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Over-winter Survival and Habitat Use by Juvenile Coho Salmon (*Oncorhynchus kisutch*) in Two Lake Superior Tributaries

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ABSTRACT. *Dramatic declines in commercial and recreational fisheries for coho salmon (Oncorhynchus kisutch) in Lake Superior have raised questions about the natural factors that limit their productivity. Snorkeling surveys were conducted during the winters of 1995–96 and 1996–97 to estimate over-winter mortality and determine winter habitat use by juvenile coho salmon in two spring-fed tributaries of Chequamagon Bay, Lake Superior. Results indicated high densities of juvenile coho salmon in pool habitats of the two streams ($\bar{x}$ = 0.85 fish/m^2) and high over-winter survival (> 45%). Regression analyses revealed no significant relationships between fish distribution and physical habitat variables (large woody debris, overhead cover, and pool size). No shift in habitat use over the winter was found. These results contrast sharply with findings from the Pacific Northwest where juvenile coho salmon generally occupy complex pool habitats during the winter. Although streams of the Great Lakes region are similar in many respects to Pacific streams, differences, particularly in stream flow regimes, indicate that the early life history of coho salmon populations in these two regions differ dramatically. These observations may have important implications on the management of stream habitats in the Great Lakes.*

INDEX WORDS: *Coho salmon,* Oncorhynchus kisutch*, winter ecology, juvenile survival, Lake Superior.*

INTRODUCTION

Coho salmon (*Oncorhynchus kisutch*) have a complex life-cycle that consists of an oceanic or lake-dwelling adult phase and a riverine rearing phase (Sandercock 1991). In both their native range of the eastern Pacific and their introduced range in the upper Great Lakes, adult salmon migrate from ocean or large lake habitats into small streams where they spawn. Upon emergence from gravel nests, juvenile coho salmon disperse throughout the stream and begin a rearing phase, which can last between 1 and 3 years. At that point, juveniles transform into smolts (silvery color, loss of lateral parr-marks) and begin a down-stream migration into a lake or an ocean. In these environments, adult coho salmon spend 2 or more years feeding before reaching sexual maturity (Sandercock 1991). As a consequence of this life-cycle, coho salmon are exposed to many different types of human threats across a range of aquatic environments. In streams, juvenile salmon reportedly require complex stream habitats (large woody debris, boulders, undercut banks and stream side vegetation, Sandercock 1991) and high water quality (cold and well-oxygenated). For these reasons, juvenile salmon are typically sensitive indicators of stream quality (Hicks *et al*. 1991, Sandercock 1991).

Since their introduction to the Great Lakes in the 1960s, coho salmon have supported commercial and recreational fisheries in Lake Superior. Although the persistence of populations in this drainage has relied upon intensive and continued stocking, several tributaries to Lake Superior, especially near Chequamagon Bay (Wisconsin), are sources of natural reproduction (Becker 1983). Recently, declines in recreational harvests have raised questions about the factors that limit the natural reproduction of coho salmon populations in this region. Over-harvesting, habitat loss and pollution threaten many salmon stocks throughout western North America (Thedinga *et al*. 1989, Hicks *et al*. 1991). Factors limiting naturally reproducing coho salmon stocks in Lake Superior are unclear. How-

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ever, based on knowledge of Pacific populations, it is reasonable to suspect that significant threats exist to the stream-resident or juvenile-phases of the life cycle.

A large number of factors contribute to variability in the abundance of juvenile coho salmon in Pacific streams. In this region, winter floods or cold temperatures can be among the most important of these factors (Bustard and Narver 1975, Swales *et al*. 1986, Thomas *et al*. 1986). Results from studies on the winter ecology of juvenile coho salmon consistently show that winter conditions can lead to high annual mortality rates, often in excess of 65% (Bustard and Narver 1975, Tschaplinski and Hartman 1983, Nickelson *et al*. 1992). Apparently stimulated by increasing water velocities in late fall (Giannico and Healey 1998), juvenile coho salmon of lowland streams typically move into protected habitats (either complex pools or off-channel ponds) in winter (Bustard and Narver 1975, Swales *et al*. 1986, McMahon and Hartman 1989, Nickelson *et al*. 1992). Similar seasonal shifts in habitat use have been documented for streams in the interior of British Columbia, which lack episodic flooding in winter (Swales *et al*. 1986). In both the regions, such shifts in distribution appear to be adaptive (Bustard and Narver 1975, Tschaplinski and Hartman 1983, Nickelson *et al*. 1992). In coastal streams, high flows and predator threats may make it difficult for fish to occupy unprotected, main channel habitats. In interior streams, warmer temperatures in off-channel ponds reduce temperature-related stress (Swales *et al*. 1986)

While high flows or low water temperatures (< 2°C) are common during the winter in Pacific streams, stream flows and water temperatures (> 4°C) during a similar period in Lake Superior tributaries are typically less severe. In this potentially important respect, coho salmon of Lake Superior inhabit streams that are very different from those in the west. Although it is unclear how the winter ecology (survival, distribution, habitat requirements) of juvenile coho salmon is affected by these conditions, it is unlikely that the model for Pacific populations is entirely appropriate for these systems.

Motivated in large part by this possibility, a study was conducted to characterize aspects of the winter ecology of juvenile coho salmon in two Lake Superior tributaries. The specific objectives were (1) to document over-winter survival, (2) to describe patterns of habitat use, and (3) to determine whether fish redistribute in fall to over winter in complex habitats. The results of this study can aid in efforts to better tailor management objectives to the specific needs of Lake Superior coho salmon populations.

STUDY AREA

This study was conducted in two low gradient, spring-fed Lake Superior tributaries located in Bayfield County, Wisconsin (46°45′00″N, 90°52′30″W). Both the Onion River and Whittelsey Creek drain small (< 10 km^2) and heavily forested watersheds. Typical of streams in this region, flows in the two study systems peak during the spring (usually late March or April) following snow-melt, and in the summer and fall in response to rain-fall events. Flows are low (< 0.5 m^3/s) and relatively constant between October and March. Fish species found in both streams include coho salmon, brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), brook trout (*Salvelinus fontinalis)*, and slimy sculpin (*Cottus cognatus*).

METHODS

Habitat Surveys

During the fall of 1995, all pool habitats in each tributary from the mouth to the first major barrier (> 1 m falls) were surveyed. Although riffle and glide habitats occur in both streams, surveys were limited to pools because juvenile coho salmon were not found in shallow-water habitats. Habitat characteristics recorded from each pool included length, width, maximum depth, substrate, the number of pieces of large woody debris (>10 cm diameter), and percent cover. Percent cover was determined by visually estimating the amount of surface area covered by shrubs, undercut banks, overhanging brush, large boulders, and large pieces of wood such as fallen trees.

Population Characteristics and Movement

During both years of the study, underwater censuses were conducted of fish in 20 randomly selected pools within each stream. Snorkeling was used as the primary survey technique partly because others have successfully employed this method in similarly clear-water streams (Hankin and Reeves 1988, Hillman *et al*. 1992, Lonzarich *et al*. 1998). Moreover, snorkeling enabled sampling many more pools with greater efficiency of effort than would have been possible with alternative methods such as electrofishing or seining. Snorkeling surveys were completed using a two-pass method in which the observer would enter a pool at the downstream end and begin moving upstream while slowly identifying and counting all juvenile coho salmon encountered. The procedure was repeated a second time 5 minutes after the original pass, and the average of the two counts was recorded. To determine the accuracy of this technique, snorkeling counts were compared with estimates obtained from electroshocking surveys in 10 study pools. Electro-fishing population estimates, which were derived by a two-pass removal method (Zippin 1956), corresponded very strongly (> 90% percent similarity) with snorkeling counts (paired *t*-test, $P > 0.50$).

Sites in the two drainages were snorkeled in fall (9 to 17 September) and spring (9 to 15 March) of both study years to quantify pool-specific changes in fish density. Surveyed pools were evenly distributed throughout the length of each stream to minimize the risk that any redistribution of fish within the streams would have gone undetected. Because the March sampling was completed well before the suspected period of salmon downstream migration into Lake Superior, it is reasonable to interpret declines in abundance as a measure of over-winter mortality. Percent changes in density were calculated for each pool and averaged each year to derive drainage-wide estimates. Differences in over-winter survival between streams and years were compared by two-way ANOVA on arcsin transformed proportion data. One limitation of this calculation was that pools lacking fish in fall surveys were omitted from these analyses even if they contained fish in spring (n = 5). Because these numbers could not be used in estimating pool-specific survival, drainage-wide estimates were derived by dividing the total number of fish counted from all pools in spring surveys by the total counted in fall.

Simple linear and multiple regression analyses were used to explore whether variability in fish density in fall or spring could be explained by pool area, amount of large woody debris, cover, and/or depth. When necessary, habitat and density data were log-transformed to meet the assumption of normality and variance equality.

To determine whether juvenile coho salmon moved from simple to complex pools during the winter, individuals from each habitat type were marked and seasonal changes in distribution were documented by underwater observation. Movement from one pool type to another was inferred by comparing pool type of origin to pool type at recapture. Simple pools were defined as those that had one to two pieces of wood (>10 cm in diameter) and less than 20% cover. Complex pools contained greater than 50% cover and more than five pieces of wood. During fall 1995 and 1996, fish from 30 pools of each type were collected throughout the Onion River study area. All juvenile coho salmon captured were given treatment-specific fin clips (adipose fin clip for complex pools, upper caudal fin for simple pools). Re-sampling the same pools in late February and early March, fish were identified by their pool of origin and the pool type in which they were recaptured. Chi-square tests of randomness (2×2 contingency table) were used to test whether marked fish moved selectively into complex habitats.

RESULTS

Habitat Characteristics

Inventories of nearly 300 sites (142 pools in the Onion River, 156 in Whittelsey Creek) revealed that pools in the two streams were similar in most physical characteristics (Table 1). On average, pools were small (range 10 to 12 m^2) and relatively shallow (40 to 60 cm). Large woody debris and other sources of cover (undercut banks and depth) were abundant in both drainages. Substrate was predominantly small gravel and sand although a few sites contained small boulders.

Population Characteristics

Significantly more fish were counted in pools of Whittelsey Creek (1.05 vs. 0.65 fish/m^2, $P < 0.05$) and in the 1995 fall survey period (1.02 vs. 0.67 fish/m^2, $P < 0.05$). In both the Whittelsey and Onion drainages, higher fish densities were recorded from upstream pools in fall 1995; however, no such trend was evident in 1996 (Fig. 1). Among the physical variables measured, only pool area ($r^2 = 0.38$, Fig. 2) showed any significant correlation (negative) with density (fall and spring combined). Juvenile coho salmon densities were not correlated with wood abundance, depth or cover when variables were tested separately or in combination with others ($P > 0.50$). However, there was a slight tendency for densities to be higher in simple pools of intermediate depth (30 to 50 cm, Fig. 2).

Patterns of overwinter survival were similar between the two streams ($P = 0.96$) and over the two winters ($P = 0.88$). Based on the percent change in fish densities within individual pools, the average

TABLE 1. Average conditions (± 1 S.E.) for different pool variables in the Onion River and Whittelsey Creek.

	Onion River	Whittelsey Creek
Number of Pools	142	156
Pool Width (m)	2.2 ± 0.1	2.2 ± 0.1
Pool Length (m)	5.0 ± 0.2	4.9 ± 0.3
Pool Area (m^2)	10.7 ± 0.1	11.9 ± 0.6
Cover (%)	18.7 ± 1.8	21.5 ± 1.6
Wood (pieces)	2.1 ± 0.2	2.4 ± 0.2
Depth (cm)	40 ± 0.2	60 ± 0.1

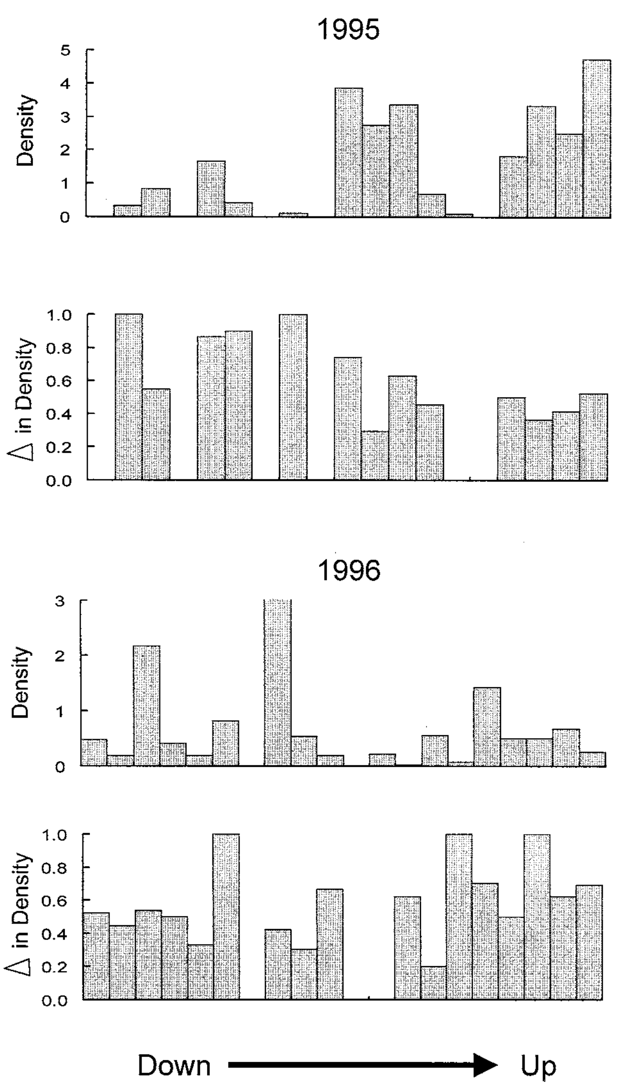

FIG. 1. Fall density estimates and over-winter declines in density (proportion) of juvenile coho salmon from individual pools of Whittelsey Creek. Results for each pool are arranged by their relative position along the stream continuum.

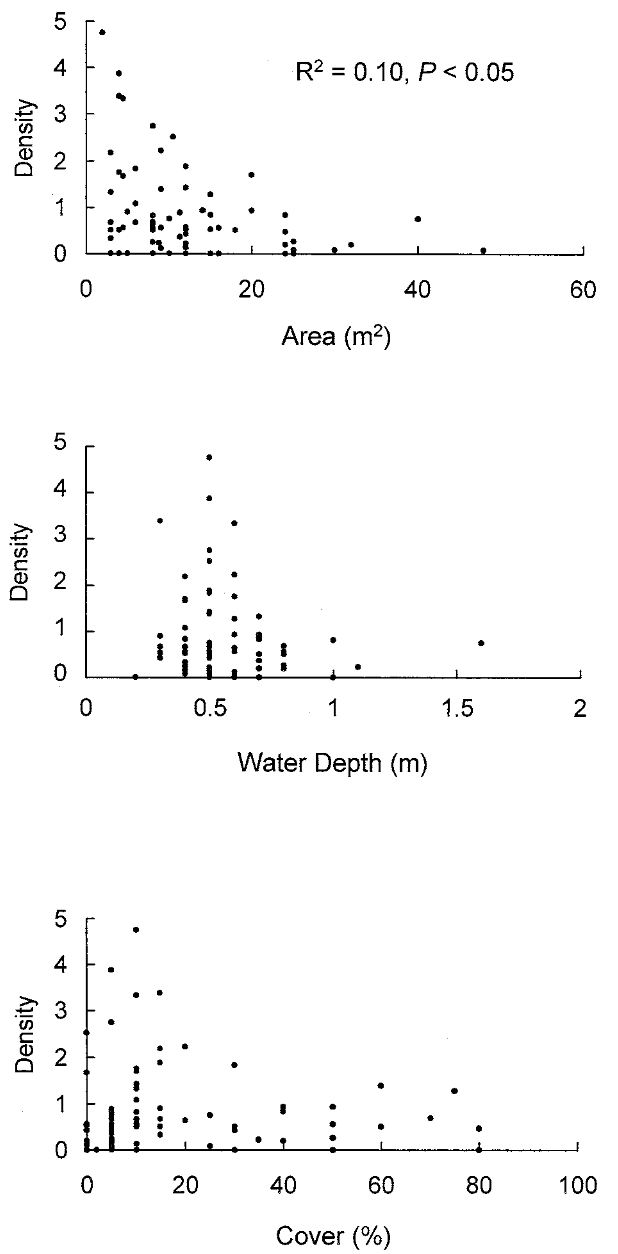

FIG. 2. The relationships between juvenile coho salmon densities (fish/m²) and habitat characteristics in the Onion and Whittelsey drainages. Results are for fall snorkeling surveys in 80 pools from the two streams.

over-winter survival estimate for the two years was 46% (± 4.2 S.E). A similar estimate was obtained when the total number of fish counted in late-winter surveys was divided by the number counted in fall (49% ± 1.3 S.E.). Using the percent change in fish densities (fall to late-winter) for each pool, significantly greater declines in density were found among downstream than upstream sites over winter 1995–96. This pattern was not apparent in winter 1996–97, however (Fig. 1).

There did not appear to be any redistribution of juvenile coho salmon into complex habitats in either winter (2 × 2 Chi-square contingency test, $P > 0.50$). Of 510 juvenile coho salmon marked from complex pools, 51 of 61 (84%) recaptured fish were taken from complex pools. By comparison, of 465 fish marked from simple pools, 86% of the 56 recaptures were collected from simple pools.

DISCUSSION

Habitat Characteristics

Physical conditions in the Onion River and Whittelsey Creek were within the range of conditions commonly encountered in salmon streams of the Pacific Northwest (Sandercock 1991, Fausch and Northcote 1992). Like many streams of that region which provide rearing for coho salmon, the two study streams were characterized by an abundance of small, structurally complex pools and dense riparian vegetation. In-stream cover, especially in the form of large woody debris, was widely distributed in pool habitats of both drainages. Furthermore, groundwater inputs, which act to moderate temperature fluctuations, keep the streams cool in summer and ice-free in winter. Although spawning habitat was not measured, riffle habitats containing small to large sized gravel are widely distributed and common in both drainages.

Population Characteristics and Movement

Mean densities of juvenile coho salmon during fall surveys were within the range of values recorded from Pacific streams but much higher than densities from three Lake Michigan tributaries (Table 2). Length measurements from a small number of fish collected in fall revealed that fish from the Onion River were of comparable size to juvenile salmon from Washington and Oregon streams but slightly larger than fish from streams of Alaska and British Columbia (Table 2).

In Pacific streams, over-winter survival rates for juvenile coho salmon vary widely among streams and over time depending on the availability of habitat refugia (complex pools, off-channel ponds) and sources of mortality (winter flows, low temperatures, and predators). Published over-winter survival rates from that region range from as low as

TABLE 2. A comparison of densities, lengths, and over-winter survival rates of juvenile coho salmon from streams throughout their North American range. FL = fork length

	Summer			Winter
	Survey Period	Densities (fish/m^2)	Size (FL, mm)	Average Survival
Great Lakes				
This study, Wisconsin	Sept	0.65–1.05	64	46[a]
Carl (1983), Michigan	Oct	0.19–0.24	86–99[b]	—
Alaska and British Columbia				
Crone and Bond (1976), Alaska	Aug	0.23–2.23	57–62	34[c]
Murphy *et al*. (1986), Alaska	Sum	0.66–1.68	51–56	–
Swales *et al*. (1986), B. C.	Win	0.4–1.8	73–85	–
Bustard and Narver (1975), B. C.	Win	–	–	35[a]
Tschaplinski and Hartman (1983), B. C.	Win	–	–	70[c]
Coastal Washington and Oregon				
Nielsen (1992), Washington	July	1.0–1.3	60–64	–
Quinn and Peterson (1996), Washington	Oct	–	78	36[a]
Scarlett and Cederholm (1984), Washington	Aug	0.37–1.01	62–68	–
Peterson (1982), Washington	Win	–	–	50[c]
Rodgers *et al.* (1992), Oregon	Sum	0.25–1.25	–	–
House and Boehne (1986), Oregon	Jun	0.18–0.88	59–61	–

[a]stream estimate, [b]total length, [c]off-channel pond estimate

34% in main-channel habitats to more than 50% in off-channel ponds or lakes (Table 2). Although comparable to these latter estimates, the results of this study (average survival of 46%) were from fish overwintering in main-channel habitats, as there are no off-channel ponds in either drainage. On this basis, winter conditions in Lake Superior streams appear to be relatively benign when compared to Pacific streams. Consistent with this view are the findings of Healy and Lonzarich (in press) who observed juvenile coho salmon maintaining dominance hierarchies during the winter in main-channel habitats of the Onion River. In comparison, juvenile salmon of Pacific streams typically redistribute into off-channel ponds and complex pools during the winter (Bustard and Narver 1975).

Though survival estimates from Lake Superior streams are comparatively high, population declines of more than 50% through the winter were observed. Given the consistency of these estimates over time and between drainages, it is unlikely that these declines are an artifact of sampling. Therefore, it is reasonable to assume that fish died from predation or physiological stress, or that they immigrated into Lake Superior. On this latter possibility, it has already been noted that such early migrations are unlikely. Several factors are linked with the down-stream migration of salmon including temperature, individual size, day length, and flow (Sandercock 1991). Migration as early as March has been documented in Pacific streams (Crone and Bond 1976, Peterson 1982, McMahon and Holtby 1992, Quinn and Peterson 1996) although the typical period of migration is usually between May and June. Two studies from the Great Lakes region have documented similar patterns of migration. Scott and Crossman (1973) indicated that smolt migrations begin in late March but peak in late May. Tripp and McCart (1983) found that peak migrations coincided with spring floods, which occur in late March or early April. No flooding occurred before the March snorkeling surveys in either study year. Another line of evidence against early smolt migration comes from the observations of fish in the late winter electrofishing and snorkeling surveys. Not one of more than 410 fish that were observed during these surveys showed any of the morphological signs (silvery color and loss of lateral parr-marks) that characterize smolts.

In the absence of evidence that fish emigrated from the streams, there is an alternative explanation: mortality caused by factors such as predation by terrestrial predators (river otter, raccoon, kingfisher, and mink) and/or temperature-related stress. Unfortunately, there is no direct evidence on the importance of these two factors in the study streams. However, Dolloff (1983) showed that otter predation on juvenile coho salmon was substantial during winter months; while Quinn and Peterson (1996) found that a negative association between pre-winter size of juvenile coho salmon and over-winter mortality. Moreover, Meyer and Griffith (1997) suggested that size-dependent over-winter mortality of two trout species was negatively correlated with winter temperatures, and Johnson and Evans (1996) reported higher over-winter mortality for age-0 white perch (*Morone americana*) at 2.5°C than at 4°C.

The findings of these studies, combined with the results of this study, indicate the need to examine more thoroughly the importance of predators and physiological stress on the regulation of salmon populations. Lake Superior streams would offer an ideal setting for quantifying the effects of such threats because they would not likely be masked by mortality arising from harsh stream flows or low temperatures. If it can be assumed that little emigration occurs during winter, then the results of this study reveal that these threats may be more substantial than previously suspected. While high rates of emigration during winter would weaken this assertion, early emigration would be significant in its own right given that such emigration is not known to occur in Pacific streams.

Unlike their Pacific coast counterparts, juvenile coho salmon in these study streams did not redistribute downstream into complex habitats to overwinter; nor could their distribution patterns be predicted by any physical habitat variables (depth, cover, or wood). In fact, juvenile coho salmon during the winter were distributed widely across complex and simple pool habitats. Together with the findings of Healy and Lonzarich (in press), who found fish in dominance hierarchies during the winter months, these results indicate that management of Lake Superior coho salmon cannot rely entirely on insights gained from Pacific populations. While over-winter survival is strongly associated with complex habitats in Pacific streams (Quinn and Peterson 1996), the results of this study suggest that physical complexity provides little if any survival benefit. This being the case, the question then becomes "what role does in-stream structure play in the winter ecology of salmon from this region?" As in other stream ecosystems, large woody debris in these streams probably affects channel morphology

(Keller and Swanson 1979), provides a substrate for aquatic invertebrates (Benke *et al.* 1984), and protects fish from predators (Lonzarich and Quinn 1995). Evidence from the Onion River also suggests that wood may reduce competitive interactions among juvenile coho salmon during the winter (Healy and Lonzarich, in press).

In conclusion, these findings, in combination with those of Healy and Lonzarich (in press), indicate significant differences in the factors limiting juvenile coho salmon of Pacific and Lake Superior streams. The life history model for Pacific populations, which predicts dramatic movements by fish during winter and high over-winter mortality in main-channel habitats, is not appropriate for populations of this region. Although high stream flows can have strong impacts on over-winter survival in Pacific streams, food availability and cover from competitors (and predators) may be much more important factors in the winter ecology of juvenile coho salmon from Lake Superior streams. For these reasons, a major management goal for Lake Superior coho salmon should be to create and maintain in-stream structure in an effort to reduce the negative effects of predation and intraspecific competition on the overwinter survival and growth of juveniles.

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