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Crosses were made between a stock of summer steelhead (Salmo gairdneri) known to be resistant to infection by Ceratomyxa shasta and stocks of summer steelhead known to be susceptible. Ceratomyxosis, the disease caused by C. shasta was initiated by exposure to Willamette River water. I found that the crosses were intermediate in susceptibility to ceratomyxosis relative to the parental stocks. There was no difference in susceptibility to ceratomyxosis between reciprocal crosses of the same stocks. Persistance of moderate susceptibility in the F_2 generation of experimental stock crosses and examples from both wild and hatchery stocks of mixed ancestry indicate long term disease problems may result from introductions of less adapted, foreign stocks.

The Relative Effects of *Ceratomyxa shasta* on Crosses of Resistant and Susceptible Stocks of Summer Steelhead

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INTRODUCTION

Historically, spring chinook (Oncorhynchus tshawytscha) and winter steelhead (Salmo gairnderi) were the only anadromous salmonids in the Willamette basin above Willamette Falls. After water quality was improved and a new fishway constructed at Willamette Falls in 1971, summer steelhead were introduced into the upper Willamette basin. Smolts were released in the North Santiam, South Santiam and McKenzie rivers, tributaries that have high summer flows. Skamania and Siletz stocks were introduced, however, only Skamania stock adults returned. It was soon discovered that Siletz stock summer steelhead are susceptible to infection by the myxosporean, Ceratomyxa shasta (Clady, undated; Buchanan et al. 1983).

Ceratomyxa shasta causes the disease ceratomyxosis in susceptible salmonids. Diseased juvenile steelhead lose their appetite, develop distended abdomens and hemorrhagic areas near the vent, darken, become lethargic, and usually die (Conrad and DeCew 1966). Ceratomyxa shasta is found in the lower Columbia and Willamette rivers and many other major river systems from northern California to British Columbia (Sanders et al. 1970; Johnson et al. 1979; Ching and Munday 1984). All that is known of the life history of C. shasta is that an undescribed infectious stage greater than 14 micrometers enters a host salmonid and after going through a trophozoite stage, produces spores. These spores cannot directly infect other fish, nor can feeding of infected tissues or cohabitation of infected fish with susceptible fish (Johnson 1979). Ratliff (1983) offers reasonable speculation about the rest of the life cycle of *C. shasta*. Although methods to eliminate the infectious stage from hatchery water supplies have been tested (Bedell 1971; Sanders et al. 1972), the only practical way to prevent ceratomyxosis outside of hatcheries is to use resistant stocks of fish (Zinn et al. 1977; Johnson et al. 1979; Buchanan et al. 1983).

Returns of Skamania summer steelhead to the Santiam system have been good, however returns to the McKenzie River have fluctuated widely. A possible reason may be that Skamania smolts released into the McKenzie River migrate through the lower Willamette River so late that in many years the water temperature exceeds 17°C. Skamania summer steelhead smolts are highly susceptible to bacterial diseases such as *Aeromonas salmonicida* and *Aeromonas hydrophila* at temperatures greater than 17°C (Buchanan et al. 1982; Fryer and Pilcher 1974) and warm water may physiologically terminate smolting (Zaugg and Wagner 1973; Wagner 1974). A stock that migrates earlier in the spring would avoid the warm water and possibly increase the percentage of smolts surviving to return as adults.

The Oregon Department of Fish and Wildlife (ODFW) has considered replacing the Skamania stock with other summer steelhead stocks. A suitable stock would be resistant to ceratomyxosis and would migrate before high water temperatures occur in the lower Willamette River. Testing of other available stocks revealed that the Umpqua stock is susceptible to ceratomyxosis (Buchanan 1977), and that the Deschutes and Clearwater (Idaho) stocks are resistant (Buchanan 1974). Unfortunately, the Deschutes and the Clearwater stocks are carriers of infectious hematopoietic necrosis (IHN) and cannot be transferred into the Willamette basin.

Resistance to ceratomyxosis is thought to be genetically transferred (Johnson 1975; Zinn et al. 1977). Zinn (1975) tested reciprocal crosses of Big Creek and Trask River fall chinook salmon along with the parental stocks for resistance to ceratomyxosis. He found resistance to be inherited as a sex-linked character. None of the Big Creek chinook salmon died, whereas 92.5% of the Trask River fish succumbed to ceratomyxosis. Only 4% of the progeny of Trask males x Big Creek females died and 33% of the progeny of Big Creek males x Trask females died.

By crossing a resistant stock (Skamania) with an early migrating but ceratomyxosis susceptible stock (Siletz or Umpqua) I hoped to produce steelhead that would be resistant to ceratomyxosis and that would retain the early smolt migration timing. A ceratomyxosis resistant, early migrating stock of summer steelhead would provide managers with another stock for use in the McKenzie River, where adult returns of Skamania stock have been low. The objectives of this study were (1) to determine the susceptibility of crosses of Siletz x Skamania and Umpqua x Skamania summer steelhead stocks to ceratomyxosis and (2) to explore how resistance to ceratomyxosis is inherited, especially if resistance is a sex-linked trait.

METHODS

An equal volume (60 milliliters) of eggs were collected from each of 19 Siletz stock summer steelhead at Cedar Creek Hatchery, 14 Skamania stock fish at South Santiam Hatchery, and 12 Umpqua stock fish at Rock Creek Hatchery in February 1981. Approximately 240 milliliters of eggs were placed in 1 liter plastic containers. Sperm was collected (10 Umpqua males, 11 Siletz males, and 11 Skamania males) by stripping milt from one male into a zip-loc bag, inflating the bag with air, and sealing the bag. All gametes were transported the same day in ice chests at 2-4°C to the ODFW's Research Laboratory at Corvallis.

From these gametes I propagated seven genetic groups of fish; Skamania, Siletz, Umpqua, and reciprocal crosses (male x female and female x male) of Skamania x Siletz and Skamania x Umpqua stocks (males are listed first in all specific stock crosses). All eggs of each stock were pooled and mixed before being divided into groups for fertilization, and 5 milliliters of sperm were pipetted from each bag into a beaker and mixed, one beaker for each stock. This was done to minimize differences within each stock in genetic contribution to the respective groups. The fertilized eggs were placed in a Heath incubator and supplied with pathogen free, 12°C well water. When the yolk sac was absorbed, each genetic group was placed in a 356 liter circular tank supplied with 12°C well water and fed to repletion several times each day. The fish were fin-clipped for group identification and each group was divided into two equal test lots on 25 September 1981 when they had grown to approximately 5-

8 cm fork length.

Exposure to water containing the infectious stage of C. shasta, such as the Willamette River near Corvallis, is the only practical way to initiate infection (Johnson et al 1979). I exposed one lot to Willamette River water in a 1.5 cu m livebox at Corvallis, Oregon (river km 212), from 30 September to 7 October 1981. Water temperature in the live box ranged from 15-16^{o}C during this exposure. A second lot was exposed at the same location from 7 October to 15 October 1981 at 12-14^{o}C. After exposure to C. shasta, the fish were transferred to pathogen free well water at 12^{o}C and fed OMP with 3% Terramycin added to prevent bacterial infections. Terramycin does not inhibit ceratomyxosis (Sanders et al. 1972). Dead fish were collected daily until 12 January 1986 and frozen or examined fresh. Fish were considered infected by C. shasta if a microscopic examination (400x) of a smear of intestinal fluid contained the characteristic spores.

Fish that survived exposure to C. shasta in the fall of 1981 were combined into one group and reexposed to C. shasta the following spring for 16 days beginning 24 May 1982 at 12-15^{o}C. Dead fish were collected and examined as before.

Fish that survived reexposure were reared to age 3+. In the spring of 1984, four males and four females were sexually mature and were bred to produce the F_2 generation (Figure 1). Since not all the F_1 fish matured at the same time I could not make all possible crosses. In addition, two groups of F_2 progeny were lost because of a failure in the water supply. The F_2 progeny were reared in pathogen free, 12^{o}C well water at the ODFW

Research Laboratory in Corvallis and exposed to *C. shasta* in the Willamette River at Corvallis for 3 weeks beginning 21 September 1984. Alsea stock steelhead, a stock that is susceptible to ceratomyxosis (Weber and Knispel 1976), were included to verify the presence of the infectious stage of *C. shasta*. After exposure the fish were transferred to pathogen free 12°C well water and fed OMP with 3% Terramycin for 86 days. Dead fish were collected and examined as before.

Differences in mortality between genetic groups were tested using X^2 for all comparisons (Cochran and Cox 1957).

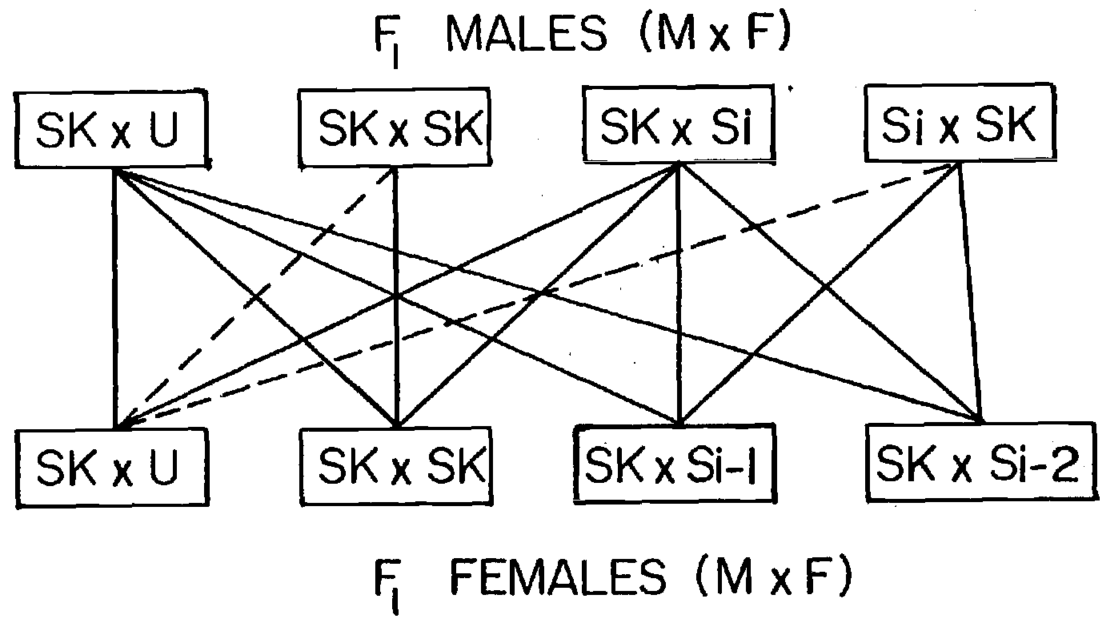

Figure 1. Crosses made to produce the F_2 generation. The dashed lines represent groups that failed. Sk = Skamania, U = Umpqua and SI = Siletz

RESULTS

Nearly all of the pure Umpqua and pure Siletz fish were dead and infected with spores of C. shasta by 105 days after the first day of exposure of the first test lot and by 98 days after the first day of exposure of the second lot (Tables 1 and 2). Only 3% of the Skamania fish in the first lot died and none of the Skamania fish in the second lot died. All four of the reciprocal cross groups in the first lot experienced intermediate levels of mortality relative to the pure stock groups. The reciprocal cross groups in the second lot incurred less mortality but were still intermediate to the pure stock groups. The differences between lots in percent mortality of the reciprocal crosses were significant (X^2=110.5, df=1, $P < 0.01$) as was the difference in mortality between the Umpqua x Skamania and Siletz x Skamania crosses (X^2=28.9, df=1, $P < 0.01$). I found no significant differences between reciprocal crosses of the same stocks and exposure ($P > 0.05$).

There were no additional effects on the Skamania steelhead from the reexposure to the infectious stage of C. shasta. (Table 3). One percent of the Skamania fish died from ceratomyxosis after being exposed to C. shasta a second time. The reciprocal crosses once again experienced a moderate level of mortality.

Mortality from ceratomyxosis on the F_2 generation is listed in Table 4. The F_2 progeny of crosses of susceptible and resistant stocks exhibited a wide range of resistance to ceratomyxosis. I found no difference ($P > 0.05$) between F_1 males mated to the same females. Large differences in resistance to ceratomyxosis of the F_2 progeny were noted between females from the same F_1 cross (Skamania x Siletz) even when they were mated to the same males.

Table 1. The effects of <u>Ceratomyxa shasta</u> on three stocks of summer steelhead and their reciprocal crosses when exposed to Willamette River water near Corvallis from September 30 to October 7, 1981 (Lot 1). SK = Skamania, SI = Siletz, UM = Umpqua.

Stocks (m x f)	Number of fish exposed	Number of fish dead	Number of fish dead and infected with <u>C. shasta</u>	Percentage of fish dead and infected with <u>C. shasta</u>
SK x SK	73	2	2	3
UM x UM	88	87	87	99
SI x SI	96	93	93	97
UM x SK	77	43	38	49
SK x UM	101	43	41	41
SI x SK	94	64	63	67
SK x SI	95	67	65	68

Table 2. The effects of *Ceratomyxa shasta* on three stocks of summer steelhead and their reciprocal crosses when exposed to Willamette River water near Corvallis from October 7 to October 15, 1981 (Lot 2). SK = Skamania, SI = Siletz, UM = Umpqua.

Stocks (m x f)	Number of fish exposed	Number of fish dead	Number of fish dead and infected with *C. shasta*	Percentage of fish dead and infected with *C. shasta*
SK x SK	101	0	0	0
UM x UM	97	96	95	98
SI x SI	88	85	85	97
UM x SK	85	12	9	11
SK x UM	94	12	9	10
SI x SK	101	22	21	21
SK x SI	95	31	29	30

Table 3. The effects of *Ceratomyxa shasta* on reciprocal crosses of summer steelhead when reexposed to Willamette River water near Corvallis from May 24 to June 19, 1982. SK = Skamania, SI = Siletz, UM = Umpqua.

Stocks (m x f)	Number of fish exposed	Number of fish dead	Number of fish dead and infected with *C. shasta*	Percentage of fish dead and infected with *C. shasta*
SK x SK	72	2	1	1
UM x SK	21	8	6	29
SK x UM	54	11	11	20
SI x SK	40	16	13	32
SK x SI	25	6	5	20

Table 4. The effects of Ceratomyxa shasta on the F_2 generation of reciprocal crosses of summer steelhead stocks. SK = Skamania, SI = Siletz, UM = Umpqua, and AL = Alsea.

Cross (F_1 ♂)	X	(F_2 ♀)	Number of fish exposed	Number of fish dead	Number of dead fish infected by C. shasta	Percentage of fish dead and infected with C. shasta
SKxSK	X	SKxSK	40	4	3	7
SKxSI	X	SKxSK	53	5	4	8
SKxUM	X	SkxSK	47	6	6	13
SKxSI	X	SKxSI-1[a]	23	4	3	13
SIxSK	X	SKxSI-1	93	34	31	33
SKxUM	X	SKxSI-1	27	17	10	37
SKxSK	X	SKxUM	6	1	1	17
SKxUM	X	SKxUM	36	17	17	47
SKxSI	X	SKxUM	60	29	29	48
SIXSK	X	SKxSI-2[a]	88	58	58	66
SKxUM	X	SKxSI-2	33	24	24	73
SKxSI	X	SKxSI-2	51	43	43	84
AL	X	AL	59	55	55	93

[a] SKxSI #1 and SKxSI #2 are different female fish from the same F_1 cross.

[b] C. shasta positive control.

DISCUSSION

By obtaining differences in resistance between stocks after rearing them in a common, pathogen free environment, I demonstrated that resistance to ceratomyxosis is an inherited trait in summer steelhead. Hoffmaster (1985) crossed male coho salmon resistant to ceratomyxosis with susceptible female rainbow trout and tested the hybrids and pure species for resistance to ceratomyxosis. She concluded that susceptibility to ceratomyxosis is inherited as a dominant genetic trait. The intermediate susceptibility of the resistant steelhead x susceptible steelhead crosses in my work and that of Hemmingsen et al. (in press) with coho does not support this conclusion. Our results suggest an additive genetic model in which each allele substitution produces an incremental increase or decrease in a particular character (Falconer 1960).

The patterns of inheritance of resistance in the F_2 generation of reciprocal crosses suggests a strong maternal influence. I do not know if this was also true in the F_1 generation because I did not test individual families. However I did not observe resistance to be a dominant sex-linked trait in steelhead as was seen by Zinn (1975) in chinook salmon.

The physiological mechanism that allows Skamania summer steelhead to prevent ceratomyxosis was partially broken down by crossbreeding with the Umpqua stock and with the Siletz stock. Differences in resistance to ceratomyxosis between the Umpqua x Skamania and Siletz x Skamania crosses demonstrate that genetic factors which make a stock susceptible are different in the

Umpqua and Siletz stocks although the pure stocks are equally susceptible at the exposure levels I tested. Differences in resistance to ceratomyxosis of the F_2 progeny of F_1 females of the same stock cross (Skamania x Siletz) when mated to the same males indicates genetic differences in susceptibility also exist within stocks.

Comparison of exposures at different locations or over different periods of the year are difficult (Ratliff 1981). Differences in the incidence of ceratomyxosis between lots 1 and 2 of the reciprocal cross groups exposed exposured in the fall of 1981 indicate that difficulties extend to comparisons of exposures at the same location and period of the year but at different times. Although the length of exposure was the same, incidence of ceratomyxosis in the reciprocal cross groups averaged 56% and 18% for lot 1 and lot 2, respectively. Differences between lots in resistance to ceratomyxosis can probably be attributed to dilution of the infective stage of *C. shasta*. Flow in the Willamette River at Albany the nearest gauging station, increased from an average of 8077 cfs during exposure of the first lot to 11,284 cfs during exposure of the second lot. The incidence of infection by *C. shasta* gradually tapers off in the fall as flows increase (Johnson 1975).

Natural selection for ceratomyxosis resistant individuals may be the mechanism by which resistant stocks evolve (Johnson 1975, Zinn et al. 1977). Threshold characteristics, such as disease resistance, can be selected for (Dempster and Lerner 1950). Differences in the F_2 progeny of F_1 Skamania x Siletz females indicate genetic differences in resistance to ceratomyxosis within stocks. A resistant stock may possibly be developed from susceptible x resistant crosses by selecting resistant families. Attempts to produce ceratomyxosis resistant hybrid steelhead should start with as many F_1 families as possible to minimize random genetic drift and reduce them to the number needed through high levels of exposure to C. shasta. This strategy would produce the largest selection differential and should produce the most ceratomyxosis resistant F_2 generation. Such an effort would require a large number of rearing tanks and may not be practical.

Even though several authors have cautioned against releasing susceptible salmonids into river systems containing the infectious stage of C. shasta (Zinn et al. 1977; Johnson et al. 1979; Buchanan et al. 1983) the ODFW, Idaho Department of Fish and Game, and Washington Department of Fisheries continue to do so (Howell et al. 1985). Of greater concern than the deaths of susceptible stocks is the possibility of genetic degradation of endemic resistant stocks. This work and that of Hemmingsen et al. (in press) with coho salmon demonstrate the intermediate susceptibility to ceratomyxosis of crosses of resistant and susceptible stocks.

If ceratomyxosis susceptible adults are released into a system they may breed with native fish and produce offspring susceptible to ceratomyxosis. An example of increased susceptibility in a wild stock may be Nehalem coho salmon. From 1965 to 1976 1.5 million fry, 40,000 fingerling, 10,000 smolt and 1,200 adult coho salmon from the North Nehalem, Trask and Alsea stocks were released into the Fishhawk Creek system, a tributary to the Nehalem River at river kilometer 106. All of these introduced stocks are susceptible to C. shasta (Udey et al. 1975; Zinn 1975; Weber and Knispel 1976). We have no record of coho being released into Cronin Creek, a tributary to the Nehalem at river kilometer 40 and these fish are thought to represent the native Nehalem coho. In 1980, age 0+ coho salmon were exposed to C. shasta by placing them in a live box in the Nehalem River (Tom Nickelson, ODFW, unpublished data). The fingerlings were from four sources 1) Trask River coho, 2) the progeny of early spawning wild adult coho from Fishhawk Creek, 3) the progeny of late spawning wild adult coho from Fishhawk Creek and 4) wild fingerlings captured in Cronin Creek. The fingerlings from Fishhawk Creek were intermediate in resistance to ceratomyxosis relative to the introduced Trask River and native Cronin Creek groups (Table 5). Native Fishhawk Creek coho may have interbred with the introduced susceptible stocks decreasing the resistance of the wild coho salmon in Fishhawk Creek to ceratomyxosis.

Table 5. The effects of Ceratomyxa shasta on four groups of coho salmon (Tom Nickelson, ODFW, unpublished).

Stock	Number of fish exposed	Number of dead fish	Number of dead fish infected by C. shasta	Percentage of fish dead and infected with C. shasta
Trask	32	23	22	69
Early Fishhawk	66	24	22	33
Late Fishhawk	36	9	7	19
Cronin Creek	55	9	4	7

An example of genetic degradation of a hatchery stock may be winter steelhead in the Cowlitz River, Washington. Historical records and chromosome studies indicate that the winter steelhead broodstock used at the Cowlitz Trout Hatchery (Washington Department of Game) is a combination of native Cowlitz River fish and the Chambers Creek stock introduced from Puget Sound (Crawford 1979, Thorgaard 1983). All steelhead stocks native to the Columbia River that have been tested are resistant to ceratomyxosis (Buchanan et al. 1983; Hoffmaster 1985). Puget Sound is outside the established range of *C. shasta* and, therefore, endemic steelhead stocks are probably susceptible to ceratomyxosis. Losses of winter steelhead reared at the Cowlitz Trout Hatchery commonly exceed 30% and sometimes exceed 80%, and *C. shasta* is thought to be the cause (Tipping et al. 1984).

These examples and susceptibility of the F_2 generation of resistant x susceptible crosses of steelhead in my experiments, even though we exposed the F_1 generation to *C. shasta* twice, indicate a danger of long term disease problems in both hatchery and wild populations following introductions of less adapted stocks.

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