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Coho Salmon Populations in the Karst Landscape of North Prince of Wales Island, Southeast Alaska

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Abstract.-Karst topography is a unique and distinct landscape and its geology may have important implications for salmon productivity in streams. The relationship between salmonid communities and water chemistry and the influence of habitat was examined in a set of streams on north Prince of Wales Island, southeast Alaska. Streams in karst landscapes showed higher alkalinities (1,500-2,300 µeq/L) than streams not influenced by karst landscapes (750-770 µeq/L). A significant, positive relationship was observed between alkalinity and density of coho salmon parr Oncorhynchus kitsutch. Backwater pools supported higher densities of coho salmon than did other habitat units. Both coho salmon fry and parr tended to be larger in most karst-influenced streams than in nonkarst streams. Although past timber harvest practices in the riparian areas of several of the streams appeared to influence stream habitat and water temperature, streams flowing through karst landscapes had a distinct water chemistry. Furthermore, these streams appeared to support more fish than nonkarst streams.

Karst topography is a unique geological feature formed by the differential dissolution of limestone (Harding and Ford 1993). The landscape typically has an irregular surface topography with sinkholes, caves, underground streams, and upwelling water (Ford and Williams 1989). Karst topography occurs in several distinct areas of southeast Alaska (Soja 1990; Busch 1994) and is best represented on the northern end of Prince of Wales Island and islands along its west coast (Baichtel 1993). Dissolution of limestone increases the alkalinity of streams as they flow through karst terrain, and higher alkalinity has been associated with increased growth rates for brown trout Salmo trutta (Campbell 1961; Neophitou and O'Hara 1986). However, no studies have linked productivity of aquatic ecosystems to karst landscape or examined its influence on salmon populations in southeast Alaska. We provide the first description of the influence of karst terrain on salmon populations. Our objectives were to describe the range of water chemistry with respect to carbonate buffering (pH, alkalinity), to determine existing habitat conditions available to salmonid populations, and to relate abundance, species distribution, and growth to water chemistry and habitat among streams. The 2-year study began in 1992 with an extensive and qualitative survey of the water chemistry and salmonid populations. This was followed by a more intensive study of the salmonid populations in a smaller number of streams in 1993.

Methods

Study area.-All the study streams are on the northern quarter of Prince of Wales Island (Figure 1) and traverse a mixture of karst and nonkarst geology. Some streams are fed directly by resurgence from limestone caves, whereas others are fed by overland flow. Hecata Limestone and Bay of Pillars are the major karst formations (Wissmar et al. 1997). Many of the streams flow along contact zones between limestone and nonlimestone formations (Table 1). For example, Jasen and Hot Calder creeks flow along a contact zone between a graywacke formation and the massive Hecata limestone underlying Mt Calder. Other streams, such as Flicker Creek, flow through mixed geologies that include the massive Hecata limestone in the upper reaches, and sandstones, graywacke and conglomerates in the lower reaches (Table 1). Wissmar et al. (1997) provide a detailed discussion

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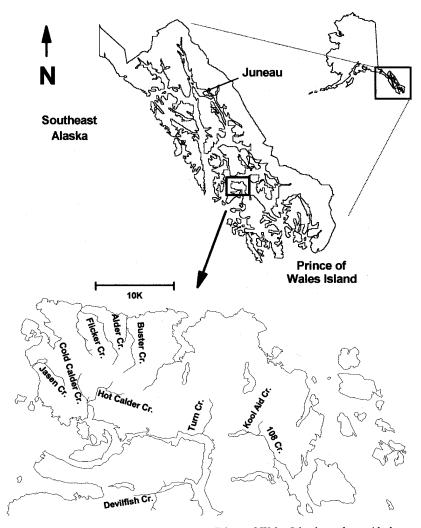


FIGURE 1.—Locations of study streams on Prince of Wales Island, southeast Alaska.

of the geochemistry of the streams in the study area.

Our study streams traverse a temperate rain forest dominated by Sitka spruce Picea sitchensis and western hemlock Tsuga heterophylla interspersed with red alder Alnus rubra (Harris et al. 1974). Wet muskegs (fens) with high acidity and anoxic soil conditions are distributed throughout the landscape (Roebuck 1985) and may increase dissolution rates of the underlying limestone and contribute to the formation of karst topography. Nearly all of the watersheds have been exposed to clearcut logging (Streveler and Brakel 1993), which may confound the responses of stream geochemistry and salmonid populations to karst geology. The small sample size and lack of undisturbed sites was insufficient to evaluate effects of logging in

our study. We wished to determine if the effects of the geology could be detected even with the effects of logging.

We report on eight streams sampled in 1993. Sample sites were generally low-gradient (<3%), second- to third-order (Strahler 1957) stream reaches. Kool Aid Creek is a tributary to 108 Creek and originates as an upwelling from a cave. We considered it to be from the same geology as 108 Creek. Of the group, 108 Creek was the only one that drained from a lake. Some streams, such as Turn Creek, were fed by water from one or more caves. We sampled from August 8 to 18. Usually two 500-m reaches were sampled of each stream. A lower reach, usually within 1-2 km of salt water, and an upper reach, at least 3 km upstream, was sampled. In some streams, access limited the sam-

Stream	Geology	Management; riparian vegetation	Tempera ture (°C)	- Conduc- tivity (μS/cm)	pН	Alkalinity (μeq/L as Ca[HCO ₃] ₂)
Hot Calder Creek	Massive Hecata limestone	Logged, second growth; alder, conifer	11	152	7.87	2,361
108 Creek	Massive Hecata limestone; con- glomerate near outlet	Logged, second growth; conifer, alder	19	110	8.11	1,570
Kool Aid Creek	Massive Hecata limestone	Logged, second growth; alder, conifer	9	a	a	a
Turn Creek	Contact between graywacke and massive limestone	Logged, no buffer; shrub	15	100	8.00	1,532
Jasen Creek	Contact between graywacke and massive Hecata limestone	Logged, buffer; old growth	10	117	8.05	1,428
Flicker Creek	Sandstone, conglomerate in low- er channel; massive Hecata limestone in headwaters	Logged, buffer; old-growth	14	160	7.99	2,217
Alder Creek	Conglomerate in upper and mid section; sandstone in lower channel	Old growth; conifer	13	75	6.77	771
Buster Creek	Conglomerate	Logged; buffer; conifer	9	60	6.84	748

TABLE 1.—Geology (listed by degree of karst influence), management status, and temperature and water quality of study streams.

ple to a single section, in which case one 500-1,000-m reach was surveyed.

Fish populations.-We made snorkel surveys of fish in six streams: Hot Calder, 108, Flicker, Turn, Alder, and Buster creeks. Fish were captured with minnow traps (3.1-mm mesh) in these streams and two additional streams, Jasen and Kool Aid creeks, to determine length frequencies and obtain scale samples. Coho salmon Oncorhynchus kitsutch and Dolly Varden Salvelinus malma were present in all streams; cutthroat trout O. clarki and steelhead O. mykiss were captured in some streams. Sample reaches started at the first pool encountered about 1 km upstream from road access. Sample sites for snorkel surveys were stratified by pool and fastwater habitats. Fish were counted in 25% of the pools and 10% of the fast-water units in each study reach. Sample units were selected randomly. Because we were unable to accurately conduct independent population estimates to calibrate the snorkel counts (see Hankin and Reeves 1988), the counts represent an index of relative abundance among the streams. Counts were made by one individual who conducted surveys at all sites. Fish were identified by species; coho salmon fry (<55 mm) and parr (\geq 55 mm) were counted separately. The size intervals were used as approximations of coho salmon age-groups; fry were young-of-theyear and parr had had at least one winter of freshwater residence. This distinction was checked against fish aged from scale analy-

Water chemistry.-Water samples of 500 mL were collected from all streams in or close to sec-

tions used for habitat and fish samples. Alkalinity was measured by the Gran titration method (Stumm and Morgan 1981). Titrations were completed within 8 h of sampling. Wissmar et al. (1997) provide detailed descriptions of the methods and analysis of water chemistry. A hand-held thermometer, a YSI¹ conductivity and temperature meter, and a Beckman¹ portable pH meter with a builtin temperature compensator were used to measure temperature, conductivity, and pH at each site. The pH meter was standardized at each sampling site with two pH buffers.

Stream habitat.-Habitat units were identified and measured with a tape or sonic distance-measuring device. They were separated into a hierarchial system, based on stream hydrology, and divided into pools (PL) - backwater (PL-BK), scour (PL-SR), off-channel (PL-OC), and side-channel (SC-PL) - and fast-water units-riffles (RF) and glides (GL) (Bryant et al. 1992). The minimum size for a habitat unit was 4 m². Area of each unit was computed from length and average width of each unit. Substrate classes were bedrock-boulder (BD-BR), >26 cm; cobble (CB), 6.4-26 cm; gravel (GR), 0.2-6.4 cm; and fines (F), <0.2 cm. Cover components were rootwads (RW),

a Not sampled.

¹ The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Agriculture of any product or service to the exclusion of others that may be suitable.

TABLE 2.—Relations of large wood debris (LWD), temperature, and alkalinity to coho salmon parr (>65 mm) densities in pools, determined by backward elimination of variables

Variable	\boldsymbol{F}	P	
All variables			
LWD	0.49	0.5563	
Temperature	2.92	0.2296	
Alkalinity	15.30	0.0596	
Temperature, alkalinity			
Temperature	3.22	0.1705	
Alkalinity	19.68	0.0213	
Alkalinity	10.98	0.0295	

large wood (LW), slash (SL), rock (RK), and undercut banks (UC). The areas of cover and substrate were estimated as proportions of each habitat unit, which were then multiplied by the respective unit area. The resulting areas of each cover and substrate type were summed over the stream reach.

Statistical analysis.-Differences in coho salmon fry and parr densities were examined independently by stream and habitat type with a two-way analysis of variance ($P_{\alpha} = 0.05$). The general linear models procedure used two classes-stream and habitat type-with six levels (six streams and six habitat types) in each class with unequal sample sizes (SAS 1988). Duncan's multiple-range test was conducted on significant results. Mean densities of coho salmon fry and parr measured in pool habitat were compared to three independent variables: alkalinity, temperature, and large wood. Multiple regression with all three independent variables and a backward elimination of nonsignificant variables was computed by the SAS regression procedure (Zar 1984). The decision criterion was $\alpha = 0.05$.

Results

Water Chemistry

Alkalinities exceeded 1,400 weq/L and pH values were above 7.8 in the karst-influenced streams Hot Calder, Jasen, Flicker, 108, and Turn creeks (Table 1). Buster and Alder creeks flowed through nonkarst terrain and had alkalinity values below 800 µeq/L and pH values below 6.9 (Table 1). Conductivity and pH were closely related to alkalinity.

Water temperatures were influenced by water source and riparian cover. Water temperatures in tributaries that originated from caves and from upwelling holes were less than 9°C at the point of origin (Bryant, unpublished data). Although Hot Calder, Flicker, and Turn creeks were partly fed

TABLE 3.—Mean densities (number/ m^2) of coho salmon fry and parr in karst- (K) and nonkarst- (N) influenced streams. Values within a column with a letter in common are not significantly different (Duncan's multiple-range test; $\alpha = 0.05$).

Fry		Parr		
Creek	Density	Creek	Density	
108 (K)	0.588 y	Hot Calder (K)	0.291 y	
Hot Calder (K)	0.514 y	Flicker (K)	0.144 z	
Alder (N)	0.269 yz	108 (K)	0.126 z	
Flicker (K)	0.168 z	Turn (K)	0.086 z	
Buster (N)	0.165 z	Alder (N)	0.079 z	
Turn (K)	0.145 z	Buster (N)	0.037 z	

by water from.caves or upwelling, these three streams flowed through logged riparian areas and had water temperatures greater than 10°C; 108 Creek was fed by a lake and had the highest temperature of 19°C (Table 1).

Salmonid Populations

Multiple regression showed a significant and positive relationship between coho parr density in pools and alkalinity (P = 0.03; Table 2). Other variables were not significantly related to coho salmon parr density. Coho salmon fry did not show a significant relationship with any of the three variables.

Significant differences among streams existed in densities of coho salmon fry (P = 0.02) and parr (P = 0.03); however, there was not a clear distinction between karst and nonkarst streams (Table 3). Highest densities of fry were observed in two karst-influenced streams-108 and Hot Calder creeks-but they were not statistically different from those in Alder Creek, a nonkarst stream. Turn Creek, also a karst-influenced stream, had the lowest densities of fry, but the study section was dominated by bedrock. Highest densities of parr appeared in the karst-influenced Hot Calder Creek, but differences in densities among the other streams were not significant. Although not always statistically different, higher densities of juvenile coho salmon were generally observed in karstinfluenced streams than in nonkarst streams. Turn Creek was an exception.

Mean densities of coho salmon fry among fastwater habitat units ranged from 0.52 fish/m^2 for glides to 0.06 fish/m^2 for riffles, but were not significantly different (P = 0.54). Overall, density of coho salmon parr differed among habitat units (P = 0.05). Highest densities were observed in backwater pools; lowest densities were observed in riffles and glides (Figure 2).

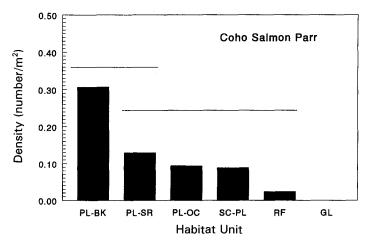


FIGURE 2.—Densities of coho salmon parr in habitat units of study streams 1993: PL-BK = backwater pools; PL-SR = scour pools; PL-OC = off-channel pools; SC-PL = side channel pools; RF = riffles; GL = glides. Thin horizontal lines extend over densities that did not differ significantly (Duncan's multiple-range test, $\alpha = 0.05$).

Coho salmon fry were larger in Hot Calder Creek than in Turn Creek (Table 4). Differences among streams were significant (P = 0.0005). Duncan's multiple-range test showed significant differences (P = 0.05) among means for three groups of streams. The largest fish were from the karst group; Hot Calder, 108, Kool Aid, and Jasen creeks (Table 4). Similar differences (P = 0.0001) among streams were observed for coho salmon parr. The mean lengths of parr in the karst-influenced streams 108, Kool Aid, and Hot Calder creeks were larger than those of parr in the nonkarst-influenced streams (Table 4). The mean length of parr in Buster creek, a nonkarst stream, was close to the mean length of those in Jasen and Flicker creeks, both of which have high alkalinities, but flow through mixed geologies (see Table 1). Turn Creek fish were the smallest of the group.

Habitat

Riffles and scour pools were the dominant habitat units in most streams (Figure 3). Kool Aid Creek was an exception, where 40% of the area was a beaver pond and classified as a backwater pool (Figure 3). Riffles made up more than 50% of the area in the reaches of the karst-influenced streams, except for 108 and Turn creeks. Scour pools (PL-SR) accounted for the greatest proportion of the area in the nonkarst Alder and Buster creeks. Habitat units commonly associated with the bank and riparian area-backwater pools and side channel units-were a small, but variable component of all streams, generally less than 10% of the area.

We did not observe clear trends for cover between karst and nonkarst streams (Figure 3). Rock was the most common cover type in Turn Creek,

TABLE 4.—Mean lengths (mm) of coho salmon fry and parr observed among streams for karst- (K) and nonkarst- (N) influenced streams. Values within a column with a letter in common are not significantly different (Duncan's multiple-range test; $\alpha = 0.05$).

Fry			Parr		
Creek	<i>N</i> .	Length	Creek	N	Length
Hot Calder (K)	14	65.2 x	108 (K)	8	95.3 w
108 (K)	11	62.5 yx	Kool Aid (K)	3	91.7 xw
Kool Aid (K)	4	59.8 zyx	Hot Calder (K)	3	89.7 yxw
Jasen (K)	8	59.6 zyx	Flicker (K)	18	81.7 zyx
Flicker (K)	10	58.2 zy	Buster (N)	17	80.0 zy
Alder (N)	9	57.9 zy	Jasen (K)	11	78.4 z
Buster (N)	5	54.8 z	Alder (N)	19	77.1 z
Turn (K)	9	54.4 z	Turn (K)	20	71.4 z

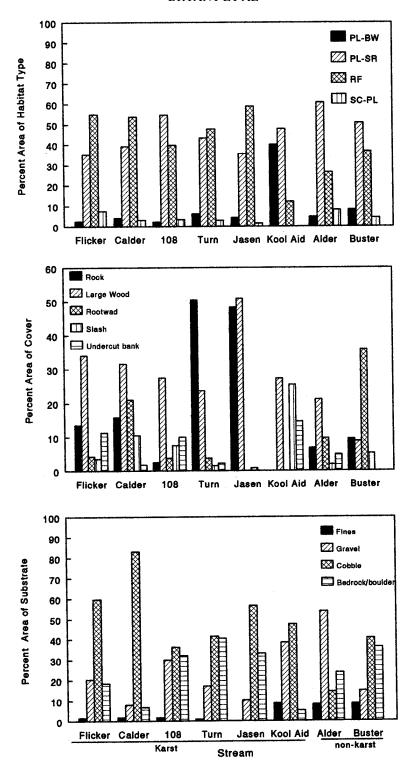


FIGURE 3.—Distribution of the percent areas of habitat units, cover types, and substrate size in each of the study streams: PL-BK = backwater pools; PL-SR = scour pools; SC-PL = side channel pools; and RF = riffles.

which also had the highest percentage of bedrock substrate of the eight streams. Large wood or root-wads appeared to be the largest cover component in the nonkarst Alder and Buster creeks. Riparian zones in both streams were forested. No relationship was observed between pools and large wood (P = 0.19).

Few of the study streams flowed directly over limestone bedrock. Most of the streams flowed through mixed geologies that tend to mask the effect of a pure limestone geology on the stream substrate composition. Cobble and gravel were the predominant substrate in most streams (Figure 3). Both Turn and 108 creeks showed high percentages of substrate area as bedrock. Although substrate may be related to the dominant bedrock geology of the watershed, we did not observe a relation between substrate and limestone.

Discussion

We observed distinct alkalinity signatures for streams flowing through karst landscapes and the relationship between alkalinity and coho salmon density in pools further suggested a positive influence of the limestone geology on fish populations. These results are consistent with observations for brown trout by Campbell (1961), and Neophitou and O'Hara (1986). Significant (P < 0.01) positive relationships were reported between both total fish and trout biomasses and alkalinity for 12 streams in the Shenandoah Valley of Virginia (J. Kauffman, Virginia Department of Game and Inland Fisheries, personal communication). In addition, concurrent studies in the limestonedominated streams of our study have shown a positive relationship between karst-influenced streams and invertebrate diversity and standing crop (M. Wipfli, Pacific Northwest Research Station, personal communication).

Karst topography did not appear to influence the distribution of habitat units among the streams that were surveyed. Karst topography is a unique landform, but its influence at the reach and habitat unit level appeared to be secondary to stream channel morphology and riparian management practices. Although we did not observe a positive relationship between number of pools and amount of large wood, a strong positive correlation was observed by Woodsmith and Buffington (1996) in a more extensive study of large wood and pools. They also documented fewer pools in streams flowing through logged riparian zones with low amounts of large wood than in undisturbed systems with intact riparian forests.

Mixed geologies will influence both riparian interactions and sediment budgets, which, in turn, determine pool and riffle development. The dissolution and chemical weathering of limestone in aquatic habitats do not generally produce broken and weathered cobbles and gravel (Ford and Williams 1989). These processes suggest that streams flowing over predominantly limestone geology tend to have smooth bedrock bottoms with small shallow pockets of gravel. This was observed only in short sections of the study streams and of other streams on the karst landscape of north Prince of Wales that flowed over pure limestone formations. We did not observe quantitative differences among the study streams. Extensive deposition of glacial till that influences gravel recruitment from surface deposits (Swanston 1969) and the mixed geology of the watersheds tend to confound many of the effects of limestone geology on stream morphol-

Differences observed in the distribution of coho salmon part among habitat types followed patterns observed elsewhere in southeast Alaska and the Pacific Northwest (Bisson et al. 1981; Bryant et al. 1992). Higher densities and greater over-winter survival were observed in backwater and off-channel habitats than in other habitats in Maybeso Creek in southeast Alaska (Bryant 1985). Nickelson et al. (1992) reported higher densities of coho salmon fry in pools, but found no statistical differences in density among pool types during the summer. They observed significantly higher densities during the winter in backwater pools. Similar results were observed by Bustard and Narver (1975), Peterson (1982), and Swales and Levings (1989). Our observations of higher densities of coho salmon part in the backwater habitats are consistent with these studies.

Although the higher alkalinities observed in karst-influenced streams may have a positive effect on aquatic productivity, other factors also affect productivity and salmonid densities. Streams flowing through karst-mixed geologies tend to have more gravel substrate than streams in pure karst that flow across limestone. Mixed-geology streams with greater amounts of large wood tend to develop deeper substrates and more pools with greater complexity than systems without large wood and sources of gravel recruitment. Deeper gravel substrate increases habitat for aquatic invertebrates and greater pool complexity provides better habitat for fish. The synergistic effects of these factors and higher alkalinities is likely to make these systems highly productive. Therefore, although higher alkalinities may increase productivity, their beneficial effects may not be observed in fish communities if other factors such as well-developed gravel substrates, large wood, and complex pools are absent.

The results from our study, based on a limited sample size, suggest higher productivity in karstinfluenced streams than in other streams, but the links among the complex factors affecting these streams are not well understood. Many of the apparently nonsignificant relationships assessed in our study may be the result of small sample sizes and low statistical power. A more extensive study to relate ranges of alkalinities, cations, pH, and geologies to salmonid diversity and production will provide a context for management of watersheds in the region. In the meantime, greater management emphasis on maintaining riparian habitats and instream habitats of karst-dominated aquatic ecosystems will ensure continued productivity of these systems. A greater understanding of aquatic ecosystem processes in karst landscapes is needed for adequate restoration of systems that have been degraded by past land management activities.

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References

- Baichtel, J. F 1993. Evolution of karst management on the Ketchikan area of the Tongass National Forest: development of an ecologically sound approach. Pages I-13 in National cave management symposium. American Cave Conservation Association, Carlsbad, New Mexico.
- Bisson, P.A., J. L. Nielson, R. A. Palmason, and L. E. Grove. 1982. A system of naming habitat types in small streams, with examples of habitat by salmonids during low flows. Pages 62-73 in N. B. Armantrout, editor. Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Western Division, Bethesda, Maryland.
- Bryant, M. D. 1985. Changes 30 years after logging in large woody debris, and its use by salmonids. Pages

- 329-334 *in* R. Johnson, C. D. Ziebell, D. R. Patton, P. F. Ffolliott, and R. H. Hamre, editors. Riparian ecosystems and their management: reconciling conflicting uses. U.S. Forest Service General Technical Report RM-120.
- Bryant, M. D., B. E. Wright, and B. J. Davies. 1992. Application of an hierarchial habitat classification system: stream habitat and salmonid distribution in Ward Creek, southeast Alaska. U.S. Forest Service Research Note PNW-RN-508.
- Busch, L. 1994. Caving beneath the Tongass. BioScience 44:215-218.
- Bustard, D. R., and D. W. Narver. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 32:667-680.
- Campbell, R. N. 1961. The growth of brown trout in acid and alkaline waters. Salmon and Trout Magazine 161:47-52.
- Ford, D. C., and P W. Williams. 1989. Karst geomorphology and hydrology. Chapman and Hall, London.
- Hankin, D.G., and G. M. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. Canadian Journal of Fisheries and Aquatic Sciences 45:834-844.
- Harding, K. A., and D. C. Ford. 1993. Impacts of primary deforestation upon limestone slopes in Northern Vancouver Island, British Columbia. Environmental Geology 21:137-143.
- Harris, A. S., and six coauthors. 1974. The forest ecosystem of southeast Alaska: 1. The setting. U.S. Forest Service General Technical Report PNW-12.
- Neophitou, C., and K. O'Hara. 1986. A comparison study of age, growth and population structure of brown trout in alkaline and acid waters in north Wales. Thalassographica 9:51-67.
- Nickelson, T E., J. D. Rodgers, S. L. Johnson, and M. F Solazzi. 1992. Seasonal changes in habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 49:783-789.
- Peterson, N. P 1982. Population characteristics of juvenile coho salmon (*Oncorhynchus kisutch*) overwintering in riverine ponds. Canadian Journal of Fisheries and Aquatic Sciences 39:1303-1307.
- Roebuck, O. W. 1985. The common plants of the muskegs of southeast Alaska. U.S. Forest Service, Pacific Northwest Forest and Range Experiment Station, Miscellaneous Publication, Juneau, Alaska.
- SAS Institute. 1988. SAS/STAT user's guide, release 6.03 edition. SAS Institute, Cary, North Carolina.
- Schmiege, D. C., A. E. Helmers, and D. M. Bishop. 1974. The forest ecosystem of southeast Alaska: 8. Water. U.S. Forest Service General Technical Report PNW-28.
- Soja, C. M. 1990. Island arc carbonates from the silurian heceta formation of southeastern Alaska Alexander terrane. Journal of Sedimentary Petrology 60:235-249.

- Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Transactions of the American Geophysical Union 38:913-920.
- Streveler, G., and J. Brakel. 1993. Cave lands of southeast Alaska: an imperiled resource. Report to Southeast Alaska Conservation Council, Juneau, Alaska.
- Swales, S., and C. D. Levings. 1989. Role of off-channel ponds in the life cycle of coho salmon (*Oncorhynchus kisutch*) and other juvenile salmonids in the Coldwater River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46:232-242.
- Stumm, W., and J. J. Morgan. 1981. Aquatic chemistry. Wiley, New York.
- Swanston, D. N. 1969. A late-Pleistocene glacial se-

- quence from Prince of Wales Island, Alaska. Arctic 22:25-33.
- Wissmar, R. C., D. N. Swanston, M. D. Bryant, and K. K. McKee. 1997. Controls on stream chemistry within a karst landscape, southeast Alaska. Freshwater Biology 30:301-314.
- Woodsmith, R. D., and J. M., Buffington. 1996. Multivariate geomorphic analysis of forest streams: implications for channel assessment of land use impacts on channel condition. Earth Surface Processes and Landforms 21:377-393.
- Zar, J. H. 1984. Biostatistical analysis. 2nd edition. Prentice-Hall, Englewood Cliffs, New Jersey.

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