn in flowing water (Heimer 1965; McPhail and Murray 1979; Oliver 1979; Leggett 1980; Goetz 1989; Pratt 1992). Apparently, bull trout avoid large rivers (e.g., the mainstem Fraser, Columbia, Peace or Liard rivers) for spawning, and instead prefer spawning sites in smaller, lower order rivers; however, this avoidance of large rivers may be more apparent than real. The difficulties inherent in observing and sampling large rivers introduce a bias against the collection of data from such environments. For example, in the Liard system there is evidence of bull trout movement from smaller tributaries to larger rivers and the mainstem Liard in the early fall (Stewart et al. 1982; Craig and Bruce 1982), and in at least one case (Adsett Creek) this outmigration occurs before spawning (Stewart et al. 1982).

Where spawning has been observed (mostly in the Columbia system), the sites are characterized (McPhail and Murray 1979; Oliver 1979; Allan 1980; Leggett 1980; Allan 1987; Fraley and Shepard 1989) by relatively low gradients, a predominance of small gravel (<20 mm), relatively low water velocity (0.03-0.8 m^{-s}), and proximity to cover (cutbanks, log jams, pools, overhanging bush, etc.). In larger streams the redds are often sited downstream of aggrading areas (Graham et al. 1981) and are associated with ground water sources (Heimer 1965); whereas, in smaller streams the redds are associated with pockets of suitable gravel (McPhail and Murray 1979; Allan 1987). Water depth over the redds varies from less than 10 cm to over 1.0 m, and the redds are relatively large (up to about 1.5 X 2 m, Brown 1984; Fraley and Shepard 1989).

Two recent studies in the Peace River system (Bustard and Royea 1995; Baxter 1995) looked at microhabitat characteristics of bull trout redd sites. In the Chowade River, Baxter (1995) found that bull trout redds were on average 2.53 m long by 1.25 m wide, and found at a mean water depth of 56.5 cm. He also found that nose velocity at the redd sites averaged 0.35 m^{-s}, cover type associated with the redds was primarily cutbanks, and substrate at the redd site was primarily large gravels. Bustard and Royea (1995) found similar results in the Kemess Creek watershed in northern British Columbia. Redds averaged 1.6 m^2 in area, and were associated with bank cover. Water depth at redd sites averaged 30.5 cm, while nose velocity averaged 39.4 m^{-s}. Bed material at 17 redd sites was primarily large gravels.

3.1.2 Season and conditions

Like all char, bull trout are fall spawners, and water temperature may be the proximate cue that initiates redd building and spawning behaviour. McPhail and Murray (1979) and Weaver and White (1985) suggest that about 9°C is the threshold temperature below which spawning activity begins. Curiously, the actual time of spawning varies little with latitude, and both northern and southern populations spawn at about the same time (Table 1). This suggests that, although there may be a threshold temperature, some other factor (perhaps the rate of change in day length) is also involved in the initiation of spawning. There is also the suggestion of a threshold temperature below which spawning ceases. In Line Creek, Kootenay River system, Allan (1987) observed that bull trout stopped spawning activities when the water temperature dropped below 5°C.

3.1.3 Behaviour

The spawning behaviour of bull trout has been observed in both stream tank environments (Leggett 1980) and in nature (Needham and Vaughan 1952; McPhail and Murray 1979; Sexauer 1994). Apparently, most redd construction and courtship occurs at night (Oliver 1979) but in both Washington and British Columbia, spawning activity has been observed during the day (Sexauer 1994; Baxter personal observation). Generally, bull trout spawning behaviour appears to differ only slightly from the spawning behaviour of Arctic char as recorded by Fabricius and Gustafson (1953); however, at least one behaviour differs among sites. Both Leggett (1980) and Sexauer (1994) describe a behaviour called "fanning" that is performed by females immediately after egg release but before post-spawning digging. This behaviour has been interpreted as an adaptation for spawning over coarse substrate. In Mackenzie Creek, where the substrate is relatively fine, "fanning" behaviour did not occur. The following account of bull trout spawning is based on observations by McPhail and Murray (1979) in Mackenzie Creek, upper Arrow Lakes. Here, males and females are paired before redd construction, and females show a behaviour similar to the "searching" behaviour described in arctic char (Fabricius and Gustafson 1953). Apparently this behaviour functions in redd site selection, and the choice of the same site by different females in different years (Baxter 1995) suggests that redd site selection is precise.

Once a site is selected, the female digs by turning on her side, arching her body and vigorously beating her tail. This action displaces gravel downstream and, after several spawnings (each one upstream of the previous spawning), this excavation is often 10-20 cm deep and over a meter long. Courtship is confined to the redd area. After a bout of digging the female drifts backwards and the male comes along side and nudges the female with his snout. Nudging is followed by the male quivering along side the female and then drifting back and crossing over to the female's other side. The female then moves forward and starts another bout of digging. This sequence is repeated, and the frequency of nudging, quivering, crossing over, and digging increases until it plateaus for about a half hour. Just before actual spawning, the male moves forward as usual but does not nudge the female. Instead he moves in front of her, arcs his body in a curve and then circles the female. She moves forward over the redd, but instead of digging she remains upright, sweeps the redd with her tail, and then lowers her erect anal fin into the redd. Fabricius and Gustafson (1953) call this behaviour "anchoring". Both male and female drop back from the redd, the male nudges and quivers, and they both move forward. They remain in close contact and the intensity of quivering increases. Eventually, both fish gape and a small number of eggs are released. The female then drifts downstream and the male moves to deeper water. After about five minutes the female moves over the redd and starts the typical salmonid post-spawning digging upstream of the eggs. The gravel displaced by this activity covers the eggs, and the female then moves upstream and rejoins the male. A complete sequence of spawnings takes several days. In the Wigwam River, females returned downstream shortly after spawning; whereas, males remained on the spawning grounds until late fall (Oliver 1979).

Table 1. Bull trout spawning season at 13 sites spanning 20 degrees of latitude.

Locality	**Latitude**	**Spawning Period**	**Author**
Metolius R.	44" 30'N	mid-July to early Oct	Ratliff 1992
Indian Cr.	460 38'N	early Sept.	Sexauer 1994
Clark Fork R.	480 20'N	mid-Sept. to late Oct.	Heimer 1965
Flathead R.	48" 50'N	early Sept. to mid-Oct.	Shepard et al. 1984a, Kitano et al. 1994
Wigwam R.	490 10'N	mid-Sept. to mid-Oct.	Oliver 1979
Line Cr.	490 50'N	early Sept. to early Oct.	Allan 1987
Mackenzie Cr.	500 40'N	mid-Sept. to late Oct.	McPhail and Murray 1979
Meadow Cr.	500 15'N	mid-Sept. to mid-Oct.	Leggett 1980
North Thompson R.	52' 05'N	early Sept. to mid-Oct.	Hagen and Baxter 1992
Pinto Lk.	520 07'N	late Sept.	Carl et al. 1989
Upper Peace R.	560 30'N	early Sept.	Bruce and Starr 1985
Chowade R.	560 41'N	mid-August to mid-Sept.	Baxter 1994a, 1995
Hoole Cr.	590 25'N	mid-Sept.	Craig and Bruce 1982

3.1.4 Sex ratio

Often only a single male and female are involved in a spawning; however, jacks (small precocious males) and subordinate males (usually bigger than jacks but smaller than the dominant male) are known from many populations (Mackenzie Creek, McPhail and Murray 1979; Flathead River, Shepard et al. 1984a; Allan 1990; Indian Creek, Yakima River system, Sexauer 1994; Squeezer Creek, Flathead system, Kitano et al. 1994; Chowade River, Peace system where subordinate males are coloured like females, Baxter 1994a). Jacks probably gain fertilizations as "sneakers" (small males that do not court females but surreptitiously take part in spawnings, Gross 1984). The sex ratio in most populations is close to 1:1, or slightly biased towards an excess of females (McPhail and Murray 1979; Oliver 1979; Fraley and Shepard 1989). In such cases, a single male may consort with more than one female. There are, however, situations where the sex ratio is biased towards males (Sun Creek, Wallis 1948 cited in Goetz 1989; Squeezer Creek, Kitano et al. 1994; Indian Creek, Sexauer 1994; Chowade River, R.L. & L. 1994, Baxter 1995). In two of these creeks (Sun Creek in the Klamath system, Oregon, and Squeezer Creek in the Flathead system, Montana), the situation is complicated by the presence of brook trout and evidence of brook trout-bull trout hybrids (Dambacher et al. 1992; Kitano et al. 1994). Leary et al. (1983) indicate that brook trout (S. *fontinalis*)-bull trout hybrids are predominately male; thus, hybridization may be involved in the male dominated sex ratio at these sites.

3.1.5 Fecundity

As in most fish, the number of eggs carried by female bull trout is a function of body size. There are not enough data available on individual fish to construct a length-fecundity relationship for any population. There are, however, some data on mean fecundity and mean female length for a number of populations, and it is clear that egg number increases with body size (Table 2).

Table 2. Mean egg number and mean female size (ranges in brackets) for six bull trout populations.

Locality	**Mean female length (range)**	**Mean egg number (range)**	**Author**
Mackenzie Creek, BC	470 mm (409-550)	1442 (1340-1607)	McPhail and Murray 1979
Upper Flathead R., Montana	645 mm	5482	Fraley and Shepard 1989
S. E. Washington	(270-620 mm)	(380-3058)	Martin 1992 (in Brown 1992)
Bull River, Montana	619 mm (455-740)	4926 (1337-8845)	Brunson 1952
Clarck Fork, Montana	544 mm (470-660)	3821 (2136-6753)	Heimer 1965
Sun Creek, Oregon	181 mm (152-201)	249 (74-337)	Wallis 1948 (in Goetz 1989)

3.1.6 Sexual dimorphism

As in many salmonids, there are differences in colour and morphology between mature males and females. In bull trout, males often are slightly larger than females (McPhail and Murray 1979; Carl et al. 1989; Kitano et al. 1994; Baxter 1995). This suggests that large male size may be advantageous in male-male agnostic encounters. In the Chowade River, the dominant male at a redd site is usually the largest fish, with satellite males usually considerably smaller (Baxter unpublished data). Aside from size, another sexually dimorphic male character is kype development. In many populations spawning males develop a grotesquely hooked lower jaw (the kype). Again, this structure may function in male-male encounters. Interestingly, the development of a male kype varies from population to population. For example, in Foley Creek (near Chilliwack) the kype is absent but in Mackenzie Creek (Arrow Lakes) it is well developed on fish of equivalent size (McPhail personal observation) and, in large males spawning in the Thutade River (Peace system), kype development borders on the grotesque (Fig. 3). In addition to the kype, in Mackenzie Creek, McPhail and Murray (1979) noticed a sexual difference in the size of the adipose fins: in males the length of the adipose fin equated its height; whereas, in females the height of the adipose fin was greater than its length.

Outside of the spawning season there are no obvious colour differences between the sexes; however, males in reproductive condition usually are brighter than females. In Mackenzie Creek, mature males develop a green back and the lateral spots brighten to a vivid lavender. The lower sides develop a coral red colour, and the head, lower jaw and operculum become black. The pelvic and anal fins develop a conspicuous tricolour pattern: white leading edges, backed by a black band that fades to grey, and is followed by a brilliant orange trailing edge (McPhail and Murray 1979). In females the general colour pattern does not change much when spawning, except for the pelvic and anal fins. These fins develop a colour pattern similar to that of males but not as strongly contrasted. Again, the development of nuptial colours, especially in males, varies from population to population (Carl et al. 1989; Haas and McPhail 1991). In the upper Arrow Lakes, McPhail and Murray (1979) observed that male colours were noticeably brighter in large tributaries (where the fish were larger and more aggressive) than in small tributaries like Mackenzie Creek. The only report of spawning colours in bull trout from an area of range overlap with Dolly Varden is for Foley Creek in southwestern British Columbia (Haas and McPhail 1991). Here, males running with milt showed no trace of either a kype or nuptial colours. It is not known whether the loss of these sexually dimorphic traits in bull trout is widespread in areas of sympatry.

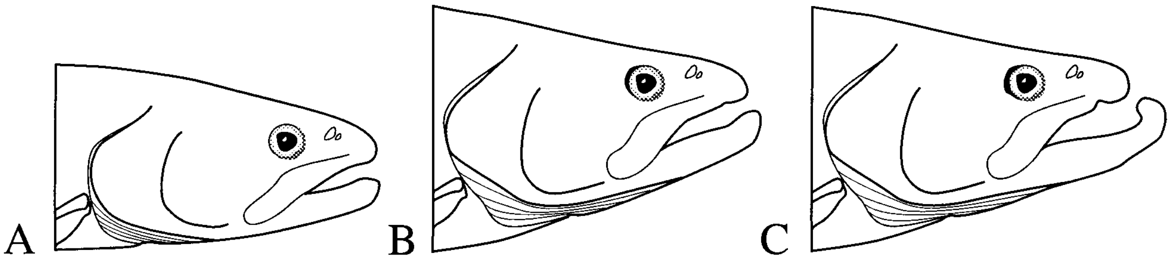

Fig. 3. Variation in kype development in reproductive males. A. Foley Lake B. Skagit River C. Chowade River.

3.2 Egg development and hatching

3.2.1 Egg size

Intraspecific variations in egg size (and egg number) are common in salmonid fishes (Craig 1985; Fleming and Gross 1990). Traditionally, fisheries biologists have argued that there are "trade-offs" between egg size and egg number associated with different sources of fry and juvenile mortality (Svärdson 1949). These trade-offs are complicated by size related changes in egg size and egg number in salmonids (Rounsefell 1957); nonetheless, egg size can be an important life-history attribute, and it is unfortunate that comparative data are not available for bull trout. The range of egg diameters (5.0-6.2 mm) given in the literature come from two sources (Heimer 1965, and McPhail and Murray 1979). More data, especially from northern and high altitude populations, are needed.

3.2.2 Development rate

Again, development rate is an important life-history trait in salmonids (Murray and McPhail 1988) that has been neglected in bull trout. Development rate is temperature dependent, but it is also sensitive to egg size, especially at low temperatures (Murray 1980). In hatchery operations, development rates usually are given as temperature units (CTU: Celsius Temperature Units). Gould (1987) indicates that bull trout eggs hatch at 350 CTU. This CTU method is useful in field incubation studies, but for interpopulation comparisons a temperature-development curve is more accurate (Murray 1980). The only temperature-development curve available for bull trout is from (McPhail and Murray 1979):

Log Development rate = 5.086 - 0.131 Temperature

This equation accurately predicts hatching at a variety of temperatures. Mackenzie Creek bull trout eggs hatched in 51 days at 10°C, and in 126 days at 2°C; however, the lower temperature produced significantly better survival than the high temperature. McPhail and Murray (1979) suggest that optimal development occurs at temperatures ranging from 2°C to 4°C. In the field, Fraley and Shepard (1989) report incubation temperatures of 1.2 to 5.4°C.

In the laboratory, bull trout emerged from the gravel approximately three weeks after hatching (McPhail and Murray 1979). In the wild, Fraley and Shepard (1989) found that fry emerged from the gravel 223 days after egg deposition.

3.2.3 Alevin size

Alevin size is, in part, temperature dependent. McPhail and Murray (1979) found significant differences in alevin size at different temperatures: 2°C produced 17 mm alevins, and 8°C produced alevins averaging 14.8 mm (standard length). In coho salmon *(Oncorhynchus kisutch),* Taylor and McPhail (1985a) demonstrated that even before emergence alevins show a startle response, and that on emergence small differences in size (e.g. 31 vs. 27 mm), can influence mortality rates (Taylor and McPhail 1985b). In Line Creek, pre-emergent fry (yolk-sac absorbed) ranged from 23 to 26 mm total length (Allan 1990). On emergence, laboratory reared fry ranged from 22.0 to 24.5 mm in standard length (McPhail and Murray 1979); while in the wild, Shepard et al. (1984a) found newly emerged fry ranged from 25 to 28 mm. In the Skagit system of southwestern British Columbia, newly-emerged bull trout alevins ranged in standard length from 17.0 to 26.3 mm (McPhail and Keeley in prep.).

3.3 Fry habitat and feeding

3.3.1 Fry habitat

Bull trout fry are relatively secretive, and often hard to find during the day (Pratt 1992; Sexauer 1994; Bonneau et al. 1995). In southeastern British Columbia and northern Montana, fry emerge from the gravel in early spring (mid-April to mid-May; McPhail and Murray 1979; Fraley and Shepard 1989; Allan 1990). Ratliff (1992) observed newly-emerged fry in the Metolius River system, Oregon, in the first week of April and, in southwestern British Columbia (Skagit system), newly-emerged bull trout fry were observed in early May (McPhail and Keeley in prep.). These fry were day active and closely associated with the shallow edges of rivers and streams, especially in areas of large, loose gravel where they used the interstitial habitat for cover (McPhail and Keeley in prep.). In the Chowade River (Peace system), fry were associated with shallow water, low velocity side-channels and instream cover (Baxter 1994b).

In the laboratory, newly-emerged fry did not fill their swim bladders until three weeks after emergence. These newly-emerged fry were strongly bottom oriented and spent much of their time in the gravel. McPhail and Murray (1979) suggested that the delay in filling the swimbladder was an adaptation that prevented the fry from being transported downstream until they were large enough to take up a feeding site. In Mackenzie Creek, once neutral buoyancy is achieved the fry concentrate in shallow, low velocity areas along the stream edge. They are most abundant in side-channels and small pools (velocity <16 cm-S) and are often associated with submerged cover (e.g., unembedded rocks, woody debris, and other velocity breaks: McPhail and Murray 1979; Pratt 1992; Allan 1987). They appear to remain in these areas at least until late fall (October).

In the Chowade River in northeastern British Columbia, Baxter (1995) measured microhabitat preference and utilization of bull trout fry during summer daylight hours. He found that fry preferred shallow, low bottom velocity areas with an abundance of cobbles and boulders that provide instream overhead cover. His results were similar to habitat preferences for fry in Smith-Dorrien Creek, Alberta (Environmental Management Associates 1993), and to those based on professional judgement (Boag 1991).

3.3.2 Fry behaviour

The behaviour of bull trout fry has been observed both in the wild and in the laboratory (undergraduate behaviour course projects, UBC). In the laboratory, fry that have just achieved neutral buoyancy are dark coloured and strongly associated with the bottom. As they grow, their colour lightens, they develop their characteristic light lateral spots, and become less bottom oriented. They still remain, however, in the lower 25% of the water column. They are not overtly aggressive, but they seem to hold focal sites, and consistently return to the same holding site after feeding forays. If another individual takes up the holding site while the original owner is on a feeding foray, the intruder usually is evicted when the original owner takes up station immediately upstream of the site and then drifts back into the intruder. Occasionally the original owner will approach the intruder head-on and, more rarely, may nip the intruder. Similar, but less detailed, observations in Mackenzie Creek led McPhail and Murray (1979) to suggest that bull trout fry hold specific sites for long periods of time.

3.3.3 Fry feeding

In Mackenzie Creek bull trout fry were observed to feed on or near the bottom, in the water column, and on the surface (McPhail and Murray 1979). Relatively few fry have been examined for stomach contents but, apparently, they take mostly aquatic insects (off the bottom or in drift) and only rarely take terrestrial insects (Nakano et al. 1992).

Not surprisingly, the growth of fry varies from site to site, but not as much as in many salmonids. For example, in Mackenzie Creek (southeastern British Columbia), McPhail and Murray (1979) record an average increase in fry size of 40 mm from late June to mid-October. Further south (Oregon), Ratliff (1992) indicates an average increase in fry length of about 28 mm from April to October, but notes that bull trout reproduction in this area is confined to cold headwater streams. Towards the northern end of their range Craig and Bruce (1982) found an average increase in length of 30 mm from early June to mid-September in Hoole Creek, while Baxter (unpublished data) observed an average increase in length of 12 mm from late July to mid-September in the Chowade River. Thus, by the end of the growing season young-of-the-year bull trout are remarkably similar in size at both the southern and northern edges of their range.

3.4 Juvenile habitat and feeding

3.4.1 Juvenile habitat

Regardless of adult habitat, most juvenile (1 +, 2+ and 3+) bull trout rear in streams (McPhail and Murray 1979; Shepard et al. 1984a; Nakano et al. 1992; Pratt 1992; Sexauer 1994). In Mackenzie Creek, during the summer, juvenile bull trout are more abundant and occupy different habitats than the young-of-the-year. Early in the summer, juveniles concentrate in pools (water velocity <25 cm7s; depth up to 1.0 m) but by August about 30% of the juveniles were in runs (water velocity >50 cni7s; depth about 25 cm). No overt aggression between juveniles was observed and, in pools, they appeared to aggregate (McPhail and Murray 1979). In Line Creek, east Kootenay region, juvenile bull trout were associated with coarse substrate, cascade flow areas, large woody debris, and shallow undercut banks (Allan 1987). In Flathead River tributaries (Montana), Fraley and Shepard (1 989) found juveniles are more abundant in pools than in runs, riffles or pocket water. Also, in the Flathead system, Nakano et al. (1992) observed bull trout juveniles holding focal sites (locations to which they consistently returned) in pools. These focal sites are strongly associated with overhead cover and are about 4 cm off the bottom (Nakano et al. 1992). In the Skagit system, bull trout spawn in the main river but juveniles (especially 2+ and 3+) move into tributary streams and remain there until they reach about 300 mm in length (McPhail and Keeley in prep.).

Sexauer (1994) collected habitat data at night on juvenile bull trout from tributaries of the Tieton and Chiwawa rivers in central Washington. She found juveniles in a variety of habitats (pools, glides and riffles) but mostly in small pools, riffle-backwaters and open side-channels with low water velocities (<0. 15m^{-s}). Unlike daytime observations (e.g., Nakano et al. 1992), at night the focal sites of over 80% of the juveniles were not associated with cover (Sexauer 1994). During winter and spring, however, juveniles were found closer to cover than in the summer (Sexauer 1994). These data indicate both diel and seasonal shifts in habitat use by juvenile bull trout.

3.4.2 Juvenile feeding

In Mackenzie Creek, juvenile bull trout forage near the substrate and in the water column, but not at the surface (McPhail and Murray 1979). In Red Meadow Creek, in the Flathead system, Nakano et al. (1992) found juvenile bull trout foraged near the bottom and in the water column. They examined benthic foragers and drift (water column) foragers separately, and found a significant difference in size between the two foraging modes: drift foragers were larger than benthic foragers. Although the two foraging types concentrate their forays at different distances off the substrate, their stomach contents are similar (Nakano et al. 1992). As they grow, juveniles shift their diet, and Pratt (1992) suggests that at around 1 10 mm they start feeding on small fish (sculpins, mountain whitefish *(Prosopium williamsoni)* and trout fry). In a small Skagit River tributary (St. Alice Creek), a 90 mm bull trout contained a 45 mm rainbow trout *(0. mykiss).*

3.5 Adult habitats and feeding

3.5.1 Adult habitats

Like many char, the bull trout occurs as a number of different life-history forms. Throughout much of its geographic distribution three life-history types are common: adfluvial, fluvial, and stream-resident populations. The adfluvial life-history involves migrations between lakes or reservoirs and spawning rivers or streams. The fluvial life-history form lives in large rivers and often migrates to smaller rivers or streams to spawn. In contrast, the stream resident form is non-migratory and spends its entire life in small streams. The least common or, perhaps, the least studied life-history form is the anadromous bull trout. Anadromous populations are suspected in the Squamish River Oust north of Vancouver) and in the lower Fraser system (McPhail personal observations; Al Stobbart, Department of Fisheries and Oceans, Pitt River Hatchery, personal communication). They probably also occur in a number of Puget Sound drainages (e.g., Nooksack, Skagit and Stillaguamish) and may once have occurred as far south as the Puyallup River (the species' type locality).

Because of this diversity of life-history forms, generalizing about the habitat requirements of adult bull trout is difficult. One thing, however, is clear: the bull trout is a coldwater species. They are uncommon wherever water temperatures rise above 15°C for extended periods (Fraley and Shepard 1989; Brown 1992; Buckman et al. 1992; Ratliff 1992; Ziller 1992; Donald and Alger 1993). The following sections deal separately with each of the known life-history types.

3.5.1.1 Stream resident populations

Stream-resident bull trout usually are separated from other populations by some barrier (typically falls or velocity barriers and in the south by areas of high temperature). Consequently, stream-resident populations are associated with headwater streams in mountainous regions where cold water and velocity barriers are common. Typically, these streams are smaller and have higher gradients than those occupied by adfluvial and fluvial populations. In these headwater streams, resident bull trout are associated with deep pools and in-stream cover. Also, most stream-resident populations are dwarfed. For example, in the Liard system, stream-resident adults average about 200 mm and rarely exceed 300 mm; whereas, adults in larger tributaries and in the mainstem average about 400 mm, and often exceed 600 mm (Craig and Bruce

1982). In addition, stream-resident fish tend to mature one or two years earlier than migratory populations in the same region (Robinson and McCart 1974; Craig and Bruce 1982).

Not all stream-resident populations occur above barriers that are insurmountable by migratory bull trout (Sterling 1978). Certainly, some lacustrine bull trout ascend Mackenzie Creek over barriers that stop rainbow trout, and spawn in a portion of the creek occupied by a stream-resident form (McPhail and Murray 1979). Given the bull trout's remarkable ability to squirm over barriers, there probably are many places where migratory (fluvial and adfluvial) and in coastal areas, anadromous, bull trout spawn alongside stream-resident fish. How much genetic mixing between different life-history forms occurs in such areas is unknown; however, some of the reports of "jacks" in this species probably include cases of stream-resident males intruding in the spawning of large, migratory individuals.

For stream resident populations, especially in northern areas, suitable overwintering sites are critical to maintaining a viable population. Craig and Bruce (1982) and Stewart et al. (1982) record the movement of char from small tributaries into larger streams in the fall. Presumably, these animals overwinter in areas of upwelling ground water or deep pools. In the Sukunka River (Peace system), Stuart and Chislett (1979) indicate that bull trout overwinter in deep pools along with arctic grayling *(Thymallus arcticus)* and mountain whitefish.

3.5.1.2 Fluvial populations

In many parts of their geographic range bull trout spend their adult lives (except when spawning) in large rivers and major tributaries (Craig and Bruce 1982; Allen 1980; Boag 1987; Fraley and Shepard 1989; Hildebrand 1991; McPhail and Keeley in prep.). Typically, juvenile bull trout rear in small streams for at least two years (and often longer) before migrating to mainstem rivers and their larger tributaries. In the southern parts of their range, mainstem bull trout concentrate in cooler areas and are often associated with the mouths of spawning streams (Buckman et al. 1992). In the central parts of their range, fluvial adults are more widespread but still associated with deep pools and instream cover (Shepard et al. 1984a; Hagen and Baxter 1992). In large, turbid, northern mainstems (e.g., the Peace and Liard rivers), fluvial adults are more widely dispersed than in other areas and not as strongly associated with specific habitats as in the south. Presumably, in these systems, bull trout are not constrained by temperature, and their relatively low numbers and dispersed distribution reflect their trophic role as top predators (Bishop 1975). For example, in two intensive surveys conducted in the lower Liard (below Liard Canyon) bull trout made up less than 1% of the total catch (McLeod et al. 1979; Irvine and Rowland 1979). In the upper Liard (above Liard Canyon) bull trout are more common but still accounted for less than 6% of the fish taken in the mainstem, and less than 3% of the catch in large tributaries (Craig and Bruce 1982). Fluvial bull trout can attain large sizes, particularly in situations where they spend a portion of their life in a large river. Perhaps the largest fluvial bull trout found occur in the Peace River system below Peace Canyon dam where several fish greater than 900 mm have been observed (R.L. & L. 1994; Baxter 1995).

3.5.1.3 Adfluvial populations

In the central part of the bull trout's range, lacustrine populations are common, especially in large oligotrophic, and high altitude lakes. Populations in lakes spawn either in tributary streams, or in the lake's inlet or outlet (Carl et al. 1989), and the spawning migrations out of large lakes can involve journeys of over 200 km (Fraley and Shepard 1989). With the exception of Flathead Lake (Montana), and a little information on the Priest lakes (Bjornn 1961) and Pend Oreille Lake (Jeppson and Platts 1959) in Idaho, remarkably little is known about the lacustrine ecology of large bull trout.

Goetz (1989) summarized what is known about the biology of bull trout in large, oligotrophic lakes. In Flathead Lake, at different seasons, bull trout use all parts of the lake: they forage in the littoral zone in fall and spring, and move to deep water in summer, most likely due to temperature constraints. In Priest Lake, Bjornn (1961) indicates that bull trout move to below the thermocline (12-18 m deep) when temperatures in the littoral zone exceed 15°C. An interim report on bull trout in Chester Morse Lake, Washington, indicates bull trout use both the littoral zone and deep water (Katherine Lynch, Seattle Water Department, Seattle, personal communication). Apparently, they also display diel, and moon-phase patterns in vertical distribution. Hydro-acoustic surveys in Chester Morse Lake detected little activity during the day and peak activity on dark, moonless nights. Chisholm et al. (1989) compared catches from floating and sinking gill nets set in the spring in Lake Koocanusa (Libby Reservoir). Catches of bull trout were low, but strikingly different in the two types of sets (averages over 9 years were: 0.0-0.2 bull trout per floating set, and 0.8-2.2 bull trout per sinking set). This result suggests that even in the spring bull trout are more abundant in deep water than near the surface.

In the large lakes and reservoirs of the upper Columbia, Fraser and Peace systems, bull trout often grow big (over 700 mm in length and 1 0 kg in weight, and commonly reach 600 mm and 7 kg in 10 or 11 years: Bjornn 1961; McPhail and Murray 1979; Al Stobbart, Department of Fisheries and Oceans, Pitt River Hatchery, personal communication).

3.5.1.4 Anadromous populations

Anadromy is the least studied life-history type in bull trout, and even the existence of anadromous bull trout is uncertain because, if there are anadromous bull trout, they occur in the area of overlap between bull trout and Dolly Varden. Thus, the specific identity of anadromous char often is uncertain. On the east coast of Vancouver Island, however, anadromous Dolly Varden occur south to about Campbell River (50' N). South of Campbell River there are no confirmed runs of Dolly Varden; however, occasional individuals are taken in the sea (Haas and McPhail 1991). In the Squamish and lower Fraser rivers, annual seasonal peaks of abundance in char suggest anadromy. These fish are silver bright and referred to by local anglers as sea-run Dollies, but the few that have been reliably identified are bull trout. The evidence that they are sea run is circumstantial (bright silver colour, and regular run timing); however, at least one char tagged in the Squamish River was recaptured in the Skagit River: a journey of about 150 kms through the sea (Poul Bech, Ministry of Environment, Lands and Parks, Vancouver, personal communication). In addition, Al Stobbart (DFO) tagged adult char in the Pitt River above Pitt Lake for several years, and obtained a number of returns from the region of the Fraser River estuary.

The evidence that these char are bull trout rather than Dolly Varden is circumstantial. Only a few individuals have been examined by scientists, and then only for morphology but, in the case of the Pitt River, all of the char examined were bull trout. Because the rivers containing what appear to be anadromous bull trout are all in the area of overlap between bull trout and Dolly Varden, morphology alone is not sufficient for positive identification, and both morphological and molecular evidence are necessary. Another observation that suggests these fish are not "pure" Dolly Varden is the size distribution in the runs. The runs consist of a relatively narrow range of sizes. In contrast, runs of anadromous Dolly Varden are characterized by a remarkable range of sizes (juveniles, subadults, and adults; Smith and Slaney 1980). Admittedly, the evidence is slim, but if anadromous bull trout are present in the Strait of Georgia and Puget Sound, they certainly warrant further investigation.

3.5.2 Adult feeding

Bull trout have a reputation as voracious predators, and for some life-history forms this is well deserved. The large body size of many lacustrine and large river populations is achieved through piscivory. Bull trout eat a wide variety of native and introduced species, but appear to have a particular propensity for sculpins (Ricker 1960; Pratt 1992), kokanee (*0. nerka)* (McPhail and Murray 1979; Bjornn 1961), mountain whitefish (Chisholm et al. 1989; Donald and Alger 1993) and, in areas of sympatry, Dolly Varden (McPhail and Keeley in prep.).

Like many salmonids, bull trout shift their diet as they grow. Consequently, most small individuals, and many stream-resident populations feed on aquatic insects. In some cases, however, this may reflect prey availability rather than prey preference. For example, in the Muskeg River, Alberta, Boag (1987) observed that bull trout above a beaver dam, where there were no other fish, fed primarily on insects; however, below the barrier they fed equally on insects and small fish. In isolated high altitude lakes, the fish community often consists of only bull trout and mountain whitefish, and whitefish are the main item in the diet of adult bull trout (Donald and Alger 1993) but, in other lakes, bull trout are the only fish and, here, they subsist entirely on benthic invertebrates and plankton (Carl et al. 1989).

In situations where fish prey species are present, the shift to piscivory takes place at between 100 and 200 mm (Stewart et al. 1982; Boag 1987; Pratt 1992) and usually involves small prey (e.g., trout fry, cottids). As they grow the proportion of fish in their diet increases, and they shift to larger prey. This tendency to exploit larger prey as they grow can cause sudden accelerations in growth, even in large individuals. McPhail and Murray (1979) observed such a growth spurt in Arrow Lakes bull trout at about 550 mm (5 years). They interpreted this sudden acceleration in growth (after three years of almost level growth) as a shift to kokanee (the dominant prey item in the largest individuals). A similar spurt in growth occurs in the mainstem Liard River for bull trout at about 400 mm (9 years). Craig and Bruce (1982) suggest this growth spurt is a result of a diet shift to large fish (e.g., suckers, grayling) and mammals (red backed voles and mice).

3.5.3 Growth and maturity

Initially, growth in bull trout is rapid and, by the end of their first summer, most populations reach a mean size of about 60-70 mm. By the end of their second summer, mean length typically exceeds 100 mm, and by the end of their third summer mean length approaches 200 mm (Sterling 1978; McPhail and Murray 1979; Oliver 1979; Craig and Bruce 1982; Fraley and Shepard 1989; Ratliff 1992; Ziller 1992). It is unusual to find individuals smaller than 200 mm in lakes, reservoirs or larger rivers (McPhail and Murray 1979; Craig and Bruce 1982; Bruce and Starr 1985; Fraley and Shepard 1989). This suggests that recruitment from rearing streams is less successful at smaller sizes (McPhail and Murray 1979). Above 200 mm, the rate of growth varies with habitat. Many stream-resident populations reach maturity at about 200 mm (Robinson and McCart 1974; Craig and Bruce 1982) and their growth rate plateaus, but lacustrine and large-river populations continue to grow and often show diet related growth spurts at ages in excess of five years (Jeppson and Platts 1957: McPhail and Murray 1979; Craig and Bruce 1982).

In habitats where bull trout achieve sizes in excess of 400 mm, sexual maturity usually is reached in their fifth summer (4+) (Bjornn 1961: McPhail and Murray 1979; Fraley and Shepard 1989). In isolated lakes and streams, however, sexual maturity can be delayed for several more years (Carl et al. 1989; Brown 1992). Not all mature bull trout spawn every year. Allan (1980) found that only 27% of the adult bull trout tagged in the Clearwater River, Alberta, returned to spawn the next year, and Fraley and Shepard (1989) suggest that in any year about 40% of the adult bull trout remain in Flathead Lake during the spawning season.

Maximum size varies greatly, but the largest recorded bull trout was taken in Pend Oreille Lake, Idaho (Goetz 1989). It was almost one metre long and weighed about 15 kg. Under the appropriate conditions, bull trout regularly live to ten years (Bjornn 1961; McPhail and Murray 1979; Kristensen 1980; Craig and Bruce 1982; Pendray 1982; Bruce and Starr 1985; Fraley and Shepard 1989), and under exceptional circumstances reach ages in excess of 20 years. The oldest bull trout recorded (24 years old) was from the upper North Thompson River, Fraser system (Hagen and Baxter 1992).

4.0 OTHER RELEVANT BIOLOGICAL FEATURES

4.1 Migration and homing

4.1.1 Migrations

Three of the life-history forms of bull trout (fluvial, adfluvial, and anadromous) make migrations as a normal part of their life cycle. The fluvial life-history form migrates from large rivers into smaller rivers to spawn. These migrations occur in late summer when water temperatures are high and water levels are low (Oliver 1979; Fraley and Shepard 1989; Hagen and Baxter 1992). Most juveniles emigrate from the spawning areas in their third summer, although some migrate as fry, and some in their fourth summer (Oliver 1979; Pratt 1992; Sexauer 1994). These juvenile migrations start in the spring and continue throughout most of the summer (Oliver 1979).

The adfluvial life-history form shows a similar migration pattern to the fluvial form: in the summer (during periods of maximum water temperature and low flows) adults migrate out of lakes into spawning streams (McPhail and Murray 1979; Fraley and Shepard 1989). Emigration from the spawning streams to lakes occurs throughout the summer, and involves fry, 1+, 2+, and 3+ juveniles (McPhail and Murray 1979). The majority of migrants to lakes are 2+ (Chisholm et al. 1989).

Bull trout are known to make long distance migrations to and from spawning area in both the Peace River (Pattenden 1992; Baxter unpublished data), and Columbia River systems (O'Brien 1996). In the Peace, bull trout that spawned in the Chowade River were angled less than one month after leaving the spawning area, having traveled a distance of over 200 km, while in the Duncan system in the Kootenays, some radiotagged bull trout traveled as far as 400 km over the study period.

Nothing is published on the migrations of the anadromous form of bull trout. In the Squamish River, the animals that may be sea run bull trout appear in the river in August (Poul Bech, Ministry of Environment, Lands and Parks, Vancouver, personal communication). If there is something akin to a smolt migration, it is protracted and probably occurs in the spring and early summer.

4.1.2 Homing

The evidence for homing in bull trout is contradictory. There are reports of tagged individuals returning to spawn in the same stream for several years (Baxter 1995), and other reports of shifting spawning sites over time (McPhail and Murray 1979; Pratt 1992). Presumably, homing is adaptive and therefore subject to natural selection. Perhaps the degree of homing is variable, and related to stream size (and stability). For example, bull trout spawning in small streams, like Mackenzie Creek, that are subject to periodic drought may be selected to switch spawning streams if they encounter difficulties. In contrast, bull trout that spawn in larger, more stable, streams may be selected to home with a high degree of fidelity.

4.2 Stocks

Leary et al. (1993) examined 51 isozyme loci in eleven Columbia system rivers and one river in the Klamath system. As expected, Klamath and Columbia bull trout are distinguishable (Nei's unbiased genetic distance of 0.032), but local bull trout populations contained little genetic variability. Thus, most of the genetic divergence is among, rather than within, populations. This type of genetic structuring implies either past population "bottlenecks" or strong local selection with little gene flow between rivers. In either case, it provides strong evidence for the existence of local stocks. Aside from this isozyme survey, there is little direct evidence of stocks in bull trout. However, site to site differences in life-history traits, nuptial colouring and spawning morphology also imply genetic differences among populations.

4.3 Population size and controls

4.3.1 Population size

Relative to coexisting species, bull trout densities usually are low, and most broad faunal surveys indicate <5% of the total catch is made up of bull trout (Irvine and Rowland 1979; McLeod et al. 1979; Kristensen 1980; Craig and Bruce 1982; Chisholm et al. 1989; Hildebrand 1991). Quantitative estimates of adult densities in lakes are rare, but hydroacoustic surveys in Chester Morse Lake, Washington suggest adult densities can be substantial (Katherine Lynch, Seattle Water Department, Seattle, personal communication). Fraley and Shepard (1989) used redd counts to establish an index of adult abundance in the Flathead system. Although there are difficulties identifying redds (Brown 1992) and the number of adults per redd varies among populations (McPhail and Murray 1979; Oliver 1979; Fraley and Shepard 1989; Pratt 1992), the technique shows promise and redd counts are beginning to accumulate from other river systems (e.g., Ratliff 1992; Baxter 1994a, 1995).

Electroshocking and snorkeling surveys in streams provide estimates of juvenile densities. Unfortunately, there is no standardized method of reporting the results of such surveys, thus, comparisons are difficult. Fraley and Shepard (1989) report 62-170 juvenile per 150 m (13 sites over 8 years) in the Flathead system. Bond and Long (1979 in Goetz 1989) found 10-20 per 100 yds (93 m) in a Klamath tributary, and Carl (1985) reports densities of 13-83 bull trout (adults and juveniles) per km in Elk Creek, Alberta. Pratt (1984) gives densities of 0.7-37.5 per 100 m^2, and Brown (1992) summarizes eight density estimates from Washington State (they range from 0.22-15 per 100 m^2). In Idaho, Schill (1992) reports a trend of decreasing bull trout densities at 112 standardized sites over a 5 year period from 0.132 fish per 100 m^2 to 0.048 fish per 100 m^2. For combined samples of juveniles and adults from Line Creek, Allan (1993) estimates densities of 1.9 to 5.2 individuals per 100m^2. Perhaps the most reliable estimates of juvenile densities are those of Sexauer (1994). Her numbers are based on night snorkel surveys of four streams on the east slope of the Cascade Mountains in central Washington. She found juvenile densities varied from 0.03 to 4.06 fish per 100m^2, with mean densities of 0.23 to 1.85 fish per 100m^2 (Sexauer 1994).

Regardless of the units used, it is clear that, on average, juvenile bull trout densities in streams are low. Given the propensity of bull trout fry to hide in the substrate during the day, it is not surprising that there are no quantitative estimates of fry density.

4.3.2 Population controls

Not much is known about the natural determinants of population densities in bull trout. For an adfluvial population in the Arrow Lakes, McPhail and Murray (1979) argue that adult population density is influenced by the carrying capacity of spawning streams. The argument is circumstantial and based on the pattern of emigration from one small stream. By June the number of fry in Mackenzie Creek is small (about 15% of the bull trout population in the creek; whereas, 1+ and 2+ juveniles make up 85% of the population). This suggests that most of the young-of-the-year produced in Mackenzie Creek emigrate to the lake as fry, probably during spring freshet. Interestingly, 15% of lake-caught adults show no stream growth, again suggesting emigration as fry. Five percent of lake-caught adults emigrated to the lake after one year of stream growth, 25% after two years and 50% after three years. Only 5% of lake caught adults show four years of stream growth. Thus, 75% of lake-caught adults show two or three summers of stream growth, even though most of the annual production, at least from Mackenzie Creek, probably emigrate as fry (McPhail and Murray 1979). This implies that fish with two or three summers stream growth have a higher probability of survival upon lake entry than fry. Why, then, do fry leave the stream? The simplest answer is that the carrying capacity of the stream is limited and that most fry simply do not find a suitable holding site. Consequently, they are displaced downstream into the lake. Although comparable data on fry abundance in tributary streams is not available, Chisholm et al. (1 989) found a similar relationship between years of stream growth and proportion of lake caught adults in each emigration class in Lake Koocanusa (Libby Reservoir). Also, in the Flathead system, 18% of juveniles emigrated from tributaries into the main river after one year, 49% after two years, 32% after three years and only 1% after four years of stream growth (Fraley and Shepard 1989). Again, this suggests that two or three years of stream residence is critical to successful recruitment of bull trout to adult habitats.

Another possible limiting factor is suitable spawning sites. In Mackenzie Creek, the majority of spawnings occurred in small, widely dispersed "pockets" of fine gravel. Suggesting, at least in this stream, that spawning sites can be limiting and, interestingly, one pair of adults left Mackenzie Creek without spawning (McPhail and Murray 1979). Also, at other spawning sites there are reports of superimposition of redds (Heimer 1965; Oliver 1979; Ratliff 1987 in Goetz 1989; Baxter 1995) and, again, this could indicate a shortage of spawning sites. In the Skagit River above Ross Reservoir and in the Chowade River (Peace system), bull trout spawning was confined to the main river and, although there appears to be several kilometers of suitable spawning area, redds were concentrated in about 500 m of river (McPhail personal observation; Baxter 1995). This suggests that bull trout are highly selective in where they spawn and, although there is remarkable consistency across rivers in the physical descriptions of spawning sites (summarized in Goetz 1989), within drainage systems it is not clear why they spawn in only a small fraction of the apparently suitable sites. Groundwater infiltration has been suggested as a factor in bull trout redd site selection (Fraley and Shepard 1989), but there is no conclusive evidence for this case.

Whatever the natural controls on bull trout populations, it is now clear that over most of the species' range human activities are the major causes of population declines.

5.0 ENVIRONMENTAL IMPACTS ON BULL TROUT

5.1 Impoundments

5.1.1 Reservoirs

There are a number of reservoirs (storage and run-of-the-river) and associated dams on the upper Columbia, upper Kootenay, and Peace rivers. The effects of these dams on bull trout are mostly negative, but there are some positive effects. On the upper Columbia and upper Kootenay, most dams are passage barriers to bull trout migrations (e.g., Bigfork, Hungry Horse, Libby, Duncan, and Revelstoke dams). These barriers have taken large sections of river systems out of bull trout production, and have been responsible for major declines in some areas (Fraley and Shepard 1989). In addition to passage barriers, there are other negative downstream effects. Gas supersaturation is a common problem associated with Columbia River dams and, although there is no direct data on bull trout, Gas Bubble Trauma can be a major source of mortality in salmonids for kilometers downstream of dams (Fidler 1985). Also, turbines probably cause some of mortality for bull trout in reservoirs. Dams also change natural flow and temperature regimes and, potentially, can alter cues used in the complex migrations that are characteristic of some bull trout life-history forms. More important, perhaps, are the effects of changes in natural flows on bull trout fry. Young-of-the-year occupy the shallow edges of rivers and streams and seek interstitial cover when disturbed. This micro-habitat is especially vulnerable to changes in water levels and, for rivers with regulated flows, sudden reductions in flow may strand large numbers of fry. In addition, many storage reservoirs in B.C. occupy U-shaped valleys. Typically, such reservoirs flood the low gradient sections of tributary streams and thus inundate spawning sites. Whatever the reasons, the long term effects of most dams on bull trout are negative. For example, Hildebrand (1992) notes the decline in bull trout numbers in the Columbia River near Castlegar since the construction of Keenleyside dam.

The positive effects of impoundments are that sometimes they provide large, lacustrine environments in areas were none were previously available. Williston Reservoir on the Peace River is an example. Before the reservoir, the upper Peace contained mostly small stream resident and fluvial populations of bull trout. With the construction of the reservoir, a lacustrine environment containing large populations of prey species was added. Bull trout now use the lake extensively and appear to be developing an adfluvial life-history (Bruce and Starr 1985). Although this response is positive, high mercury levels are present in

Williston Reservoir bull trout with 60% of the samples exceeding the Canadian federal guideline of 0.5 ppm (Watson 1992). On the Deschutes River, Oregon, the Round Butte Dam created a large lake (Lake Billy Chinook). Ratliff (1992) notes that juvenile bull trout that reach the lake grow at rates of 1.4 cm per month, which is much faster than in other habitats in the same system.

5.2 Other impacts

5.2.1 Logging, pipe lines, oil exploration, and road construction

The impacts of these activities on bull trout are dependent on the nature of the terrain and the care exercised by the operators but, if careful controls are not in place, they typically produce general habitat degradation. They all increase siltation, and increased siltation, especially in small, spawning streams is a major problem. The survival of bull trout eggs is a function of the proportion of fines (<6.35 mm) in the incubation gravel (Weaver and White 1985). Shepard et al. (1984b) found that incubation mortality increased abruptly with 30% fines, and survival with 50% fines was zero. A serious secondary effect of siltation is that it cements gravel into the substrate. Loose substrate is essential to young-of-the-year bull trout as cover, and for the community of aquatic insects that provide the major food source for bull trout fry and juveniles (Nakano et al. 1992). An unexplored, but potentially important, impact of the temporary increases in turbidity associated with construction is their effect on the social structure of bull trout fry. Although not overtly aggressive, in the laboratory bull trout fry occupy focal sites from which they displace intruders (McPhail personal observation). Consequently, even a temporary increase in turbidity may cause the break-down of social structure and lead to increased fry mortality.

Logging, and pipeline construction right-of-ways, often remove riparian vegetation and decrease the frequency of occurrence of large instream woody debris. Focal sites in juvenile bull trout are strongly associated with overhanging vegetation (Nakano et al. 1992), and woody debris provides cover for juveniles, stream-resident adults, and migratory spawners. Loss of riparian shade in the summer can increase temperatures to above 15°C and removal of vegetation results in increased variation in flow. This leads to low flows in summer and fall, scouring flash floods in spring, and substrate freezing in winter. Regardless, the distribution and abundance of bull trout have been associated with patterns of habitat condition that suggest habitat disruption has directly influenced many populations (Riemen and McIntyre 1993).

Also, these activities lead to increased access, especially to the upper reaches of streams. In late summer, migratory bull trout characteristically ascend tributary streams up to some impassable barrier (often a falls) and then hold in deep pools for up to a month before spawning. At this time they are particularly vulnerable: they are large, conspicuously coloured, good to eat, and will take almost any lure. Poaching and other forms of harassment are a problem wherever access to tributary streams is increased.

5.2.2 Recreational fisheries

In common with other long lived, voracious species, bull trout are vulnerable to recruitment overfishing. Recruitment depends, at least in part, on the number of spawners, and adult bull trout are relatively easy to catch. Cross (1985) estimates that in Flathead Lake a minimum of 30% of the adult bull trout tagged in a spawning run were caught by anglers in the lake, while O'Brien (1996) noted that 10% (5 of 49) of bull trout that were radiotagged in the Duncan Lake system were harvested by anglers within 6 months. Recreational fisheries target adult bull trout, and except in a few large lakes, sustaining fisheries for this species is a problem. For example, Martin (1986) reviewed creel survey results for a high elevation lake in southeastern B.C. Access to the lake was improved in the 1970s. At first the fishery took 80% cutthroat trout and 20% bull trout, but by 1986 bull trout made up only 10% of the catch, and Martin (1986) estimated that most of the bull trout catch were new recruits.

There are two recent studies that indicate restrictive angling regulations have a beneficial effect on bull trout populations. Allan (1993) suggests that the increase in the number of bull trout spawning in Line Creek over the last decade, may be attributable to changes in fishing regulations, specifically a reduction in the daily bag limit from eight fish to two. In a more detailed study in Lower Kananaskis Lake, Alberta, Stelfox and Egan (1995) found that with a change in angler harvest of bull trout to zero, the percentage of repeat spawning by bull trout over a three year period increased from 52% to 82%. They directly attribute this increase to the zero bag limit.

5.2.3 Interactions with other species

5.2.3.1 Competition

Leathe and Graham (1982) suggest that because of their piscivorous habits, adult bull trout show little food overlap with other salmonids. This may be true in many natural situations, but Donald and Alger (1993) document the replacement of lacustrine bull trout by introduced lake trout *(Salvelinus namaycush)*. Originally, many of the high altitude (>1300 m) lakes on the east slope of the Rocky Mountains in Alberta contained only two fish species: bull trout, and mountain whitefish. In these lakes, bull trout made up about 12% of fish sampled by gill nets. One such lake was Bow Lake. In 1964, lake trout were introduced to Bow Lake and by 1984 bull trout had vanished. Lake trout then dispersed downstream from Bow Lake and reached Hector Lake sometime in the 1970s. By 1984, bull trout made up only 6% of the gill net catch in Hector Lake, and by 1992 they were gone. Donald and Alger (1993) attribute the replacement of bull trout by lake trout to competition. In the same vein, Marnell (1985) suggests that the decline of bull trout in some Glacier National Parks lakes may be a result of lake trout introductions.

Presumably, the bull trout's interactions with native species have co-evolved over time, and therefore are less severe than the interaction with lake trout. For example, Marnell (1985) suggests that in the Isabel Lakes, Glacier National Park, where native populations of cutthroat trout and bull trout coexist, they show well developed habitat partitioning. Nakano et al. (1992) record resource partitioning between stream dwelling bull trout and native cutthroat. Similarly, in Mackenzie Creek, McPhail and Murray (1979) found clear differences in habitat use by sympatric bull trout and rainbow trout. Seasonally, adult bull trout and adult squawfish *(Ptychocheilus oregonensis)* show strong diet overlap (Jeppson and Platts 1959; Thompson and Tufts 1967), but the thermal preferences of these species are so different (squawfish abruptly reduce their rate of intake below 12°C; whereas, bull trout avoid temperatures above 15°C) that severe competition between these species is unlikely.

5.2.3.2 Hybridization

Hybrids between bull trout and introduced brook trout are known from Oregon (Markle 1992), Montana (Leary et al. 1983), Alberta (Nelson and Paetz 1992), and British Columbia (McPhail and Taylor 1995). Apparently, most bull trout-brook trout hybrids are males (Leary et al. 1983) and perhaps they are sterile; however, Markle (1992) reported a female hybrid from Oregon, and one of the two hybrids found in the Skagit system also was a female (McPhail and Taylor 1995). An imbalanced sex ratio (a deficiency in the heterogametic sex) is a common observation in hybrids (Haldane 1932). If the bull trout-brook trout cross is sterile (or has significantly diminished fertility relative to the parental species), occasional hybrids probably are of little genetic consequence except in small, isolated populations of bull trout. If, however, the hybrids are fertile and capable of back-crossing, introgression (fusion of genomes) could result in the genetic swamping of bull trout in areas were brook trout are introduced. So far, in British Columbia, there is no evidence of introgression between bull trout and brook trout.

In contrast, there is evidence of introgression between bull trout and Dolly Varden in areas where their geographic distributions overlap (McPhail and Taylor 1995; Baxter et al. in prep.). In such areas (e.g. the Skagit system in southwestern BC and northwestern Washington, and Thutade Lake system in northern B.C.), there is both morphological (Brown 1992) and molecular evidence not only of hybridization but also of gene exchange between the species (McPhail and Taylor 1995; Baxter et al. in prep.). The situation is complex, however, and although the mitochondrial genome shows hard evidence of gene flow, the morphologies of the two species clearly map onto two distinctive habitats (McPhail and Keeley in prep.; Bustard and Royea 1995). This suggests that the morphological differences between the species are adaptive and, in the area of overlap, a Dolly Varden-like morphology predominates in small stream drift foragers while a bull trout-like morphology prevails in lacustrine and large stream piscivores,

6.0 OPPORTUNITIES FOR HABITAT COMPENSATION AND IMPROVEMENT

6.1 Spawning habitats

In small streams, or hydro impacted rivers, spawning habitat may be limiting and, consequently, in some areas site enhancement may be a viable option. Bull trout will spawn in small pockets of suitable gravel (McPhail and Murray 1979). Thus, strategically placed stop-logs or other instream modifications such as large boulders that trap gravel and create holding sites may increase the number of available spawning sites. On a larger scale, however, not enough is known about the spawning requirements of bull trout to make the construction of artificial spawning sites feasible. As mentioned earlier, in many systems (e.g., Chowade and Skagit rivers) bull trout use only a small fraction of what appears to be suitable, available spawning habitat. Thus, although the flow and substrate characteristics of redds have been measured (reviewed in Goetz 1989), it is not clear what factors govern the choice of spawning sites by bull trout. What this suggests is that reconstruction of appropriate spawning habitat may not necessarily enhance spawning. If artificial spawning sites become technically feasible, there still would have to be solid evidence that fry production was limiting population size, or that a proposed development would impact spawning habitat, before such a project was attempted.

6.2 Egg development habitat

6.2.1 Natural propagation

The two major sources of incubation mortality are silt and freezing. Sometimes, human sources of silt can be controlled by regulation of activities in vulnerable watersheds. In natural systems, seasonal floods act to scour silt from gravel. In flow-regulated rivers, occasional water releases that mimic natural surges may help to maintain suitable spawning habitats. For activities that produce temporary silt loads (e.g., pipeline construction), confining construction activity to specific time periods may be the only feasible strategy. But, because of their dependence on interstitial cover in their first year of life, safe "construction time windows" for bull trout may be narrower than for most salmonids.

The freezing of redds can be prevented by requiring human activities to assure sufficient winter flows. In nature, bull trout show a propensity to spawn in areas with ground water (Fraley and Shepard 1989). In some cases, it may be possible to prevent eggs from freezing by diverting nearby ground water sources into spawning areas, or identifying ground water sources and limiting activity in these areas if they are critical for spawning.

6.2.2 Artificial propagation

Artificial propagation of bull trout has been tried in British Columbia at the Kootenay Hatchery (Brown 1985). Optimal incubation temperatures are lower than found in most trout hatcheries, and newly fertilized eggs are especially sensitive. Even with these limitations, however, reasonable hatching success and fry survival are possible (Brown 1985). Survival of juveniles under hatchery conditions is still a problem, but with research this can probably be solved. Certainly, there was no problem rearing bull trout from eggs to adults under laboratory conditions (McPhail and Murray 1979). Given the present concern about wild stocks of salmonids, and the poor performance of hatcheries in other enhancement programs, artificial propagation probably is not a desirable enhancement tool for bull trout.

6.3 Fry habitat

Since bull trout have evolved in environments with fluctuating flows, the fry probably have behavioural mechanism to cope with changes in water levels, provided the changes reflect the natural seasonal flow regime and are not too sudden. Low velocity side channel areas with an abundance of instream cobbles for cover have been identified as critical habitat for summer rearing (Baxter 1995), and perhaps these habitats could be enhanced.

6.4 Juvenile habitat

The carrying capacity of streams for juveniles is thought to be a major "bottleneck" in bull trout production (McPhail and Murray 1979). Consequently, any modifications in tributary streams that increase juvenile habitat may increase recruitment to lakes and large rivers. Nakano et al. (1992) describe the characteristics of juvenile holding sites in a small stream. Their study, and others, emphasize the importance of cover, especially overhead cover, to juvenile bull trout. Consequently, the carrying capacity of small streams might be enhanced by providing more overhead cover in association with devices that break stream-flow.

6.5 Adult habitat

For lacustrine populations not a lot can be done to improve adult habitat. In run-of-the-river reservoirs it may be possible to prolong water retention time and thus increase plankton production. Such a strategy could increase prey species like kokanee and mountain whitefish, and secondarily increase growth and survival of bull trout. The same is true for fluvial populations, although in some moderate size rivers properly placed debris catchers might provide more cover, primarily in the form of log jams. For adults, protection from poaching and over-fishing by catch restrictions, gear regulation and closures, is the surest way to improve adult survival.

6.6 Public education and involvement programs

The turn around in the bull trout's public reputation is remarkable. In anglers', and provincial and state fisheries biologists, eyes the bull trout has gone from "trash fish" to "trophy fish" in less than two decades. It is not that large bull trout were scorned, there has been a trophy fishery in large lakes in Idaho, Montana and B.C. for years but, generally the species was held to be inferior to trout and a menace to young trout. Now that the bull trout's reputation has been polished, the main public education problem is restraint. Because of their habit of ascending streams in the summer and holding in deep pools (often below a barrier), large bull trout are exceptionally vulnerable to poaching and over-fishing. The public must be made aware that the species is in serious decline, and that the standard mitigation "techno-fixes" (e.g., hatcheries and artificial spawning sites) either will not work or are undesirable for bull trout. The only practical management tool for the species is regulation, and this requires not only public participation but also public understanding of why the regulations exist and what they are meant to accomplish. An example of the efficacy of regulation as a restoration tool for bull trout is provided by Line Creek in southeastern British Columbia. Allan (1993) analysed the upward trend in the number of bull trout spawning in Line Creek since the mid-1980s and attributed the increase to a change in regulations in 1985 that reduced daily bag limits from eight to two fish, only one of which could be larger than 50 cm.

6.7 Essential biological research

There are several major gaps in our knowledge of bull trout biology. First, in common with many species, we do not know what controls bull trout recruitment. It is relatively easy to obtain adult mortality rates, numbers of spawners, fecundity and even egg survival, but more difficult to measure fry and juvenile survival rates. The problem is especially acute in the adfluvial life-history form. What happens between recruitment to the lake or reservoir and recruitment to the fishery? The ecology of juvenile bull trout in large lakes is still a black box of unknowns. In the same vein, we are ignorant about the behaviour and ecology of bull trout fry. The few studies that report the relative numbers of young-of-the-year and juveniles suggest that by late summer juveniles out-number fry by about five times (McPhail and Murray 1979; Allan 1993). Do these numbers simply reflect the difficulty of enumerating fry, or do they implicate cannibalism as an important source of fry mortality?

A second obvious gap in our knowledge of the biology of bull trout involves the anadromous life-history form. We are not certain it even exists, but if it does, there are many questions regarding the ecology, physiology and behaviour of downstream migrants that require investigation. In addition, the duration of the marine phase and the distance of marine migrations are a mystery. Do they remain in the Puget Sound-Strait of Georgia region, or do some actually migrate out to sea? On their return to the river do they home precisely, or is there a high rate of straying? These questions will have to be answered before a rational management program for anadromous bull trout can be crafted.

Lastly, the vexing question of the relationship between bull trout and Dolly Varden needs clarification. In areas outside the region of overlap, species identification is not a problem, for management purposes the taxonomic status of the fish is irrelevant as long as there is only one species in an area. It is in the zone of overlap that the question of whether there is one, or two, species becomes important. If there are two coexisting species, they are likely to have slightly different habitat requirements and life-histories and, consequently, may require slightly different management plans.

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