Prevalence of the Sockeye Salmon Brain Parasite *Myxobolus arcticus* in Selected Alaska Streams

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Prevalence of the Sockeye Salmon Brain Parasite *Myxobolus arcticus* in Selected Alaska Streams

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ABSTRACT: Over 10,000 spawning sockeye salmon *Oncorhynchus nerka* throughout Alaska were examined for the presence of the brain parasite *Myxobolus arcticus* to evaluate its potential as a natural marker to separate mixed stock fisheries in Alaska. Prevalence of the parasite (proportion of fish infected by the parasite) differed widely among sampling locations. The brain parasite, previously reported as common in southeastern Alaska, infected sockeye salmon primarily in coastal lake systems of eastern Prince William Sound and the Copper River area. Brain parasites were present in >85% of the fish returning to lakes east of Cook Inlet, whereas <20% of fish returning to glacial and riverine habitats in the same region were infected. Sockeye salmon systems west of Prince William Sound, such as Bristol Bay and Cook Inlet, were largely devoid of the parasite. Prevalence of the parasite in southeastern Alaska systems appeared stable over the last decade in lake systems but was more variable in riverine habitat. In the Taku River parasite prevalence varied widely between sites but was similar among years for most locations within the river. The restricted geographic distribution and potential for low interannual variability suggest that *M. arcticus* could serve, especially when used in conjunction with other techniques, as an effective biological marker for estimating origins of sockeye salmon caught in high seas and coastal fisheries.

INTRODUCTION

Salmonid parasites enable fishery managers to separate groups of fish in mixed stock fisheries because parasites acquired in fresh water reflect differences in the rearing environment. The myxosporean parasite *Myxobolus arcticus* (formerly identified as *M. neurobius*), present in the brain tissue of salmonids, has proven useful in assigning stock of origin for sockeye salmon *Oncorhynchus nerka* and chinook salmon *O. tshawytscha* because of its distinct geographic distribution (Margolis 1982; Urawa et al. 1998). This parasite is present in nearly all sockeye salmon in the coastal lake habitats of southeastern Alaska and British Columbia (Moles et al. 1990; Rutherford et al. 1992). Because it is largely absent from Canadian stocks of sockeye salmon that emanate from the extensive transboundary rivers (Bailey and Margolis 1987; Wood et al. 1988), parasite prevalence is used in conjunction with scale pattern analysis for stock composition estimation in the mixed stock fisheries in southeastern Alaska. *Myxobolus*, along with other parasites, has also been used to differentiate up to 7 stocks of sockeye salmon on the Fraser River system with precision (Bailey and Margolis 1987). In addition, the distribution of this and other parasites provides information on the migratory route of sockeye salmon (Bailey et al. 1988). However, the distribution of the parasite in the larger and more complex riverine systems that characterize much of the sockeye salmon habitat in the rest of Alaska is not well documented.

Myxobolus is acquired in the freshwater environment and persists for the life of the host (Quinn et al. 1987). There is some decrease in swimming performance among infected fish, but the parasite causes little other damage to host function (Moles and Heifetz 1998). The presence of the parasite in some fish but not in others in the same river is thought to be due to differences in freshwater habitat or early life history

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of the host. The probability of parasitism by *Myxobolus* increases as the habitat becomes less variable and the length of freshwater residence increases (Moles et al. 1990). Evidence from the Stikine River suggests parasite prevalence may be affected by the length of freshwater residence (Wood et al. 1987b). Thirty-nine percent of age-0 fish were parasitized, whereas 55% of age-1 fish in the Stikine River were parasitized. In the Iskut River 16% of age-0 fish and 23% of age-1 fish were parasitized (Wood et al. 1987b).

If factors influencing distribution of *Myxobolus* were understood better, distribution of parasitized sockeye salmon could be predicted, and its use as a stock-separation marker could be enhanced without costly annual resampling of reference stocks. Our objectives were to determine the prevalence of *Myxobolus* in the majority of sockeye salmon-producing lakes of Alaska, estimate the interannual variation by comparing current parasite prevalences in southeastern Alaska lakes with prevalences in the same lake systems a decade ago, and establish whether a relationship exists between freshwater residence time (inferred from scale age determination) and the prevalence of *Myxobolus* in adults returning to their natal streams in southeastern Alaska. We examined parasite prevalence from sockeye salmon systems in Alaska ranging from lake systems with long freshwater residence periods to rivers with virtually no freshwater rearing period. Some systems were single, short rivers associated with a nursery lake, whereas others were large, complex riverine systems containing a variety of rearing habitats.

METHODS

Fish were sampled in 1989 and 1990 from 86 lakes and streams from Kuskokwim Bay to Prince William Sound to establish the baseline distribution of *Myxobolus* in sockeye salmon in Alaska. The Kuskokwim River, Bristol Bay, and the Alaska Peninsula were sampled in 1989; Cook Inlet, Prince William Sound, and 2 systems in the Kodiak area were sampled in 1989 and 1990. Approximately 50 spawners were captured from each lake or stream with seines, gillnets, or spears by personnel from the Alaska Department of Fish and Game, National Marine Fisheries Service, and the U.S. Fish and Wildlife Service. A sample size of 50 is required to detect the presence of the parasite in large populations with >10% overall prevalence of that parasite (Anonymous 1984). Sampling locations were chosen to cover a wide geographic range and to select streams with sizable runs of sockeye salmon. Fish heads were removed, individually bagged, and frozen for shipment to the laboratory.

To determine interannual variability in parasite prevalence, sockeye salmon spawners were also sampled in 1997 for the prevalence of *Myxobolus* from 19 lakes in southeastern Alaska previously assessed in 1986 and 1987 (Moles et al. 1990). These were some of the most productive sockeye salmon systems in southeastern Alaska. The few systems previously characterized as having low parasitism were sampled because variation in parasitism is more discernable in systems with low prevalence. The Mann-Whitney rank sum test was used to determine the significance of the variation in prevalence between years. The Taku River and neighboring Port Snettisham were also sampled during 1986–1999 at 15 locations to evaluate parasite prevalence of stocks that contribute sockeye salmon to the District 111 gillnet fishery. The Fisher exact test was used to assess significance of changes occurring over the sampling period. Linear regressions of the arc sine-transformed prevalences were computed for systems with significant Fisher tests.

In the laboratory brains were removed and analyzed for parasites using a variation of the pepsin digest method developed for detection of whirling disease (Anonymous 1984). After a pepsin digest in a horizontal shaker bath, the digest was centrifuged at 1,200 g for 5 minutes. The pellet was examined for spores using a phase contrast microscope at 250×; slides with <10 spores were reexamined to confirm the presence of spores. Presence or absence of the parasite in each fish was recorded. A minimum of 10 spores in 300 microscope fields was required for a positive sample. Intensity of infection was not estimated.

The influence of freshwater residence time on parasitism was examined for selected streams using estimates of age from scales. Freshwater age and the presence or absence of the brain parasite were determined for fish sampled in 1987 from 10 Taku River sites as well as for fish sampled from the Situk, Old Situk, and East Alsek Rivers. The Taku River was chosen because of the wide variability in parasite prevalence noted previously. A variety of habitats were sampled in the Taku River ranging from glacial channels to slow, clear beaver ponds similar to lakes. Situk, Old Situk, and East Alsek Rivers are geographically adjacent, but the sockeye salmon in the rivers have different parasite prevalences and life history strategies. For each fish sampled from these systems, 3–4 scales were collected for aging. Scale impressions were made in the laboratory and examined at 85× to determine the length of freshwater residence. Prevalence values were arc sine-transformed, and a Kruskal-Wallis one-way analysis of variance on ranks was used to determine whether infection rate varied by age group

Table 1. Prevalence of *Myxobolus arcticus* in sockeye salmon systems in central Alaska in 1989–1990.

System	Sample Size	Proportion of Fish Infected
Kuskokwim		
Goodnews River, near fork	50	0.00
Goodnews River, main fork	50	0.00
Kagati Lake	50	0.00
Telaquana Lake	50	0.00
Bristol Bay		
Nushagak drainage		
Igushak River	50	0.00
Wood River	50	0.00
Kulik Lake	50	0.00
Nushagak River	50	0.00
Nushagak Lake	50	0.00
Ugashik drainage		
Blade Creek	50	0.00
Ugashik Narrows	50	0.00
Ugashik Lake	50	0.00
Deer Creek	50	0.00
Ugashik Creek	50	0.00
Egegik drainage		
Featherly Creek	50	0.00
Becharof Lake	50	0.00
Naknek drainage		
Margot Creek	50	0.00
Naknek Lake	50	0.00
Brooks Lake	50	0.00
Iliamna drainage		
Copper Creek	50	0.00
Kvichak River	50	0.00
Gibraltar Creek	50	0.00
Iliamna River	50	0.00
Belinda Creek	50	0.00
Battle Creek	50	0.00
Lake Clark drainage		
Kijik River	50	0.00
Tazimina River	50	0.00
Togiak River	50	0.00
Alaska Peninsula		
Urilia Bay	100	0.00
Thin River	50	0.00
Nelson Lagoon	50	0.56
Hoodoo Lake	50	1.00
Bear Lake	50	0.00
Sandy River	50	0.00
Ilnik River	50	0.00
Chignik Lake	32	0.00
Meshik River	50	0.00
Kodiak		
Karluk River, Kodiak	50	1.00
Thumb River, Kodiak	50	0.00
Pauls Bay, Afognak Island	26	0.85
Cook Inlet		
Chenik Lake	50	0.00
Crescent River	50	0.00
Big River Lake	50	0.00
Packers Creek Lake	50	0.00
China Poot Bay	50	0.00
Kasilof River	50	0.00
Tustamena Lake		
Nikolai Creek	50	0.00
Bear Creek	50	0.00
Glacier Flats	50	0.00
Moose Creek	50	0.00
Crystal Creek	50	0.00
Clear Creek	50	0.00
Seepage Creek	50	0.00
Daniels Lake	50	0.00
Kenai River		
Main stem	50	0.00
Hidden Lake	50	0.00
Russian River	50	0.00
Susitna River		
Main stem	50	0.00
Yentna River	50	0.00
Hewitt Lake	50	0.00
Chelatna Lake	50	0.00
Big Lake	50	0.00
Port Dick Lake	50	0.00
Nuka Bay	50	0.00
Aialik Bay	50	0.00
Prince William Sound		
Jackpot Creek	50	0.00
Eshamy Creek	50	0.00
Main Bay (jacks)	50	0.00
Coghill River	50	0.00
Miners Lake	50	0.48
Billys Hole Lake	99	0.90
Ragged Point	100	0.59
Twentyseven Mile Slough	100	0.17
Robe Lake	43	0.91
Copper River (main stem)	100	0.08
McKinley Lake	100	0.93
Eyak Lake	100	0.99
Chitina River	150	0.05
Martin River Slough	100	0.19
Martin Lake	100	0.91
Little Martin Lake	100	0.97
Bering Lake	100	1.00
Kushtaka Lake	100	0.96
Lake Tokun	100	0.98
Thirtynine Mile Slough	100	0.06
Pleasant Creek	50	0.74

in the Taku River. Pairwise multiple comparisons between age groups were made using Dunn's test.

RESULTS

Of the 3,258 sockeye salmon examined from 65 river systems west of Prince William Sound in Alaska, only 150 fish (<5%) from 3 systems (Nelson Lagoon/Hoodoo Lake, Karluk River, and Pauls Bay) were parasitized by *M. arcticus* (Table 1). The parasite was absent in samples from all 24 Bristol Bay systems examined. These systems represent the major sockeye salmon river drainages in Bristol Bay and are among the most productive sockeye salmon streams in the world. *Myxobolus* was also absent from the 4 Kuskokwim River sites and all Cook Inlet sites. On the Alaska Peninsula the parasite was present only in the Nelson Lagoon/Hoodoo Lake system. Prevalence of the parasite in Hoodoo Lake was 100%, but was only 56% in Nelson Lagoon into which Hoodoo Lake flows. The systems examined from these 3 areas represent the majority of the sockeye salmon production of Alaska. In contrast, fish from 2 of the 3 systems examined from Kodiak and Afognak Islands were heavily (≥85%) parasitized. Prevalence of the parasite was 100% in the Karluk River but was absent from the Thumb River which feeds Karluk Lake. In Pauls Bay on neighboring Afognak Island, 85% of the sockeye salmon were parasitized. The many other stocks on these 2 islands were not sampled.

In Prince William Sound parasitism with *Myxobolus* was more common. Many of the 1,792 fish examined from the river systems of eastern Prince William Sound and the Copper River area just east of the sound were parasitized with *Myxobolus* (Table 1). In contrast, fish from 4 locations sampled in western Prince William Sound were devoid of the parasite. Nine locations in Prince William Sound had a parasite prevalence ≥90%. These were shallow coastal lakes similar to many sockeye salmon-producing lakes of southeastern Alaska. The rivers and sloughs had prevalences ranging from 5–74% incidence, and the Copper River had <10%. Fish from the remaining coastal systems of Alaska to the south and east were also heavily parasitized with *Myxobolus* (Moles et al. 1990).

Baseline resampling of 19 of the southeastern Alaska sockeye salmon systems found no significant shift ($P = 0.534$) in parasite prevalence between reported values from 1986–1987 and our sampling a decade later (Table 2). Fourteen systems were heavily (>88%) parasitized, Lace River was lightly parasitized (21%), and 4 systems were unparasitized (Chilkat Lake, Chilkoot Lake, Ford Arm Lake, and Steep Creek).

Table 2. Proportion of fish infected by *Myxobolus arcticus* in adult sockeye salmon returning to selected southeastern Alaska systems.

Location	Year	Sample Size	Proportion of Fish Infected
Auke Lake	1987	99	1.00
	1997	50	1.00
Chilkat Lake	1983	73	0.00[a]
	1997	19	0.00
Chilkoot Lake	1983	80	0.00[a]
	1997	18	0.00
Crescent Lake	1987	100	0.87
	1997	50	0.92
Ford Arm Lake	1987	68	0.00
	1997	50	0.00
Hugh Smith Lake	1987	127	0.99
	1997	38	1.00
Karta River	1987	99	0.99
	1997	51	1.00
Kegan Lake	1986	50	1.00
	1997	10	1.00
Klakas Lake	1988	50	1.00
	1997	50	0.98
Lace River	1987	50	0.20
	1997	34	0.21
McDonald Lake	1987	97	0.98
	1997	50	1.00
Petersburg Lake	1986	50	1.00
	1997	49	0.88
Red Lake	1986	53	0.96
	1997	50	1.00
Salmon Bay Lake	1986	51	0.96
	1997	47	1.00
Sarkar Lake	1986	44	0.98
	1997	5	1.00
Speel Lake	1986	100	0.85
	1997	42	0.98
Steep Creek	1987	50	0.16
	1997	69	0.00
Thoms Lake	1987	60	0.98
	1997	54	0.98
Windfall Lake	1987	50	0.90
	1997	50	1.00

[a] Leo Margolis, Canadian Department of Fisheries and Oceans, Nanaimo, British Columbia, personal communication.

Substantial variation in parasitism exists within the Taku River and Port Snettisham systems, depending on sampling locations (Table 3). For example, prevalence of *Myxobolus* in 1987 at 10 discrete locations in the Taku River ranged from 10% in the glacial Chum Salmon Slough to 81% in South Fork Slough. However, prevalences were more stable within a given location in the river. Fish in Tuskwa Slough, sampled

Table 3. Variation in the prevalence of *Myxobolus arcticus* at selected sites in the Taku River and Port Snettisham systems.

System	Year	Sample Size	Proportion of Fish Infected
Taku River			
Nahlin River	1988	31	0.00
Nakina River	1987	43	0.12
Takwahoni Slough	1986	20	0.25
	1987	17	0.29
Honakta Slough	1986	41	0.15
	1987	33	0.15
	1992	11	0.18
Shustahini Slough	1986	128	0.13
	1987	93	0.16
Chum Salmon Slough	1986	7	0.14
	1987	97	0.10
Coffee Slough	1986	30	0.00
	1987	33	0.18
Chunk Slough	1991	3	0.33
	1996	35	0.14
Tuskwa Slough	1986	60	0.13
	1987	147	0.12
	1991	12	0.12
	1992	8	0.13
	1993	33	0.12
	1995	97	0.18
	1996	27	0.19
Yellow Bluff	1995	19	0.21
	1996	16	0.13
South Fork Slough	1986	59	0.78
	1987	53	0.81
	1993	38	0.82
	1995	126	0.33
	1996	43	0.42
Fish Creek	1986	20	0.40
	1987	19	0.11
Yehring Creek	1986	89	0.12
	1987	195	0.12
	1991	20	0.05
Port Snettisham			
Crescent Lake	1987	100	0.87
	1988	100	0.81
	1991	61	0.90
	1992	56	1.00
	1993	105	0.93
	1994	94	1.00
	1995	100	0.98
	1996	131	0.94
	1997	50	0.92
	1998	83	0.99
	1999	105	0.97
Speel Lake	1986	100	0.85
	1987	100	0.74
	1988	104	0.82
	1992	94	0.95
	1993	66	0.89
	1994	87	0.97
	1995	100	0.98
	1996	79	0.98
	1997	42	0.98
	1998	12	1.00
	1999	93	0.97

Table 4. Prevalence of the brain parasite *Myxobolus arcticus* in adult sockeye salmon by spawning site and freshwater age group in the Taku River.

Location	Freshwater Age	Sample Size	Proportion of Fish Infected
Nakina River	0	10	0.10
	1	30	0.13
	2	3	0.00
Takwahoni Slough	0	9	0.11
	1	7	0.43
	2	1	1.00
Honakta Slough	0	22	0.09
	1	9	0.22
	2	2	0.50
Shustahini Slough	0	48	0.08
	1	44	0.23
	2	1	1.00
Chum Salmon Slough	0	41	0.05
	1	48	0.17
	2	3	0.33
Coffee Slough	0	15	0.00
	1	13	0.31
	2	5	0.40
Tuskwa Slough	0	66	0.08
	1	28	0.18
	2	1	0.00
South Fork Slough	0	34	0.62
	1	19	0.89
Fish Creek	0	8	0.00
	1	11	0.18
Yehring Creek	0	9	0.00
	1	117	0.13
	2	9	0.00
Total	0	262	0.14
	1	326	0.21
	2	25	0.24

7 out of 10 years between 1986 and 1996, had an average parasite prevalence of 14% (SD = 3). In contrast, fish in South Fork Slough, sampled in 1986, 1987, 1993, 1995, and 1996 had an average parasite prevalence of 63% (SD = 24). Crescent and Speel Lakes, both sampled 11 years out of 14 years, had prevalences of 94% (SD = 6) and 92% (SD = 8), respectively. Only 3 of the systems (South Fork Slough, Crescent Lake, and Speel Lake) had significant differences in parasite prevalences ($P \leq 0.001$) among years sampled. Prevalences decreased in South Fork Slough but increased in both Crescent and Speel Lakes; the regression was significant ($P = 0.0002$) only for Speel Lake.

Within the Taku River drainage returning adults with a longer freshwater residence were more likely to be parasitized than those that migrated directly to sea after emergence. Only 14% of the age-0 fish, but 21% of the age-1 and 24% of the age-2 fish, were

Table 5. Prevalence of the brain parasite *Myxobolus arcticus* in spawning sockeye salmon by river and freshwater age group.

Location	Freshwater Age	Sample Size	Proportion of Fish Infected
Situk River	0		
	1	6	1.00
	2	41	0.95
Old Situk River	0	31	0.32
	1	2	0.00
East Alsek River	0	88	0.10
	1	6	0.16
Pooled all rivers	0	381	0.14
(includes Taku River)	1	340	0.23
	2	66	0.68

parasitized (Table 4). Mean parasite prevalences were 11% (SD = 18, n = 262) for age-0 fish, 29% for age-1 fish (SD = 23, n = 362), and 40% for age-2 fish (SD = 42, n = 25) in 10 locations sampled in the river. Parasite prevalence in fish that spent one year in fresh water was significantly higher (P = 0.038) than fish that migrated to sea shortly after emergence. Presence of the parasite in 14% of the salmon that had migrated to the estuary within a few months of emergence (age 0) indicated infection can occur soon after hatching.

Among the 3 adjacent systems of the Yakutat area, parasitism rates differed among systems rather than among age groups within a system (Table 5). The Situk River system has a nursery lake and no age-0 sockeye salmon. Nearly all fish in our sample (87%) overwintered 2 years, and 96%, regardless of age, were parasitized. The Situk River system was similar to the heavily parasitized coastal lakes of southeastern Alaska. The nearby Old Situk River, primarily an age-0 system lacking a nursery lake, had a prevalence of 32% among the 31 age-0 fish examined. The age-1 (n = 2) fish from the Old Situk River were not parasitized. The East Alsek River can also be characterized as primarily an age-0 system; 10% of the age-0 fish (n = 88) and 16% of the age-1 fish (n = 6) were parasitized.

DISCUSSION

The coastal nursery lakes where many of the parasitized fish were found are typically wet, monomictic, oligotrophic, and have low phosphorus content, longer food chains, and rivers that run less than 50 km to the sea (Hyatt and Stockner 1985). Previous studies in British Columbia (Rutherford et al. 1992) and southeastern Alaska (Moles et al. 1990) also found that sockeye salmon from the coastal lakes had *Myxobolus* prevalences near 100%. In contrast, systems such as Bristol Bay are typically combinations of riverine and lake rearing areas containing many different habitats. Some larger river systems, such as the Taku and Stikine Rivers, contain little lacustrine habitat, and sockeye salmon must rear in the river.

Differences in geographic distribution of the parasite may be the result of physical characteristics of the lakes. Differences in parasite communities often reflect differences in aquatic habitat. Lake depth is an important determinant of parasite assemblages in oligotrophic salmon lakes (Marcogliese and Cone 1991). Aquatic oligochaetes appear to be intermediate hosts of *Myxobolus arcticus* (Kent et al. 1993). These worms feed on decaying spawning salmon and provide an environment for the myxosporean to transform into the infective triactinomyxon stage of the parasite (Urawa 1994). Sockeye salmon engaged in benthic feeding would be more likely to be exposed to the triactinomyxon stage. Additionally, gulls and aquatic waterfowl are more likely to visit coastal lakes with clearwater access to benthic feeding than other types of rearing habitat. These birds, which are often vectors for parasites, may also factor in the distribution of *Myxobolus*.

Lacustrine habitat provides the type of feeding environment conducive to infection. The brain parasite is seldom found in coho salmon *O. kisutch*, even when all sockeye salmon in the same lake are parasitized. Sockeye salmon rearing in lake-like habitat feed on Cladocera and Copepoda (Birtwell et al. 1987). Coho salmon, which may share the same habitat, typically feed on insect larvae (Koski and Kirchhofer 1984). Similarly, sockeye salmon in the Taku River feed largely on insect larvae (Brownlee 1991) rather than crustaceans. A triactinomyxon stage of *Myxobolus* would probably be consumed by salmon feeding on similarly shaped crustaceans.

The Taku and Stikine Rivers also have extensive glacial habitat. Turbidity can reduce visual feeding of Alaska salmon (Lloyd et al. 1987). If visual feeding plays a role in parasitism, the low prevalence of *Myxobolus* in these systems might be the result of turbidity reducing host–parasite interactions. As visual feeders sockeye salmon in glacial systems must feed near the surface, reducing the potential for infections from benthic intermediate hosts such as oligochaetes.

A second factor in structuring parasite communities in freshwater systems is the risk of exposure. Presumably, if sockeye salmon all shared the same lake environment they would also share the same potential for exposure to the parasite. Lake rearing, crowding,

and benthic feeding probably lead to increased opportunities for contact between parasite and host. In contrast, fish within riverine or glacial habitat would not share the same risk of exposure, and we would expect more variability in parasitism. In riverine habitats of southeastern Alaska parasitism by *Myxobolus* is more variable, as is the distribution of sockeye salmon in such systems. In much of the Taku River, for example, fish do not have access to lakes and instead rear in side channels. Side-channel habitats in the Taku River, such as beaver ponds and sloughs, provide rearing habitat for 39% of the sockeye salmon in the river, but account for only 5% of the river's area (Murphy et al. 1989). Within these areas, Murphy et al. observed fish densities in excess of 150/100 m^2, more than sufficient to ensure infection. Additionally, lakes, sloughs, and beaver ponds tend to retain more carcasses than faster-moving rivers, resulting in the presence of more spores.

Interannual stability of parasite prevalence is necessary for the parasite to be used as a population marker. Lake systems do not have to be resampled as frequently if the baseline prevalences are stable. Sophisticated stock separation methods combining parasite prevalence with genetic and freshwater age data require stability of the markers for accurate allocation of stocks (Pella et al. 1998). Several of these systems were lakes (Hugh Smith, McDonald, Kegan, Karta, Red Bay, Salmon Bay, and Thoms Lakes) that had also been sampled for *Myxobolus* by the Canadian Department of Fisheries and Oceans in 1983. Parasite prevalence reported by Wood et al. (1988) was similar to our values in Table 2, suggesting prevalence of *Myxobolus* in coastal lake systems of southeastern Alaska remained similar for 15 years, although the mechanism for this apparent stability is still a matter of speculation. Low variability in parasite prevalence in lake systems probably reflects the uniformity of habitat. In contrast, riverine areas such as South Fork Slough on the Taku River can vary annually in the carcass-washout rate, spawner density, and flow. Areas devoid of the parasite may therefore lack elements such as an intermediate host or sufficient density of host or parasite to allow successful infection of the population, or the parasite may not have been introduced into that lake or river. Prevalence changes in Speel and Crescent Lakes from a low of 74–81% in the mid 1980s to nearly 100% in 1999 suggests the parasite may become ubiquitous with time once it is established in a lake system.

The factors needed to establish infection in a lake are still largely unknown, and infection prevalence can change quickly. Baseline sampling for *Myxobolus* in Great Central Lake on the western coast of Vancouver Island from 1977 to 1984 characterized the lake as having a low prevalence (<5%) of *Myxobolus*. In 1993 to 1995 prevalence rose from 52% to 75% (Margolis 1998). Two nearby lakes remained stable with 100% prevalence suggesting the increase in parasitism might be due to fish straying to a nearby system. Or, conditions in the lake that precluded the parasite changed and now favor its development.

Prevalence, especially in systems with little or no evidence of *Myxobolus*, is subject to change, and baseline characterizations must be reestablished periodically if prevalence data are used to monitor mixed stock fisheries (Margolis 1998). There is presently no evidence to indicate a lake system characterized as heavily parasitized will show a substantial decline in parasitism over time. This suggests individual stocks do not have to be sampled frequently, but, in view of Margolis' results, should be examined periodically. In complex riverine habitats that support several stocks, such as the transboundary rivers originating in Canada, establishing interannual variability is more difficult. Spawning and rearing areas are geographically separate, and the risk of infection for a given fish may vary depending on the clarity of the water, carcass-washout rates, and the presence of stable rearing areas such as beaver ponds and sloughs.

Although the differences in parasitism among returning adults differed statistically between age-0 and age-1 fish, care should be taken in interpreting these results. The mixture of clear water and glacial habitat within the Taku River drainage confounds the issue. Age-2 spawners are more abundant in glacial lake populations in the similar Stikine River (Wood et al. 1987b), and fish from glacial habitat within the Taku River had lower levels of the brain parasite.

This mixture of glacial and clear habitats was not a complicating factor in the 3 Yakutat streams, but each system was primarily an age-0 or age-1, so no one system had enough fish of all ages to provide definitive answers.

Length of freshwater residence is determined by the amount of rearing habitat available (Wood et al. 1987a). In the absence of suitable lake habitat, some juvenile sockeye salmon rear in riverine or estuarine habitat. Wood et al. suggest 3 life history strategies for sockeye salmon. "Lake-type" fish are associated with the nursery lake–short river combination and rear for 1–3 years in fresh water. "River-type" fish rear in the ponds and sloughs of large rivers for a year. "Sea-type" fish migrate to sea as underyearlings and rear in the estuaries adjacent to the stream. Some larger rivers such as the Stikine and Taku Rivers contain many

fish using each strategy (Wood et al. 1987a). The rate of infection was greatest among lake systems with 2 years of freshwater residence and least among age-0 populations. The parasite was occasionally present in adults that spent only a few months in fresh water, indicating infection can take place soon after hatching because these fish leave rearing areas by early to mid summer.

The presence of *Myxobolus* in age-0 fish supports the theory that an intermediate host facilitates infection of sockeye salmon. An intermediate host such as an oligochaete has been implicated in the transmission of *Myxobolus* (Kent et al. 1993) and would provide the necessary mechanism for infecting newly emergent sockeye salmon long after the carcasses of returning adults had deteriorated. Our data also support Dana's (1982) findings that infection can take place soon after hatching, because sea-type fish leave rearing areas by early to mid summer before adults return (Heifetz et al. 1989).

Because lake-reared sockeye salmon share the same environment, they share the same risk of infection. Parasitism in such a system, whether 100% or 0%, is also less variable from year to year. In contrast, fish rearing in more complex systems occupy widely differing habitats and have differing risks of infection. The *M. arcticus* infection in coastal lake habitats of Alaska may be stable enough to justify its use as a biological marker without annual resampling of the individual stocks. Within complex habitat, all major contributing systems should be included in the baseline with periodic resampling of habitat types within the river.

Within the studied systems, prevalence of *M. arcticus* among sockeye salmon is probably related to the habitat of the host fish. The most important factors governing the prevalence of the parasite are probably access to the benthos and the presence or absence of a nursery lake; these factors are interrelated and difficult to examine individually. Parasite prevalence is generally highest in lake-type fish and lowest in sea-type fish. The parasite has a strongly disjunct distribution and prevalences appear stable, at least for lake systems. The absence of *Myxobolus* from many western Alaska fish and its high prevalence among eastern Gulf of Alaska stocks should prove useful, particularly in combination with scale pattern analysis and genetic markers, in separating stocks of Alaska sockeye salmon. Future research should concentrate on expanding the baseline resolution, particularly in the Kodiak region. The presence of infected and uninfected stocks in adjacent areas may provide opportunities for smaller scale stock separation. If data from the present study were correlated with existing limnological data, perhaps some of the underlying causes for disjunct distribution and variability of the parasite could be determined.

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