REVIEW OF LITERATURE ON

COMPETITIVE AND PREDATOR-PREY INTERACTIONS WITH JUVENILE SALMONIDS IN THE CONTEXT OF REDUCED STREAM FLOWS

prepared for the
DEPARTMENT OF FISHERIES AND OCEANS
West Vancouver, B.C.

Aquatic Resources Limited

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The diversion of Nechako River flows may significantly change the quantity usable habitat for all species in the fish community. Except for juvenile chinook salmon, the nature of these changes are at present unknown. For chinook salmon, the preliminary studies done to date suggest that rearing habitat will increase (Envirocon Ltd. 1984; Russell et al. 1983). This increase is based largely on the depth and velocity requirements of the species. The influence of other biotic and abiotic factors such as food abundance and availability of cover have not been considered. Thus, whether the number of rearing chinook will increase accordingly is unknown. Because the quantity of suitable habitat in a particular system is limited, it follows that an increase in habitat for one species must occur at the expense of other species. Thus some of the species residing in the Nechako River will inevitably suffer a loss in habitat.

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Significant changes in the thermal characteristics of the Nechako River may occur. Water releases from the Kenney Dam and the dam at the outlet of Murry Lake are to be used in the regulation of river temperatures. The projected changes in temperature along the length of the Nechako River are presented in Appendix II. In general, flow reductions are expected to cause a slight increase in water temperature during the months of April through June. Extensive reductions in temperature are proposed for the months of July and August by the controlled release of surface and hypolimnion waters of the Nechako Reservoir. During the remainder of the year, river temperatures are to remain either at their current pre-developement levels or drop slightly to lower values.

From a review of the effects of river flow regulation in 81 river systems in the Pacific Northwest, Burt and Mundie (1986) concluded that the habitat loss and changes in temperature conditions could dramatically affect juvenile salmonid populations in the Nechako River. However, Burt and Mundie (1986) provided little information as to how these affects would be manifested. One likely mechanism is through changes in the interrelationships between the species of the Nechako River fish community.

Aquatic systems are generally considered to be in a state of equilibrium whereby the nature and extent of predation and/or competition allows for a stable coexistence of all species in the community (Arthur 1987; Pimm and Hyman 1987). This state of equilibrium however, is largely dependent on prevailing environmental conditions and is therefore susceptible to shifts as these conditions change. In the case of riverine systems, reduction in stream flow can cause significant changes in habitat structure and would surely shift the system's state of equilibrium. This could in turn affect the stable coexistence of species. For example, in one of the few studies of it's kind, Schlosser (1985) examined the community structure of a second-order stream in central Illinois

1984; Rieman et al. 1986; Stauffer 1977; Vondracek and Moyle 1983; Wood 1987a, b). Much of this predation on juvenile salmonids is largely a consequence of their small size, which renders them susceptible to a large group of predators (Belford 1978; Nilsson 1978; Patten 1971, 1977). As these smaller individuals grow in size however, the number and type of predators which have mouth gapes large enough to consume them lessens, and therefore predation rates decline. Another size related factor of importance is swimming performance. Bams (1967) and Taylor and McPhail (1985) have found that the survival of young salmonids was directly related to swimming performance, and that this in turn was size dependent (i.e. larger individuals swim faster and thus evade predators more effectively than smaller individuals). This is particularly evident in newly emerged fry. Bams (1967) and Fresh and Schroder (1987) have noted that predators may selectively prey on salmonids which still retain much of their yolk reserves. In addition to increasing the fry's visibility to predators, the orange-red yolk apparently impairs swimming performance as well.

Less common and not as readily quantifiable is the mortality which can be attributed directly to competitive interactions. Although fish displaced from stream positions conducive to positive growth may ultimately die of starvation, malnutrition, injury or other stress related causes, it is generally felt that these individuals will succumb to predation before any of these extreme conditions arise (Chapman 1966; Chapman and Bjornn 1969; Dill et al. 1981; Everest and Chapman 1972; Fausch 1984; McFadden 1969; Miller 1958). Peterson et al. (1990) noted that northern squawfish, a major predator of juvenile salmonids, selectively prey upon injured (descaled) individuals when given a choice in an artificial stream environment. Some studies suggest that stress alone (due to handling) can increase the susceptibility of juvenile salmonids to predation (M. Mesa, U.S Fish and Wildlife Service, personal communication, Congleton et al. 1985). However further studies are required to provide more conclusive evidence. An additional consequence of competition may be the slower growth rates that are accrued by fish forced to occupy stream positions that are less than optimal for growth (Fausch 1984, Hillman pers. comm., Reeves et al. 1987). As noted above, smaller fish are more susceptible to predation than larger fish. Thus, slower growth rates can prolong a fish's exposure to high predatory pressures (Fausch 1984).

As in predation, size can have a significant influence on the outcome of competitive interactions. This is particularly evident in intraspecific interactions - larger fish tend to dominate over smaller fish (Larkin 1956). In addition, intraspecific competition (in particular territoriality and social hierarchies) appears to be most intense among similarly sized individuals. Presumably, the greater the size disparity between individuals, the sooner these interactions are resolved. Size mediated competition however, is not necessarily the case for interspecific competition. For example, Allee (1981) found that juvenile coho salmon were able to out compete juvenile steelhead trout regardless of size.

Gibson (1981) observed similar size-independent responses when he compared the agonistic behaviors and competitive outcomes of interactions between coho salmon, Atlantic salmon, brook trout and steelhead trout. Thus the level of aggression inherent in the genetic makeup of the species may also be a strong determinant in the outcome of competition. This genetic component was clearly demonstrated by Taylor and Larkin (1986) when they compared the agonistic behaviors of ocean- and stream-type populations of chinook salmon. They found that stream-type chinook were inherently more aggressive to mirror images (intra-specific competition) and coho fry (interspecific competition) than the ocean-type chinook. Similar inherited differences in agonistic activity were reported by Rosenau (1984) for two distinct populations of coho fry.

METHODS

The information contained in this review was collected in two steps: first through a search of the published literature and second through a series of interviews and discussions with other people engaged in research or other activities relevant to the subject.

LITERATURE SEARCH

The initial information collection phase included a computerized literature search, a manual search of major journals, and the distribution of letters to institutions supporting work in the area of juvenile salmonid studies.

Computer Search

The computer search was performed by L.M. Warren Inc. The databases searched included:

AQUAREF	(1970 - 1990)
BIOSIS	(1970 - 1990)
ASFA	(1978 - 1990)

The following keywords were used:

- predation
- prey
- forage
- interaction
- competition
- territoriality
- interspecific
- intraspecific
- interference
- flow
- stream river
- regulated
- reduced
- reduction
- varying
- temperature
- density
- thermal
- rearing
- salmonid
- salmon
- stream flow
- altered
- resource
- sympatric
- displacement
- coexist

Manual Search

In addition to the computer search, a number of major journals were searched manually from the year 1970 onwards. These included:

Transactions of the American Fisheries Society
North American Journal of Fish Management
Canadian Journal of Fisheries and Aquatic Science
Canadian Journal of Zoology
Environmental Biology of Fishes
California Fish and Game
Progressive Fish Culturist
Journal of Fish Biology

In addition, various technical publications associated with these journals were also searched. A manual search of the Indexes of Canadian Journal of Fisheries and Aquatic Science, Zoological Record, Fisheries Review, Sportfish Abstracts, and the IPSFC publication index (1970-1990) was also performed.

Letters of Inquiry

To increase the breadth of the search, letters of inquiry were sent to institutions engaged in salmonid research. These were directed towards the state fish and wildlife agencies and universities of Alaska, Washington, Oregon, Idaho and California.

INTERVIEW PROGRAM

At the onset of the program it was assumed that published literature would be sparse, and that the bulk of the information would come from either the 'grey literature' contained in agency and university technical reports or the unpublished observations of people directly involved in the study of behavioral interactions or juvenile salmonid ecology. A list of potential sources was developed through the contacts of the study team and later expanded to include the authors of papers located in the literature search and individuals that responded to our letters of enquiry. These contacts often led to further contacts and other sources of information. All of these people were initially contacted by telephone. Generally the discussions were casual, but where warranted, a more formal interview was conducted. The people contacted are listed in the acknowledgements.

INTERPRETATION AND ASSESSMENT

Initially a complex system was established to sort and discuss the information by species, life history stage, type of behavioral interaction (interspecific versus intraspecific and predatory versus competitive interactions), stream flow effects and temperature effects. However, as the literature search progressed, it became evident that there were not enough data to support such a scheme. The paucity of information required that a different approach be used.

Based on the findings of Burt and Mundie (1986) and the available literature, stream flow reductions were equated to a joint loss of habitat (overcrowding) and reductions in water velocity. Consequently, literature, observations, and individual suggestions collected during the literature review and interviews were cross referenced by these two latter variables along with the effects of altered thermal regimes. The information was further subdivided by the nature of the interaction (i.e. predation or competition). Following the discussion on stream flow related effects is a cursory description of the life history and ecology of all Nechako River fishes. Along with the available literature, this formed the basis from which potential predators and competitors of chinook salmon were identified.

EFFECTS OF REDUCED STREAM FLOW

OVERCROWDING

Flow reductions in riverine systems are generally accompanied by reductions in overall wetted width and depth. Consequently, both rearing and spawning habitat may suffer major losses (Hamelton 1985; Newcombe 1985). The immediate effects of such losses in habitat would be the forced crowding of all species - referred to as "species packing" (Werner 1977). Under such crowded conditions, fish are in closer proximity to one another and in turn, the potential for competitive and predatory interactions may increase. There may also be an intensification of previously existing interactions. Over time however, these crowded conditions abate as fish emigrate from the system, die of 'natural' causes, or succumb to predation and a new state of equilibrium is established (Clothier 1953, 1954; Kraft 1972; Miller 1958; Pimm and Hyman 1987; Schlosser 1985).

Competition

Little is known about the effects of overcrowding on the structure of fish communities, particularly at the level of competitive interactions. Few studies have explored the issue (Eck and Wells 1987). An understanding of multispecies competitive interactions and how they may regulate fish community structure is still a fledgling science, and to date much of the research appears to be restricted to closed systems such as ponds and lakes (Cohen 1987; Colby et al. 1987; Pimm and Hyman 1987). Riverine systems on the other hand, are open systems where considerable emigration and immigration can take place. Unlike the more complex work done in lakes, most of the research concerned with the effects of overcrowding in riverine systems have dealt primarily with specific two-species interactions. Further, these studies have generally been restricted to salmonid interactions, primarily because of the wide spread use of stocking programs and the fact that competitive interactions are generally considered to be more intense between closely related species, and therefore of greater concern, than more distantly related species (Arthur 1987; Baltz and Moyle 1984). Consequently, the discussion which follows on the effects of crowding on competitive interactions is largely within the context of intraspecific salmonid interactions.

Soon after emergence, stream resident juvenile salmon and trout become aggressive and establish territories or social hierarchies. Because rearing habitat is limited, riverine system can only accommodate a certain number of such territories and in turn, can only support a finite number of fish (Backiel and LeCren 1978; Chapman 1966; Grant and Kramer 1990; Larkin 1956). Assuming that food is not a limiting factor, it follows that the carrying capacity of a stream is determined largely by the amount of available rearing habitat and the size of each territory (Grant and Kramer 1990). Obviously, a reduction in rearing habitat, such as that caused by a reduction in stream flow, would reduce the carrying capacity of a stream and displace a proportional number of 'surplus' individuals (McFadden 1969). This displacement is thought to be one of the primary mechanisms (outside that associated with the inherent motivation to migrate seaward) leading to the emigration of salmonid populations from stream and river habitats (Bjornn 1971, 1978; Chapman 1962; Clothier 1953; Clothier 1954; Erman and Leidy 1975; Hillman and Griffith 1987; Irvine 1988; Kraft 1972; Lister and Walker 1966; McFadden 1969). There are exceptions however. For example, when Jenkins (1971), and later Hume and Parkinson (1987), released large numbers of hatchery-reared rainbow trout into empty streams, they found that dispersal was more a function of individual differences in preferred habitat than social interactions. When Heggenes (1988) introduced wild brook trout to an existing population further upstream, no substantial changes in movement or stream habitat choice occurred among the original residents. In addition, no emigration was observed among the planted or wild trout. The reason for this apparent lack of dispersal is unclear. It may be that the carrying capacity of the stream was not reached and that greater numbers were required to initiate emigration. Alternatively, it may reflect differences in feeding and aggressive behavior between the two populations. Hume and Parkinson (1987) cite several studies which demonstrate such differences in behavior between planted and wild stocks.

In some cases, overcrowding has been shown to inhibit growth as well. (Backiel and LeCren 1978; Miller 1958). Fraser (1968) found that the growth rates of coho salmon and steelhead trout were inversely related to rearing density. Because food limitations were not a factor in the experiment, it was concluded that reduced growth was due to increased intraspecific competition. Fraser (1968) suggested that agonistic behaviors directed toward competitors may have interfered with feeding activity and therefore reduce food consumption rates. Martin and Wertheimer (1989) reported that both growth and food conversion efficiency was density dependent in chinook salmon. Based on the density dependent conversion efficiency factor, it was suggested that greater proportions of the consumed energy was directed towards the activities associated with competitive interactions rather than growth. Tripp and McCart (1983) reported density dependent growth among the coho salmon stocked in streams containing cutthroat trout. Further, they noted that stocked coho had a negative effect on the growth of resident cutthroat trout. Reduced food consumption rates due to the shared use of limited food resources was cited as the likely reason for this reduction in growth. As noted earlier, size is an important factor mediating predator-prey interactions. Reductions in growth rate can prolong the time juvenile salmon and trout are exposed to high predation risks.

Among juvenile salmonids, territories and social dominance are established through agonistic behaviors and may include both displays and physical contact. Studies have indicated that these agonistic behaviors increase with population density (Fenderson and

Carpenter 1971; Fraser 1968; Grant and Noakes 1988; Hartman 1965). High levels of aggression may lead to stress (Congleton et al. 1985), and if physical contact is involved (e.g. nips) physical injury as well. As was noted earlier, stress and injury can increase a fish's vulnerability to predation. Some species, such as northern squawfish have been found to selectively prey on injured (descaled) prey (Peterson et al. 1990). Although not conclusive, predators may also be selectively prey on stressed individuals (M. Mesa, personal communication, Olla and Davis 1989)

Predation

From the food habit information collected over the years, it has become clear that fish do not restrict their diets to one particular type of prey. Rather, a variety of prey types are eaten (Larkin 1956). However, the number and proportion of particular prey types included in a fish's diet can vary considerably. Such responses range from a clear preference for one type of prey over another to a random consumption of prey regardless of species (Pyke et al. 1977). One of the primary factors which can govern these response patterns is prey density.

In general, when one particular prey type is more abundant than other types (species) of available prey, fish will consume that prey type exclusively. This is due in part to the fact that abundant prey are simply encountered more often. These frequent encounters however, allow fish to gain experience in the pursuit, capture and consumption each prey. In turn, this increases the likelihood of capturing the prey once encountered and minimizes the time and energy spent in the process. Thus, there is a clear advantage to selective predation under such conditions (Pyke et al. 1977; Hyatt 1979; Ware 1971)

A shift in abundance from one prey type to an other generally causes a corresponding shift in the prey type consumed by a particular fish species. Such prey switching responses are a common aspect of fish foraging behavior (Hyatt 1979). This phenomenon is of particular relevance to juvenile salmonid predatory interactions. The concentrations of emerging fry and downstream migrants which commonly occur among salmonids make them particularly attractive as prey to both piscivorous fish and birds (Elson 1962; Poe et al. 1988a; Slaney et al. 1985; Vondracek and Moyle 1983). Overcrowding due to a sudden drop in stream flow, or the consequential emigration of large numbers of fish could also elicit prey switching responses. However, the literature search failed to uncover studies which have examined these specific response to flow reductions.

Although changing prey densities may result in prey switching responses among predators, the consumption of such prey is rarely in direct proportion to their abundance. Rather, the response of predators to changes in prey density have been characterized into four types. (Types I - IV) and are collectively referred to as predatory functional responses (Holling 1966; Mace 1983; Peterman and Gatto 1978; Woodsworth 1982) (Figure 1). These functional responses attempt to qualify the effects of prey density on predation rate by considering it's effects on the various sub-components which constitute an act of predation. Although many have been identified, the most fundamental components appear to be the rate of effective search, handling time (time required to pursue, capture and consume prey) and the time of exposure a predator to prey. (Holling 1966; Peterman and Gatto 1978; Woodsworth 1982; Mace 1983).

The functional responses that appear to be of particular relevance to salmonid predator-prey interactions are Types II, III, and IV (Figure 1). In a Type II response, the rate at which prey are consumed by a single predator increases as prey density increases but, in a decelerating fashion. Eventually an asymptote is reached whereby further increases in prey density cause no further changes in predation rate. This basic response to prey density is thought to be a function of handling time and gut capacity (Holling 1966; Woodsworth 1982; Mace 1983). In a Type III response, predation rate initially accelerates as prey density increases from very low values. However, at a critical density, there is an inflection in the relationship and predation rate begins to decelerate. Like the Type II response an asymptote is eventually reached. The initial acceleration phase of a Type III response is due either to a gradual switch in prey type preference (Oaten and Murdoch 1975) or to a gradual increase in effective search and capture rates gained through experience (Hollings 1966, Begon and Mortimer 1981). Because they differ only in their initial response to prey density increases, it is often difficult to distinguish between Type II and III response curves, particularly in salmonid predator-prey interactions (Woodsworth 1982). In contrast to the latter two functional response types, a Type IV response involves an initial increase in predation rate which eventually peaks and is followed by a gradual decrease in predation rate. This decrease in predation rate with increasing prey density is generally thought to be a function of prey schooling and associated confusion effects (Partridge 1982), although other factors such as the "distastefulness" of a prey species which becomes more pronounced at higher densities (Holling 1966) or by the direct interference of prey during an attack (Woodsworth 1982). Finally, a modified Type II response curve has been described whereby a sudden switch in prey species causes a positive displacement in the x-intercept of the curve (Peterman 1977). Based on the discussion above, it is clear that the response of predators to prey density is varied and complex. Further, the functional response of a particular predator species to prey density is not necessarily unique. Rather, it may change as prevailing biotic and abiotic conditions change (Holling 1966, Mace 1983).

In addition to functional responses, there may also be a numerical response to increasing prey densities. The latter response simply refers to an increase in the number of a particular predator species in response to prey density increases. Such numerical responses can occur at two levels; 1) over the short term where predators are attracted

Figure 1
Predator functional response curves (After Woodworth, 1982).

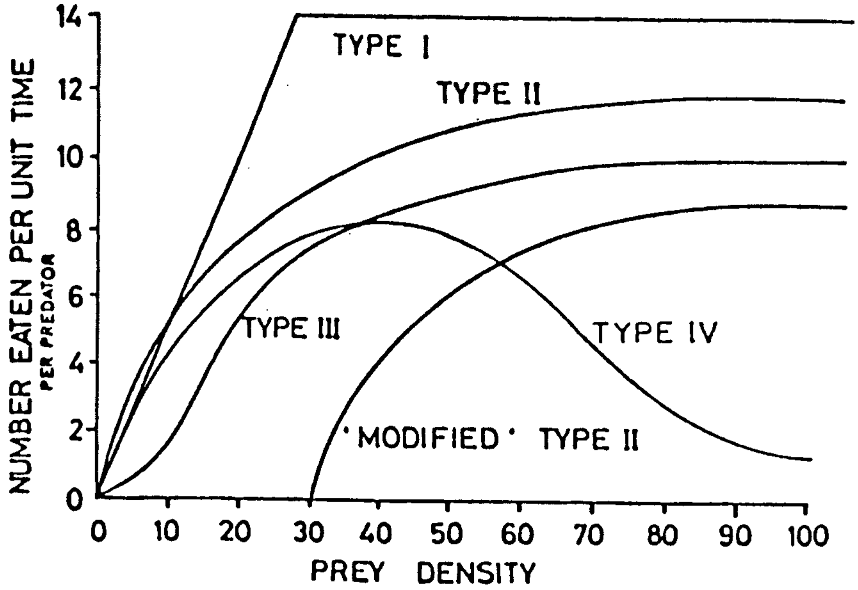
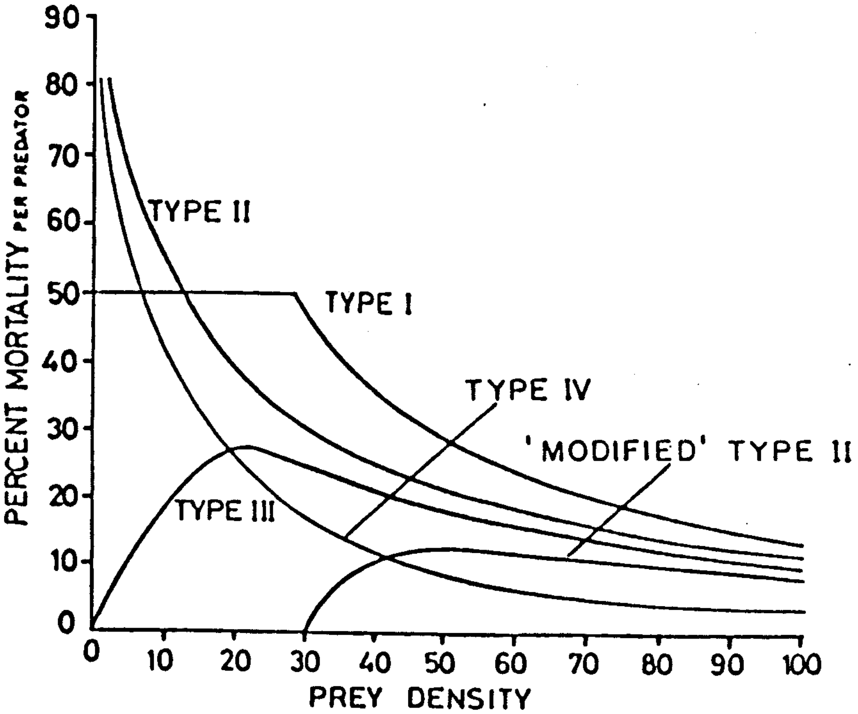


Figure 2
Mortality of prey as a function of predator functional response (After Woodworth, 1982).



from surrounding areas by the high prey densities and form aggregates which concentrate their feeding efforts on particular prey and; 2) over the long term which involve changes in the population size of predators. As pointed out by Vondracek and Moyle (1983) and Beamesderfer and Rieman (1988), migration routes blocked by dams and other diversion structures may also concentrate predators. In the presence of abundant prey, this concentration of predators may remain the area to feed rather than search for alterative spawning habitats.

The effects of predation on prey abundance have been similarly qualified and quantified (Neave 1953). These responses are classified in to three general categories: depensatory, compensatory and extrapensatory effects. Whereas extrapensatory mortality is independent of prey density, depensatory mortality refers to an inverse relationship between mortality and prey density and compensatory mortality to a direct relationship. Only the latter two types of mortality appear to be of concern with respect to salmonid prey-predator interactions (Slaney et al. 1985).

Depensatory and compensatory mortality is intimately related to the functional responses of predators to prey (Woodsworth 1982). In a Type II response, mortality will be depensatory over the full range of prey densities, i.e. as prey density increases, predation rate will increase but not proportionately, resulting in a continuous decrease in percent mortality (Figure 2). In a Type III response, mortality will initially be compensatory since, as predators switch to more abundant prey and gain search and handling experience, a progressively greater proportion of prey are taken as prey density increases. However, as predators approach their limits of handling and gut capacity, percent mortality will become depensatory as in the Type II functional response. A Type IV functional response will result in depensatory mortality over the full range of prey densities. Because predation rate decreases at higher densities in a Type IV response, the drop in mortality will occur at a much faster rate than in a Type II situation. A modified Type II response is likely to yield a mortality curve similar to that associated with the Type III response, but with a positive shift in the x-intercept.

These mortality curves are of particular relevance to emerging and migrating salmonid juveniles. During these phases of their life cycle, they are found in large numbers which may in turn elicit prey-switching, numerical and functional responses among predators. Despite the resulting increase in depredation, the mortality suffered by these fish generally decreases as population density increases (Fresh and Schroder 1987; Mace 1983; Vigg 1988; Wood 1987a, b; Wood and Hand 1985; Woodsworth 1982). As noted above, predators can only consume a limited number of prey per unit time. Thus swamping predators with a high number of prey will allow the majority to escape predation.

VELOCITY

The effect of stream velocity on the behavioral interactions between or within species has not been well documented. Much of the research has been directed towards intraspecific competition rather than interspecific competition or predation. In addition, current velocity is often related to food abundance which may further complicate its effect on behavioral interactions.

Fish respond to current in different ways. Among salmonids, current response (rheotaxis) is apparently related to the extent of their stream residence (Hoar 1951; Taylor and Larkin 1986). For example, pink, chum and 'ocean-type' chinook which move to estuary areas soon after emergence do not respond to current as strongly as coho, steelhead and 'stream-type' chinook which have an extended stream residence pattern. In the latter group of salmonids, current velocity is an important component of their microhabitat and differences in velocity preferences and may lead to spatial segregation of both salmonid and non-salmonid species (e.g. Taylor 1988). Changes in flow will invariably alter the velocity characteristics of streams and may increase or decrease the areas of preferred velocity. This may in turn lead to changes in the intensity of intraspecific competition for space. Interspecific competition may also rise if there is overlap in preferred velocities.

Rheotaxis is not the only relationship which exists between fish behavior and current. Changes in stream velocity can have significant effects on the social and foraging behaviors of salmonids as well. In fast waters, stream resident trouts and salmonids are aggressive, maintain territories (feeding stations), and adopt a 'sit-and-wait' foraging strategy (i.e. feeding on drift). In slower or stagnant waters, they are less aggressive, may form loose schools and adopt an active foraging strategy (Gibson 1978, 1981; Grant and Noakes 1988; Kalleberg 1958; Newcombe 1985; Reimers 1968; Taylor 1988). Reductions in stream velocity appear to influence the cover seeking response of some salmonids as well. This response however appears to differ among species. For example, juvenile coho salmon become more closely associated with cover at high velocities than at low velocities (Taylor 1988). Chinook salmon on the other hand, appear ambivalent while Atlantic salmon tend to seek cover more readily in slow waters (Gibson 1978; Taylor 1988).

Changes in aggression and foraging behavior that occur as a function of current velocity are apparently related to the abundance of drift organisms and the energetic costs of territory defence (Grant and Noakes 1988). As current velocity increases, there is initally a corresponding increase in the abundance of drift organisms. Thus as velocity increases, it becomes more profitable for fish to establish territories and adopt the sit-and-wait foraging strategy than to actively forage for food since the energetic costs of territory defence in relation to energy intake is less than that for swimming while in search for food. In conjunction with these shifts in behavior, there may also be changes in the size of territory that is defended. Slaney and Northcote (1974) found that reductions in available drift increases the territory size of juvenile rainbow trout. Chapman and Bjornn (1969); Dill et al. (1981), Mason (1976) and Symons (1971) noted similar responses in coho salmon and other salmonids. Apparently, these fish must forage over a greater area when food availability is low. As pointed out by Grant and Kramer (1990), the primary consequence of an increase in territory size is a reduction in the carrying capacity of the system and therefore, a displacement of subordinate individuals (i.e. emigration).

These shifts in habitat preference, social behavior and territory size in response to current velocity can potentially alter predator-prey and competitive interactions. A switch in microhabitat may bring fish into contact with new competitors or may intensify existing interactions by reducing the extent with which species are spatially segregated. Changes in cover use can increase or decrease the susceptibility of fish to predation depending on the species and may evoke density dependent responses on the part of the predator (i.e prey switching and functional responses). Similarly switches from stationary to active foraging strategies or the expulsion from a territory may themselves alter susceptibility to predation. Symons (1974) found that Atlantic salmon given the opportunity to establish territories were less vulnerable to predation by large brook trout than salmon which were not. Escalated intraspecific competition may also lead to increased levels of stress and injury and which in turn increase susceptibility to predation (Peterson et al. 1990; Symons 1974).

Changes in microhabitat use in response to altered stream velocities are not restricted to salmonids. A case in point is the response of northern squawfish to various flow regimes in the Columbia River Basin. At high velocities, squawfish generally inhabit nearshore areas where velocity is lowest. At lower velocities squawfish may move into the deeper mid channel. Since chinook salmon during their outward migration are found principally in the mid-channel area, this shift in habitat by squawfish puts them in a position to consume large numbers of these migrating fish (Faler et al. 1988).

Changes in predator-prey interactions may also be mediated through velocity dependent levels of turbidity. Fast waters can carry a high silt load and the resulting turbidity may impair the visual acuity of predators. This in turn can afford prey a certain degree of protection. A reduction in velocity would reduce steam turbidity and therefore expose prey to a greater risk of predation (Brannon et al. 1987; Ginetz 1972; Ginetz and Larkin 1976; Rensel et al. 1984).

Reductions in stream flow will cause the waters edge to move away from existing overhanging and instream vegetation. Several studies have shown that both types of vegetation provide important sources of cover for fish, and can reduce significantly the risk of predation (e.g. Mittelbach 1986; Savino and Stein 1989). Thus, stream flow reductions can increase the incidence of predation through the loss of potential cover. This loss may be particularly important to newly emerged chinook salmon fry which occupy the shallow, sheltered margins of rivers during the initial phase of their life-cycle (Nechako River Project 1987).

TEMPERATURE

Increases in maximum water temperature and prolonged periods of elevated temperature are usually associated with reductions in stream flow. The magnitude of these temperature changes depends on a variety of factors and may vary from system to system.

Temperature is a pervasive factor in the life history of fish (Beitinger and Fitzpatrick 1979). Because biochemical processes are temperature dependent, changes in the thermal environment would invariably alter a fish's physiology. Like all organisms, there are limits to how much thermal change fish can tolerate. Outside of these limits physiological responses begin to breakdown. These limits are commonly referred to as upper and lower incipient lethal temperatures and as the name implies, temperatures beyond these extremes ultimately culminate in death (Reynolds and Casterlin 1979).

Within these thermal extremes, changes in ambient temperature can affect physiological processes in different ways; some increase continuously as temperature increases while others plateau or peak at a particular temperature. The sum of these thermal responses is thought to yield a dome shaped curve, the peak of which is thought to represent the temperature at which all physiological activities collectively operate with maximum efficiency (Beitinger and Fitzpatrick 1979; Brett 1971; Brett and Groves 1979). As ambient temperatures move away from this optimum, the overall performance and well being of an individual fish declines rapidly.

The physiological response to changes in ambient temperature can have a significant impact on competitive and predator-prey interactions. The nature of these mediating effects however, are varied. This depends largely on the direction and magnitude of the temperature change and on the thermal physiology the interacting species. Further, fish express preferences for certain temperatures that are species specific. This provides an axis along which coexisting species can potentially segregate (Baltz et al. 1982; Baltz et al. 1987). Disruption of a thermal continuum along a stream can dramatically alter these patterns of segregation.

Competition

The most obvious effect of temperature on the competitive interactions between two species occurs when it changes their physiological performance in such a way that it provides one with a competitive advantage. This was clearly demonstrated by Reeves et al. (1987) in a study investigating competitive interactions between juvenile steelhead trout and redside shiners. When temperatures of their artificial stream were held between 12-15 °C, the trout were strongly territorial, forced the competing shiners in to deeper and slower waters and severely restricted the shiner's access to food. When temperatures were increased to 19-22 °C, the relationship between the two species reversed. The shiners were quicker to respond to food and forced the trout to abandon attempts at establishing territories. In addition, a large proportion of the trout emigrated from the system as consequence of the red shiner activities. A similar, but more dramatic thermal response was observed in interactions between chinook salmon fry and redside shiners exposed to the same experimental protocol (T.W. Hillman, Idaho State University, pers. comm.). Chinook salmon juveniles apparently dominated redside shiners in cool waters (12-15°C), but were in turn dominated by the redside shiners at warm temperatures (18-22°C). Consequently, production was high for chinook salmon at the cooler temperatures, and for redside shiners at the warmer temperatures.

Altered thermal regimes can also affect competitive interactions in less direct ways. Fish, in expressing a preference for certain temperatures, are able to segregate spatially along a thermal axis. Through discriminant function analysis, Baltz et al. (1987) found that temperature was one of the prime factors governing the distribution of rainbow trout, Sacramento sucker (*Catastomas occidentalis*), Sacramento squawfish (*Ptychocheilus grandis*) and hardheads (*Mylopharodon conocephalus*) in a California stream. Temperature was also found to be responsible for the segregation of speckled dace (*Rhinichthys osculus*) and riffle sculpin (*Cottus gulosis*), two species which occupy similar habitats. Sculpins apparently thrived in the cooler waters and were capable of excluding dace from their preferred stream positions. In the warmer waters located downstream, dace were found to predominate, primarily because the sculpins tended to avoided these high temperatures. In the Sixes River of Oregon, temperature apparently played a role in the spatial segregation of coho salmon and chinook salmon fry (Stein et al. 1972). Upon emergence, both species were found to occupy similar microhabitats, but as the river temperatures increased over the course of the summer, coho were observed to move into the much cooler waters of the tributaries while the chinook remained in the mainstem. Clearly, disrupting the thermal continuum of streams could seriously affect the distribution of these fish. Depending on the magnitude and direction of temperature change, an increase or reduction in the incidence or intensity of competitive interactions can ensue.

In addition to spatial segregation, temperature may also influence the temporal segregation species. A case in point is the competitive interaction between juvenile rainbow trout and coho salmon in the Big Qualicum River (Lister and Genoe 1970). Fry of both species occupy similar microhabitats when they are of the same size. Newly emerged fry initially occupy stream margins and move to progressively deeper and faster waters as they grow older. However, because the chinook fry in the system emerge approximately one month earlier and grow faster than coho fry, they are larger than coho at any given time. The difference in size allows both species to coexist through spatial segregation. Shifts in incubation temperatures over the winter months however, can delay or accelerate emergence times in the two species and in turn, interfere with this time related spatial segregation.

As ambient water temperatures increase, the metabolism of fish accelerates exponentially. As a result, the energy required by fish to maintain a positive growth rate increases as well. Because competitors must search for greater amounts of food, such an increase in energy demand can intensify competitive interactions. Among conspecifics, this may lead to increased competition for space. Slaney and Northcote (1974) found that territory size among stream resident rainbow trout increased when food abundance was low. Similar observations were reported by Dill et al. (1981) and (Wilzbach 1985). It follows that an increase in food demand without a corresponding increase in food abundance can result in a similar situation - i.e. high food demands lead to increases in territory size. As noted earlier, increases in territory size can displace subordinate fish and therefore reduce the overall density of young salmonids in streams. In this respect, altered temperature regimes can either compound or ameliorate the effects of crowding.

Temperature can also mediate competitive interactions by influencing the growth rate of fish. For example, Stein et al. (1972) found that the outcome of competitive interactions between juvenile coho and chinook salmon were at least in part determined by size. In cool temperatures, coho salmon were found to grow much faster than chinook and this provided a competitive edge over chinook salmon. An increase in water temperature may reverse the situation. Chinook salmon grow better at warm temperatures and this growth advantage may alter the size relationship between the two species. In turn, chinook may be able to out come coho for profitable stream positions.

Predation

Changes in temperature regime can affect the outcome of predatory interactions much in the same way it can affect competitive interactions, i.e. through changes in overall physiological performance. A change in temperature towards the optimum for a given species can increase the effectiveness with which it can prey on other organisms or avoid predation (Coutant et al. 1979). This was apparently the case when Yocum and Edsall

(1974) examined the predator-prey interaction between juvenile lake whitefish and yearling yellow perch at different temperatures. At cool temperatures, the number of prey caught per attack by perch was relatively low. However, as ambient temperatures increased towards the thermal optimum, the number of prey caught per attack increased accordingly. Sylvester (1972) reported a similar thermal response in the predator-prey interaction between yearling coho salmon and sockeye fry. As acclimation temperature increased from 7°C to 17°C, the coho yearlings increased the number of fry consumed per unit time and in turn reduced their survival rate. The high predation rate of squawfish observed below an impoundment structure on the Eel River, California is thought to be in part related to the river's high water temperature. These warmer waters apparently favour the activity of Sacramento squawfish and enhance the success with which they can capture and consume juvenile salmon (L. Week, Personal communication). Conversely, a shift towards the thermal optimum of the prey species can reduce their vulnerability to predation. Burst swimming performance is an important factor in predator avoidance (Bams 1967; Howland 1974; Taylor and McPhail 1985). Because performance varies as a function of temperature (Pritchard 1936; Webb 1978), shifts in temperature towards the species' optimum would enhance their avoidance response and therefore render them less susceptible to predation. Thus, shifts in temperature away from their respective thermal optima in either of a pair of interacting species can inhibit their predatory or predator-avoidance capabilities. Obviously, the outcome of predator-prey interactions at different temperatures will depend largely on the thermal physiology of each of the interacting species.

Brief exposure to potentially lethal temperatures can also increase susceptibility to predation. Coutant (1973) exposed chinook salmon and rainbow trout fry to a larger trout predator following short term exposure to lethal temperatures. In both species, thermal stress increased their vulnerability to predation by larger trout. In addition, the predators appeared to selectively prey on the stressed individuals. Abnormal swimming behaviors were apparently the primary means by which predators were able to discern the disabled prey.

Warmer temperatures accelerate the metabolism of fish and therefore increase their demands for energy. In response, food consumption rates increase. However, the increase occurs only up to a certain temperature, after which thermal stress appears to reduce appetite (Brett 1979). The importance of the temperature-consumption relationship in mediating predatory interactions was clearly demonstrated in the recently published study of Beamesderfer et al. (1990). Following years of research on the predatory activities of northern squawfish in the Columbia River basin, they developed a model of predation which enabled them to examine the joint effects of water temperature and other parameters on juvenile chinook salmon losses. Sensitivity analysis showed that temperature and it's effects on food consumption rate was, along with the number of potential predators, a major factor governing the mortality of chinook salmon through predation. This appears to be the only study which has carefully examined the role of temperature dependent consumption rates as a factor affecting salmonid survival.

Increased energetic demands due to warming temperatures can also affect the behavior of the prey species. When there is ample food to satisfy their energetic demands, fish tend to adopt foraging strategies that minimize the risk of predation. In the classic studies of Milinski and Heller (1978) and Werner et al. (1983), it was noted that fish tend to expose themselves to greater risks of predation in search of food when it is difficult to procure. This is apparently the case among salmonids as well (Wilzbach 1985). When ample food was provided, cutthroat trout were found to rarely venture far from cover. This was interpreted as an adaptive response to reduce predation. With a reduction in available food however, most of the trout abandoned the areas of cover - presumably in search of food - and therefore increased their potential exposure to predators.

As noted earlier, the temperature preferences expressed by fish can lead to a spatial segregation of species in riverine systems. In the same way that it can minimize competition, spatial segregation can also minimize the interaction between predators and prey. Coho salmon smolts are typically piscivorous in nature and are known to prey on salmonid fry when present (Rensel et al. 1984). However, in the Sixes River in Oregon where both coho and chinook reside in sympatry, the differences in temperature selection behavior appear to restrict the distribution of coho smolts to the cooler waters of the tributary streams and away from the chinook salmon which tend to occupy the warmer mainstem (Stein et al. 1972).

NECHAKO RIVER FISHES AND SPECIES INTERACTIONS

There are a total of 20 fish species that reside in the Nechako River system (Table 1). Non-salmonid fish are the most abundant species, particularly northern squawfish, redside shiners and various suckers species (of which largescale suckers appear to predominate). Among the salmonids, chinook salmon fry are the most numerous, followed by Rocky Mountain whitefish. The remaining species occur only in relatively low numbers (Envirocon Ltd. 1984).

Table 1
Common and scientific names of fish species in the Nechako River (Modified after Envirocon Ltd. 1984).

Family	Common Name	Scientific Name
Salmonidae	Chinook salmon	*Oncorhynchus tshawytscha* (Walbaum)
	Sockeye salmon	*Oncorhynchus nerka* (Walbaum)
	Coho salmon [a]	*Oncorhynchus kisutch* (Walbaum)
	Rainbow trout	*Oncorhynchus mykiss* (Richardson) (formerly *Salmo gairdneri*)
	Dolly Varden	*Salvelinus malma* (Walbaum)
	Rocky Mountain whitefish	*Prosopium williamsoni* (Girard)
Catostomidae	Largescale sucker	*Catostomus macrocheilus* (Girard)
	Longnose sucker	*Catostomus catastomus* (Forster)
	White sucker	*Catastomus commersoni* (Lacepede)
	Bridgelip sucker	*Catostomus columbianus* (Eigenmann and Eigenmann)
Cyprinidae	Redside shiner	*Richardsonius balteatus* (Richardson)
	Longnose dace	*Rhinichthys cataractae* (Valenciennes)
	Leopard dace	*Rhinichthys falcatus* (Eigenmann and
Eigenmann)		
	Northern squawfish	*Ptychocheilus oregonensis* (Richardson)
	Peamouth chub	*Mylocheilus caurinus* (Richardson)
	Brassy minnow	*Hybognathus hankinsoni*
Cottidae	Prickly sculpin	*Cottus asper* (Richardson)
Gadidae	Burbot (ling)	*Lota lota* (Linnaeus)
Acipenseridae	White sturgeon	*Acipenser transmontanus* (Richardson)
Petromyzontidae	Pacific Lamprey	*Entosphenus tridentatus* (Gairdner)

[a] Found occasionally in Nechako River tributaries (Nechako River Project 1987).

SALMONIDAE

Chinook salmon

The distribution of chinook salmon along the Pacific coast extends from the northern streams of Alaska to the Ventura River of Southern California (Scott and Crossman 1973). In coastal streams, newly emerged chinook fry generally migrate directly into estuarine habitats and therefore spend little time in freshwater. However, in more inland streams, chinook fry may adopt one of a complex array of life cycles - spending anywhere from months to years in freshwater before migrating seaward. Nechako River chinook are typical in this regard, and extended freshwater rearing is an important segment of their life history (Envirocon Ltd. 1984; Emmet 1989; Emmet and Convey 1990).

The Nechako River has been extensively studied in the past, particularly in reference to chinook salmon (Nechako River Project 1987; Russell et al. 1983). As a result much is known about the early life history of chinook salmon during their freshwater phase in the Nechako River.

Upon emergence from gravel, chinook fry in the Nechako River initially form tightly packed schools in the shallow, sheltered margins of the river. Shortly afterwards, the fry become territorial and occupy progressively deeper and faster waters as they increase in size. As a consequence, they move into areas further away from shore (Nechako River Project 1987). The data also suggest that chinook fry may rear in some of the larger tributaries of the Nechako River and remain there for much of the summer.

During the latter part of their freshwater phase, juvenile chinook in the Nechako River undergo diel inshore/offshore migration. They occupy the shallow river margins at night to feed and move to offshore areas by day, where loose schools are formed in the vicinity of log jams and other sources of cover. Despite these extensive movements, juvenile chinook still maintain a clear preference for river margins. They rarely venture further than 6-8 m from shore or waters greater than 1 m in depth (Nechako River Project 1987). Because fish other than chinook salmon are more abundant in the mid-channel areas than along the river margins, it is thought that this restriction in distribution may serve to reduce interspecific competition. Furthermore, it has been suggested that the migratory and schooling behaviors may provide a certain degree of protection from potential predators, whether it be piscivorous fish or birds (Nechako River Project 1987).

The distribution of chinook in the Nechako River appears to change over the course of their residence in the system. In Spring and early summer, chinook fry are found throughout the system including all major tributaries (Nechako River Project, 1987). By Late summer/early fall, many of the chinook in the tributaries migrate into the Nechako mainstem, mostly due to severe reductions in tributary flows. In addition, there is also a migration of rearing chinook from the upper reaches of the Nechako River to its lower reaches and the Fraser River (Envirocon Ltd. 1984, Nechako River Project 1987). The chinook apparently overwinter in these latter areas, hiding among the larger substrate and other sources of shelter (Emmet 1989; Emmet and Convey 1990). Come spring, the remaining chinook continue their seaward migration out of the Nechako River and into the Fraser River.

Chinook Salmon in the Nechako River and it's tributaries are opportunistic feeders, consuming primarily aquatic insects (Diptera and Ephemeroptera) and copepoda in proportion to their abundance (Russell et al. 1983, Envirocon Ltd. 1984). Chinook appear to feed primarily on drift organisms although benthic organisms may also be taken. This feeding pattern of Nechako River chinook is reflected in their preference for stream positions between 10-20cm above bottom.

Sockeye salmon

Sockeye salmon typically spawn in the inlet tributaries of lakes during the fall months. The eggs incubate during winter and hatch in spring. Soon after emergence, the fry migrate out of the spawning streams to rear in the open waters of lakes. Seaward migration of sockeye smolts generally occurs in the spring months of their second to fifth year of freshwater residence (Scott and Crossman 1973).

Within the Nechako River system, sockeye salmon have only been reported in the Nautley and Stuart Rivers, two major tributaries of the Nechako River which drain a series of lakes. Because juvenile sockeye spend most of their freshwater life in lakes, encounters with the rearing chinook salmon are minimal. The residence time of juvenile sockeye salmon in the Nechako River is limited to a period of 2-4 days in spring during their seaward migration (Envirocon Ltd. 1984). Although competitive interactions are possible, they are not likely to significantly affect the chinook population. Furthermore, because sockeye smolts are primarily plankton feeders, they pose a minimal predatory threat to chinook. Reductions in steam flow are not likely to affect the limited interactions between the two species.

Coho salmon

Coho salmon generally spawn in the fast, shallow waters of river tributaries in late fall/early winter. Fry emerge from gravel in spring and generally remain in their natal streams for the first year in life. During their first year, fry initially congregate in schools and occupy shallow, gravel habitats near shore. As they increase in size, they become more aggressive and territorial (Reimers 1968; Scott and Crossman 1973). Although coho fry may be found in pool habitats throughout the freshwater phase of their life cycle, the trend is particularly prominent during late fall and winter (Hartman 1965). In the following spring, juvenile coho begin their outward migration, leaving their natal streams behind only to return in 3 to 5 years to spawn. Juvenile Coho migrate mainly at night and in small schools. They are generally considered to be bottom feeders and consume a variety of aquatic insects larvae. Coho smolts are known to feed on salmonid fry, including their own, when they are abundant (Scott and Crossman 1973).

To date, coho have only been caught in the tributaries of the Nechako River (Nechako River Project 1987). Despite extensive sampling over the years, none have been caught in the Nechako River mainstem (Envirocon Ltd. 1984, Nechako River Project 1987). The reason for this is unclear. This has raised some question as to whether the species was properly identified (C. Levings, pers. comm.). However, Stein et al. (1972) reported a similar pattern of coho and chinook fry distribution in the Sixes River, Oregon. They cited temperature differences between the tributary streams and the mainstem as the main factor causing this spatial segregation pattern. Coho apparently prefer the cooler waters of the tributaries over the warmer mainstem, which is preferred by the chinook salmon. Whether this type of spatial segregation occurs in the Nechako River system is not known. However, the collective spot temperature data of Russell et al (1983) and Nechako River Project (1987) suggests that it may be possible. During the months of May through to September of 1980-81 and 1985-86, tributary temperatures were generally cooler than the mainstem by 2 to 5°C. Regardless, the fact that juvenile coho are found primarily in the Nechako River tributaries rather than the mainstem limits the extent with which they interact with chinook. Furthermore, because most chinook fry migrate to the lower sections of the Nechako River mainstem by fall, and later migrate seaward in the following spring, coho smolts are unlikely to encounter chinook fry in significant numbers to considered as a major predatory threat.

Among the chinook fry found rearing in the tributaries however, competitive and predatory interactions with coho fry can be intense. Stein et al. (1972) found that juvenile coho salmon were able to out compete chinook salmon fry in an artificial stream under all experimental conditions. Lister and Genoe (1970) found that the microhabitat preferences of coho and chinook fry of the same size are very similar. In addition, both species express similar changes in habitat preference with size. Thus the potential for competition between the two species is very high. However, Lister and Genoe (1970) noted that in the Big Qualicum River, British Columbia, chinook salmon emerged one month earlier than the coho and were consequently larger at any given time. The size difference apparently resulted in a high degree of spatial segregation. This time related spatial segregation of species may also occur in the Nechako River. However, because temperature conditions, a major factor determining the time of egg hatching, is likely to differ from that of the Big Qualicum River this may not necessarily be so. Because chinook rearing in the tributaries commonly migrate to the mainstem by late summer, the time spent together would be limited. This may reduce the extent with which the two species compete.

Rainbow trout

Life histories of rainbow trout vary considerably depending on region, habitat and variety. There are anadromous steelhead trout, non-anadromous stream resident rainbow trout and lake dwelling kamloops trout (Scott and Crossman 1973). In the Nechako River system, the stream resident rainbow trout appears to predominate, although lakes in the system may contain the lake dwelling form (Envirocon Ltd 1984). There is no compelling evidence to suggest the system also supports anadromous steelhead trout.

Studies carried out by Envirocon Ltd. (1984) indicate that rainbow trout spawn in the Nechako River in spring. Spawning takes place primarily in tributary streams where redds are formed in the fine gravel substrate of riffle habitats. Eggs usually hatch in 4 to 7 weeks and the newly emerged fry commence feeding about two weeks later (Scott and Crossman 1973). In the Nechako system, the fry rear almost exclusively in tributary streams. Rainbow trout at the parr stage however, rear both in tributary streams and in the river mainstem. Adults apparently reside primarily in the mainstem. The vast majority of trout outside of the tributaries were found in the upper reaches (1 - 5) of the Nechako River, coincident with the distribution of juvenile chinook salmon. However, they are found only at low densities (Envirocon Ltd. 1984).

Like other stream resident trout, rainbow trout are territorial (Allee 1981; Edmundson et al. 1968; Everest 1969; Everest and Chapman 1972; Gibson 1981; Hartman 1965; Rose 1986; Slaney and Northcote 1974). Newly emergent fry typically occupy slow, shallow waters near stream margins and move into progressively faster and deeper waters as they grow in size. Coincident with these size related shifts in microhabitat is an increase in territory size. These territories however, break down during winter as water temperatures cool and stream velocities abate. Rainbow tend to congregate in deep pools and often hold among the interstices of large rubble substrate (Bjornn 1971; Chapman and Bjornn 1969; Edmundson et al. 1968; Everest and Chapman 1972; Gibson 1981; Swales et al. 1986).

Rainbow trout prey on a variety of organisms. As young, they feed primarily on benthic prey such as insect larvae crustaceans and snails, but will also consume drift organisms. With increasing size, fish become a more important component of their diet. Included among their piscine prey are other salmonids. Rensel et al. (1984) noted that rainbow trout, in addition to coho salmon and cutthroat trout, are the most often reported predators of juvenile salmonids, particularly of pink, chum and sockeye salmon where mortalities may be as high as 97%. Rainbow trout are also known to prey on chinook (Patten 1971). The extent of this predation however, is not well documented, but it is likely to depend on predator and prey numbers as well as the size distribution of the trout (Fresh and Schroder 1987; Patten 1971; Rensel et al. 1984).

The number of trout currently residing in the Nechako River, in particular adults, is not well known. From 1983 to 1986, a closure of the trout fishery and a stocking program were initiated to restore the trout population to previous levels. Preliminary data suggest that the population of trout is increasing (Slaney 1986). Regardless, because large predators such as adult trout can consume high numbers of prey per individual, they pose a serious predatory threat to chinook fry even at low numbers (Fresh and Schroder 1987).

Juvenile rainbow trout are often found in conjunction with chinook salmon. Thus the potential for competition exists. In a 14 year program studying the effects of steelhead and chinook stocking regimes in the Lemhi River Idaho, Bjornn (1978) found that steelhead trout production, when stocked jointly with chinook salmon, was considerably less than when they were stocked alone at a comparable density. Bjornn cited competition as the reason for the loss in steelhead production. However, the intensity of competition was not high enough to prevent their coexistence since the joint production of the two species far outweighed the production of each species alone, regardless of stocking density. Everest and Chapman (1972) compared the microhabitat preferences of chinook salmon and steelhead trout and found that they were very similar at any given size. However, because spawning and emergence times differed between the two species (steelhead spawn in spring while chinook spawn in fall), chinook salmon were always larger at a given time than the steelhead. Thus chinook were always in deeper and faster waters than the steelhead and this permitted their coexistence. A similar time related segregation pattern is likely to exist in the Nechako River. In addition, as was evident in the surveys done by Envirocon Ltd. (1984), there may also be considerable spatial segregation between the two species. Rainbow trout fry rear primarily in the tributary streams while the majority of chinook are thought to rear in the mainstem. Thus competitive interactions between the two species may be of concern only in those few tributaries where chinook fry are known ascend and subsequently rear for a short period of time. (Envirocon Ltd. 1984).

Dolly Varden

Like many other trout and salmon, Dolly Varden may be anadromous or non-anadromous. They spawn in the fall and the fry emerge from the gravel in spring. Dolly Varden generally spend up to 4 years in their freshwater spawning streams before migrating seaward or lakeward. Adults may also reside in larger river systems (Scott and Crossman 1973).

Dolly Varden fry initially remain in the shallow waters of stream margins where they stay on or near the bottom. As they grow older, they move to progressively deeper waters, but maintain their close association with bottom. In addition, their association with cover (large organic debris, cutbanks and large boulders) increases (Dolloff and Reeves 1990). They do not appear to be highly territorial (Dolloff and Reeves 1990; Newman 1956; Schutz and Northcote 1972). Both the young and old alike are opportunistic predators, consuming a wide variety of insects, isopods, gastropods, amphipods, leeches, fish eggs, fish and other small vertebrates (Scott and Crossman 1973). Dolly Varden have earned a reputation as being an intense predator of salmonid fry, particularly during periods of downstream migration (Pritchard 1936; Scott and Crossman 1973).

The number of Dolly Varden found in the Nechako River is very low (Envirocon Ltd. 1984, Nechako River Project 1987). All Dolly Varden that were sampled were greater than 20 cm in length. No fry or parr were caught suggesting that the Nechako River is not an important spawning or rearing ground. It has been suggested that the Dolly Varden found in the Nechako River may be from tributary populations or other parts of the Fraser River System (Envirocon Ltd. 1984). Thus, although a potentially serious predator, Dolly Varden do not pose a major threat to Nechako River chinook salmon fry. Further, because no fry or parr reside in the system, they are of unlikely to compete with chinook fry at that stage. Even if there were juvenile Dolly Varden, their close association for bottom would vertically segregate the two species, therefore minimizing the potential for competitive interactions (Dolloff and Reeves 1990; Schutz and Northcote 1972)

Rocky Mountain whitefish

Rocky Mountain whitefish occur in a wide variety of habitats. They feed mainly on bottom organisms, but will feed at any level, including the surface, if there is a shortage of food. Whitefish typically spawn in the fall and early winter over gravel substrate. Fry emerge in spring. Little is known of their early-life history and microhabitat preferences (Scott and Crossman 1973). In the Nechako River, Rocky Mountain whitefish were observed primarily in the deeper mid-channel of the river (Nechako River Project 1987). There is some evidence which suggests that whitefish may undergo diel inshore-offshore migration during summer - occupying areas closer to the river's margin during the day and mid-channel areas at night (Envirocon Ltd. 1984). This pattern of diel migration is opposite that expressed by chinook fry. Because of this spatial and temporal segregation of species, competitive interactions between mountain whitefish and juvenile chinook salmon are likely to be minimal. Further, because whitefish are not considered to be piscivorous, they pose no predatory threat to chinook.

Flow reductions and the increased carrying capacity of the Nechako river for rearing chinook is likely to increase competition for food and space between the two species by reducing habitat partitioning. The magnitude of this increase however is unknown as little is known about the microhabitat preferences of mountain whitefish during the various phases of their life-cycle.

CATOSTOMIDAE

There are four species of suckers found in the Nechako River (Table 1). However, because little is known of their individual life history patterns, particularly in the Nechako River system, their general biology and potential to interact with chinook salmon are discussed as a group.

Suckers typically spawn in spring when water temperatures increase to 5-10°C. Depending on temperature, the eggs hatch within in a two week period and become free swimming fry about two weeks later. Their mouths are initially terminal in location and the fry feed on a variety of drift organisms. Once they reach 12-18 mm in length, their mouths migrate to the sub-terminal position. This is accompanied by a gradual shift in microhabitat from a position higher up in the water column to a close association with the bottom. As benthic feeders, suckers consume a wide variety of invertebrate prey depending on their size, season and location. All species are found in larger river systems and their tributaries. Except for the bridgelip sucker, they are also found in lakes (Scott and Crossman 1973).

Both white and largescale suckers undergo strong diel inshore/offshore migration - feeding near shore during the day and moving offshore at night (Scott and Crossman 1973; Envirocon Ltd. 1984). McPhail and Lindsey (1970) note that these diel movements are also expressed at the fry stage. Whether longnose and bridgelip suckers express similar diel shifts in habitat preference is unknown.

Suckers as a group are the most abundant fishes in the Nechako River (Envirocon Ltd. 1984). Because few of the surveys carried out in the Nechako River differentiated between the four sucker species, their relative abundances are not well known. From the limited data however, it appears that largescale suckers are the most numerous of the four species (Envirocon Ltd 1984).

There are few studies which have examined the interactions between suckers and salmonids. In general, dietary overlap is minimal and there a high degree of vertical segregation between the two groups (Baltz and Moyle 1984; Dettman 1976; Holey et al.

1979). At one time, suckers were considered to be a major predator of salmonid eggs. However, this may be an exaggeration. Scott and Crossman (1973) cite a number of studies which indicate otherwise. It would appear that the eggs eaten by these species may only be those exposed by superimposition of salmonid redds. This is likely to be the case for chinook salmon since their eggs are buried deep in the substrate (Russell et al. 1983; Scott and Crossman 1973).

Because of their subterminal mouth and close association with river bottoms, it is doubtful that suckers pose a predatory threat to juvenile salmonids. This was evident in the behavioral response of juvenile coho to the chemical stimulus of largescale suckers compared to that of northern squawfish, a major predator of juvenile salmonids (Rehnberg and Schreck 1986). Coho actively avoided areas where the squawfish stimulus was released but was relatively indifferent to the sucker stimulus.

As pelagic feeding fry, suckers may compete with juvenile salmonids for food and space. Baltz and Moyle (1984) compared the microhabitat preferences of juvenile trout and Sacramento suckers at various ages and sucker densities. Both species shared a common preference for maximum water depths, mean velocities, focal point velocities, surface velocities and substrate types regardless of sucker age. Among the newly emerged sucker fry, there was also considerable overlap in preferred focal point depths indicating that the two species may compete for space as well as food. However, as the suckers grew in size and their mouths moved to the subterminal position, they became vertically segregated and the potential for competition was minimized. Since chinook fry share similar microhabitat preferences (Everest and Chapman 1972), it is conceivable that competition between this salmonid species and suckers is also possible.

As noted above, some suckers undergo diel inshore-offshore migration which may also be expressed by young fry. Chinook salmon fry also move inshore and offshore depending on the time of day, but opposite in phase. Thus temporal segregation may exist between the two species, particularly the white and largescale suckers. This would minimize the extent of chinook interactions with suckers.

Suckers and juvenile salmonids may compete for space during the winter. Many salmonids, including chinook fry, hold among the interstices of large rubble substrate when water temperatures and velocities drop to winter lows (Bjornn 1971). These areas however, may also be occupied by suckers. Gibson (1978), in examining this hiding behavior among brook trout and Atlantic salmon, noted that longnose suckers could limit the number of potential hiding places for these fish. The nature and intensity of these potential interactions have not been explored within the Nechako River.

CYPRINIDAE

Northern squawfish

Northern squawfish are found primarily in lakes, but may also reside in larger river systems. During winter, lake populations typically occupy the deeper offshore areas while river populations tend to move downstream into deeper waters. During late spring and summer, squawfish move inshore to spawn in shallow waters over gravel substrate. In the absence of suitable spawning habitat, squawfish may migrate considerable distances (several 100 km) up or into rivers and may even ascend tributary streams (Beamesderfer and Rieman 1988; Brown and Moyle 1982; Scott and Crossman 1973; Vondracek and Moyle 1983). At the end of spawning, squawfish tend to disperse into summer feeding areas which generally consist of low velocity shoreline habitats.

Squawfish eggs hatch in about a week, but may be longer or shorter depending on water temperature. The young generally remain near shore during summer but migrate into deeper waters by fall. In riverine habitats, the young tend to avoid strong currents and remain near shore or in pools (Scott and Crossman 1973). Larger squawfish appear to express a similar avoidance of fast waters, remaining near shore except when velocities drop due to reductions in stream flow (Beamesderfer and Rieman 1988, Faler et al. 1988). When this occurs, northern squawfish will move further offshore to feed.

Northern squawfish are opportunistic feeders. Young under 10 cm in length feed almost exclusively on aquatic insects and other aquatic invertebrates (Scott and Crossman 1973, Poe et al. 1988, Vigg et al. 1988). As the young grow in size, crayfish and fish become increasingly important, particularly individuals between 200 and 350 mm in length. In squawfish greater than 350 mm in length, fish become the dominant prey (Poe et al. 1988, Vigg et al. 1988). Diets may also vary in accordance to season. Ricker (1941) noted that during their spring and summer residence close to the shores of Cultus Lake, British Columbia, a wide variety of organisms, including fish, crustaceans, insects and other aquatic invertebrates, were consumed. During the fall when offshore areas were inhabited, fish were consumed almost exclusively. Changes in prey composition were also observed by Poe et al. (1988) in the Columbia River. During the months of April and May, fish comprised approximately 90% of their diet. In June this percentage dropped to about 60%, but increased to 90% again in July. In August, the percentage of fish included in their diet was comparable to that in June. Unlike the situation in Cultus Lake where habitat shifts were implicated (to and from offshore areas), the changes in prey composition of Columbia River squawfish were apparently related to changes in prey availability. Eggers et al. (1978) arrived at a similar conclusion with regard to a Lake Washington population of squawfish and implicated prey-switching responses as a mediator of northern squawfish predation.

Because of this largely piscivorous diet and their often sympatric existence with salmonids, northern squawfish have earned a reputation as a major predator of juvenile salmonids, particularly during their outward migrations when they are found at high densities (Eggers et al. 1978; Jeppson and Platts 1959; Poe et al. 1988a; Ricker 1941; Rieman et al. 1986; Simms et al. 1977; Thompson 1959; Thompson and Tufts 1967; Vigg et al. 1988). However, a review of the available literature on squawfish predation lead Brown and Moyle (1982) to concluded that, although great numbers of salmonids may fall prey to squawfish in lacustrine habitats, this predatory reputation may not be deserved by squawfish in riverine habitats. There are several studies which suggest that squawfish predation of juvenile salmonids may not be as significant in streams (Buchanan et al. 1980, 1981; Kirn et al. 1986; Poe et al. 1988). As pointed out by Brown and Moyle (1982), the high incidences of salmonid predation were generally associated either with a recent release of hatchery reared fish which supplemented natural stocks, or with dams and other diversion structures where conditions apparently facilitate predation. In the former case, the reportedly high rates of predation may have been due to an inundation of fry that were above natural levels and caused a quicker prey switching response among the resident squawfish. Alternatively, the squawfish may have been selectively preying on the hatchery fish which are generally considered to be less "fit" overall, and thus more susceptible to predation, than wild fish (Slaney et al. 1985). With respect to dams and other diversions, both prey-switching and numerical responses may be involved. Dam structures which accommodate migratory activities can act as partial barriers and cause mass aggregations of migrating salmon (Hall 1979; Poe et al. 1988a; Simms et al. 1977). In passing through fishways, fish may become injured, stressed and disoriented and therefore become more susceptible to predation (Peterson et al. 1990; Poe et al. 1988). Both factors could induce the prey switching response of squawfish. These conditions may also attract squawfish from surrounding areas, and cause local populations to increase. Additionally, as noted above, squawfish sometimes migrate to upstream areas to spawn during the spring and summer months. Dams may block this migration and, with the migrating fry providing abundant food, compound the numerical response (Beamesderfer and Rieman 1988; Vondracek and Moyle 1983).

In the Nechako River, the conditions which aggregate both predators and prey in diverted rivers presently do not exist. Overflow from the Nechako Reservoir above the Kenney dam enters the Nechako River via Cheslatta system which is located approximately 8 km downstream. The river bed between Kenney Dam and the Cheslatta confluence contains only residual flows and few fry rear in the area (Envirocon Ltd. 1984). However, there is a plan to reactivate this part of the river ~~for at least part of the year~~ (Appendix II). What this will do to the distribution of chinook fry and northern squawfish immediately below the dam is unknown. Because there are no other diversion structures below the Kenney dam which impede the outward migration of chinook, predation by squawfish throughout most of the Nechako River is likely to be similar to the levels noted for undiverted or

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unstocked systems. The extent of squawfish predation on chinook fry immediately below Kenney Dam cannot be determined without more information on their future distributions. Regardless, because northern squawfish are one of the more abundant species found in the Nechako River (Envirocon Ltd. 1984), they still can pose a significant predatory threat.

Juvenile squawfish tend to reside in low velocity habitats and probably do not compete intensely with chinook salmon for space or food, despite the fact the both species consume similar prey items. Unlike squawfish, chinook salmon are found in slow waters only at an early age. Because squawfish fry emerge during summer, much later than chinook, the fry are unlikely to share the same habitat. This type of temporal segregation appears to be a common phenomenon among stream dwelling fish, particularly salmonids (Rensel et al. 1984).

Redside shiner

Redside shiners are found in a wide variety of habitats, from ponds and lakes to streams and rivers of various sizes, and are able to tolerate a wide range of temperature and trophic conditions. They spawn in spring and early summer in equally diverse habitats. The eggs hatch in 3 to 15 days depending on water temperature and the fry begin feeding within 10 days (Scott and Crossman 1973). Both young and adults form schools, but may disperse temporarily under some conditions (Reeves et al. 1987). The behavior of redside shiners shifts with the time of day. In lakes, they are found primarily in near shore where they feed and move offshore at night (Scott and Crossman 1973). In streams, shiners move into deeper and faster waters containing larger substrates by day and move back to calmer and shallower waters at night (Reeves et al. 1987).

Redside shiners are active and opportunistic feeders which forage in both pelagic and benthic habitats. As fry, they feed on a number of small planktonic and demersal crustaceans as well as diatoms and other small organisms. Larger shiners are mainly insectivorous, but will consume algae, molluscs, eggs and small fish, including their own and other minnows and trout (Scott and Crossman 1973).

Redside shiners are not considered to be major predators of trout and salmon juveniles, although predation on chinook fry is possible among the larger shiners. The extent of this predation however, has not been studied. Shiners are more commonly viewed as fierce competitors of trout and salmon fry. Both share common microhabitat preferences and prey on the same organisms (Johannes and Larkin 1961; Reeves et al. 1987; Scott and Crossman 1973).

Redside shiners are one of the most abundant fishes in the Nechako River (Envirocon Ltd. 1984). Thus competitive interactions with chinook salmon may be a significant factor. Water temperature in the Nechako system generally ranges between 15 and 20 °C during the summer. Given the results of Reeves et al (1987) and Hillman (Idaho State University, pers. comm.), the potential for redside shiners to out compete chinook and rainbow trout for food is quite high and therefore should be of concern. Clearly further research is required to investigate the nature and impact of this competitive interaction.

Longnose dace

Longnose dace spawn during late spring and summer in riffle areas over gravel substrate. The eggs hatch within 1-2 weeks, but may be longer depending on temperature. The young emerge from the gravel in about a week and commence their existence as pelagic feeders in calm, inshore waters. This pelagic stage lasts for about four months after which they switch to a benthic existence. Longnose dace are generally found in clear, fast flowing gravel or bouldery streams, but may also take up residence along the shores of lakes (Scott and Crossman 1973). In the Nechako River, they are found throughout the system, including many of the tributaries (Envirocon Ltd. 1984).

During their pelagic existence, longnose dace feed largely on small planktonic organisms and other demersal crustaceans. Adults, on the other hand, feed primarily on benthos and this is reflected in their subterminal mouths. The type of prey consumed depends largely on availability and abundance, but is generally comprised of insect larvae (Scott and Crossman 1973). Longnose dace are not known to be piscivorous.

Because of the strong vertical segregation, competition between longnose dace and chinook fry is minimal during summer. Chinook fry are generally found in the water column (Nechako River Project 1987) while dace maintain a close association with bottom. During their pelagic stage, longnose dace and chinook may compete for food. However it is likely to be minimal since salmonid fry move offshore into swifter waters soon after emergence. Differences in emergence times (early spring versus summer) may also minimize the potential for interaction with juvenile chinook. There may be some competition for space during winter. Both species seek shelter among the larger rubble substrates at this time of the year (Emmet 1989; Emmet and Convey 1990; Scott and Crossman 1973). However, there has been no documentation of this type of competition in the literature.

Leopard dace

Leopard dace, like the longnose dace, are found throughout the Nechako River system, but are considerably more abundant (Envirocon Ltd. 1984). Little is known about the ecology of leopard dace, except that they prefer slower waters than longnose dace and occupy benthic stream positions (Scott and Crossman 1973). Their diet consists mainly of aquatic insect larvae. Young of the year apparently feed exclusively on dipterous larvae, but increase the breadth of their diet to include other insect larvae and terrestrial insects as they grow larger. The data of Envirocon Ltd. (1984) suggest that they are active inshore only at night. During the day, they either move offshore or hide among the substrate. Their preference for slow waters in riverine habitats would suggest the latter.

Their small size and insectivorous diet preclude leopard dace as potential predators of chinook fry. There may be some competition for food, however, given the preference for slow waters and their close association with bottom, it is not likely to be significant. As with the longnose dace, there may be some competition with chinook for space during the winter.

Peamouth

Peamouth appear to spawn during late spring and early summer. Newly hatched young form schools near shore but move into deeper water later in the summer. These fish are commonly associated with the weedy shallows of lakes and rivers where they tend to school in large numbers. They feed on a variety of aquatic and terrestrial insects, including their larvae. They also consume a variety of planktonic crustaceans, molluscs and, on occasion, small fish (Scott and Crossman 1973).

The extent with which peamouth interact with juvenile salmonids is not known, nor have any cases been documented. Based on their preference for invertebrate organisms, peamouth are unlikely to prey significantly on juvenile salmonids. There is a possibility however, that they may compete with juvenile salmonids for food. Their preference for shallow waters also indicate that there may be some competition for space. No documented cases of competition between peamouth and chinook were found. No peamouth were caught in the fisheries surveys carried out by Envirocon Ltd (1984). However, some were caught during the surveys of Russell et al. (1983). Thus, it would appear that few peamouth reside in the system. Consequently, competitive interactions with chinook are probably of little consequence.

Brassy minnow

The brassy minnow is only sparsely distributed in northwestern Canada. Little is known of their spawning habits except that they appear to spawn late in spring. They are found mainly in slow cool streams, boggy lakes, shallow bays and in overflow ponds (McPhail and Lindsey 1970). In the Nechako River, no brassy minnows were caught in the baseline fisheries surveys of Envirocon Ltd (1984), although the presence was noted. This suggests that there are very few of them in the system.

Based on their long looped intestine and black peritoneum, McPhail and Lindsey (1970) suggested that brassy minnows are primarily vegetarian. As a result, they pose no predatory threat, nor are they serious competitors with chinook salmon for food. Competition for space is possible, however there have been no documented cases of this.

COTTIDAE

There is reportedly only one species of the family cottidae in the Nechako River - the prickly sculpin. They usually spawn in the spring, forming nests under large boulders or flat rocks. The eggs hatch in 2-3 weeks depending on temperature. Newly emerged fry are initially pelagic for the first month, following which they metamorphose and begin their existence as bottom dwellers, hiding among the interstices of larger substrate and sometimes partially bury themselves (Patten 1971). Prickly sculpins tend to occupy areas of low velocity and the margins of pools. They are most active at night.

Planktonic crustaceans form a major component of the diets of young free-swimming sculpins. Following their metamorphosis, aquatic insect larvae and other bottom invertebrates are the main food organisms. In sculpins greater than 70 mm, fish become a more important source of food.

Sculpins are noted predators of juvenile salmonids (Foerster 1968; Fresh and Schroder 1987; Glova and Mason 1977; Hunter 1959; Mace 1983; Moyle 1977; Patten 1971; Rensel et al. 1984; Woodsworth 1982). In comparing several freshwater cottid species (coastrange, prickly, reticulate and torrent sculpins), Patten (1971) found that the prickly sculpin was the greatest consumer of salmonid fry, primarily because of their larger size. The highest reported average predation rate was 14% of the total number of emerging pink and chum fry over a 10 year period (Hunter 1959). As pointed out by Woodsworth (1982), this estimate may be high since "the fry and sculpins were caught together and concentrated in traps and seines, where a good portion of the predation could have occurred". In an extensive study carried out by Patten (1971) with hatchery released chinook fry, a predation rate ranging from 1 to 4% of the total number of fish released was observed. Following the release of large numbers of chum fry into Big Beef Creek, Washington, analysis of the stomach contents of prickly and coastrange sculpins showed that they were negligible predators of chum fry (Fresh and Schroder 1987). Predation levels may even be less under more natural conditions. In a review of sculpin predation on salmonid fry, Moyle (1977) notes that, of the 7,785 sculpin stomachs that were examined in 15 different studies carried out in unstocked streams, only 35 contained salmonid remains.

Predation by sculpins on salmonid fry appears to be restricted to those periods of time when they are highly concentrated (e.g. during outward migration). Woodsworth (1982) reported that prickly sculpins consume sockeye salmon fry in proportion to their relative abundance and that this followed a Type II response curve. A numerical responses are also possible. Hunter (1959) found that the up- and downstream movements of sculpins correlated with shifts in prey density.

Predation by prickly sculpins on chinook fry appears to be size related (Patten 1971, 1977). Only the larger individuals (>65mm) appeared to consume salmon fry, consistent with the observations of Scott and Crossman (1973). Patten (1971) noted that this size relationship can be expressed as a function of the mouth gape of these fish - the larger fish having mouths large enough to consume the fry. Mouth gape may also place a limit on the size of chinook consumed. Patten (1971, 1977) found that the average size of chinook found in the stomachs of sculpins was much smaller than the average size of chinook fry released. Thus the extent of sculpin predation on juvenile chinook may decrease over time as they grow in size.

The extent of sculpin competition with juvenile salmonids for space and food in riverine habitats is relatively unknown. With respect to space, competition is likely to be minimal during summer as sculpins occupy benthic positions and chinook salmon mid-water positions. There may be some overlap in the prey types consumed however, since juvenile salmon are known to feed on benthic organisms. Ringstad (1974) noted that sculpins at high densities may crop benthos sufficiently so as to severely reduce drift densities and in turn, limit the growth of juvenile coho salmon. A similar interaction may occur with chinook. During winter, competition for space is possible between chinook and prickly sculpins. Chinook fry tend to seek shelter among the interstices of large substrate during this season (Emmet 1989; Emmet and Convey 1990), which is also the preferred habitat of sculpins (Patten 1971; Ringstad 1974). This close association between chinook and sculpins may intensify predatory interactions.

Prickly sculpins were caught only in relatively low numbers in the Nechako River (Envirocon Ltd. 1984). Actual numbers however, may be substantially higher since sculpins are difficult to capture and enumerate by beach seine or electroshocker. In addition, because of their hiding behavior, they are difficult to observe visually while snorkeling. As pointed out by Moyle (1977) and Patten (1971), the size of the sculpin population is one of the more important determinants of salmonid predation. Clearly, reliable population estimates of Nechako River sculpins are required to determine the extent with which they contribute to the mortality of chinook salmon juveniles during their freshwater residence.

GADIDAE

Burbot are mid-winter spawners. Their eggs hatch in about 30 days depending on ambient temperatures. They are found mainly in lakes but occupy larger river systems.

In riverine habitats, they generally remain in the deeper mid channels, larger pools and back eddies (Breeser et al. 1988).

Burbot are considered to be voracious predators, feeding principally off the bottom and at night. The younger individuals (less than 500 mm) feed mainly on insects and other invertebrates. The adults (greater than 500mm) however feed almost exclusively on fishes (Scott and Crossman 1973). In the Tanana River, Alaska, the diet of adult burbot includes pike, chubs, sculpins, lamprey, grayling and whitefish. Burbot will feed on young salmon as well, but apparently they are not consumed in large numbers (W. Dardar, University of Alaska, personal comm., McCart 1967; Scott and Crossman 1973; Withler 1948). This is apparently due to the strong vertical segregation between the two species. In riverine habitats, young salmonids are generally associated with river margins, shallow pools and riffle habitat. Burbot, on the other hand, forage mainly near bottom in deep waters.

Very few burbot have been caught in the Nechako River. This however may simply reflect the limitations of the sampling techniques used (mainly beach seine and snorkeling) (Envirocon Ltd. 1984, Nechako River Project 1987). Because burbot are generally associated with the deep waters of the mid channel and are close to the bottom, they are inaccessible by beach seine and difficult to spot visually. Thus the actual numbers in the Nechako River may be higher than what the catch data suggest. The fact that no burbot were caught near the river's margin or in shallow pools suggest that they, whether young or old, rarely venture into these areas. For this reason burbot are probably negligible predators of chinook salmon. In addition, the differences in habitat and food preferences are likely to be sufficient to ensure that they do not interact competitively either.

ACIPENSERIDAE

Moderate numbers of non-anadromous white sturgeon have been reported in the Nechako River. They are limited in distribution to reaches below the Nautley River and are found principally in deep back eddies. There is some evidence which suggests that they may move into the shallower areas of the main channel at night to feed (Envirocon Ltd. 1984). They vary in length from 70 to 114 cm in length and range 5 to 20 years of age. Little is known of the early life history or of their spawning habits in the Nechako River. Sturgeon may undergo extensive migrations in addition to those commonly associated with spawning. The functional significance of these movements however remain unclear (Envirocon Ltd. 1984).

White sturgeon are mainly bottom feeders. This is reflected by their subterminal, protrusible, sucker mouth. The food of smaller sturgeon consists of a variety of bottom dwelling invertebrates. As sturgeon grow in size, fish become an increasingly more important component of their diet. It is generally assumed that these are sucked off the bottom and are either dead (e.g. carcasses left from spawning) or bottom dwelling (Scott and Crossman 1973). In a laboratory test tank, Brannon et al. (1987) found that white sturgeon could capture chinook, coho, pink and chum salmon fry with ease provided that the ability of the fry to detect its approach was hampered (i.e. high turbidity and darkness). The extent of sturgeon predation on salmon fry has not been documented. It is conceivable that white sturgeon predation of chinook fry may be more intense during winter. The fry become closely associated with the bottom during this time of the year.

Because of the apparent absence of sturgeon less than 5 years of age in the Nechako River, the obvious close association with bottom, and the preference for deep slow waters, sturgeons are unlikely to compete significantly with chinook fry for food or space.

PETROMYZONTIDAE

Little is known of the biology of Pacific lampreys in the Nechako River. Few have been caught (Russell et al. 1983). In general, the Pacific lamprey migrates from the sea to spawn during late summer after which they die. The eggs hatch within a 2 to 3 week period and the young ammocoetes remain in fresh water burrowed in the mud for periods of up to 5 or 6 years. During this phase of their life cycle, they feed primarily on drift organisms. Following transformation, they move out of their burrows and head seaward for a period of 1 to 2 years, after which they migrate back to their natal streams. During this later part of their life cycle, they are parasitic, consuming the body juices of large fish, including salmonids (Scott and Crossman 1973). Because of their unique biology, the pacific lamprey pose neither a competitive or a predatory threat to Nechako River juvenile chinook fry.

BIRD PREDATION

Bird predation on juvenile salmonids and other fish species has not been studied as intensely as fish predation. (Mace 1983). Nevertheless, it is evident that avian predators are subject to the same principles which govern fish predation (Elson 1962; Mace 1983; Wood 1987a,b; Wood and Hand 1985). Prey-switching, functional responses and numerical responses are all expressed by piscivorous birds. In addition, their impact on juvenile salmonid populations follows the same mortality patterns described earlier for fish predators (see p.14).

Studies which examine the extent that birds prey on juvenile salmonids are few. Mortality estimates range from immeasurable levels to 39% (Elson 1962; Mace 1983; Wood 1987a,b) and appear to vary depending on the system. For example, Mace (1983) found that piscivorous birds were able to consume up to 32% of the chinook released by a nearby hatchery on the Big Qualicum River, B.C. However, when a similar study was carried out on hatchery releases to the Capilano River, bird predation was found to be insignificant. Reasons for these systemic differences are unknown but species composition of the avian community and the relative numbers and type of prey that are available seem to play a role (Elson 1962; Mace 1983; Wood 1987a,b). Few of the birds reported to prey on fish appear to do so exclusively. Rather, they express varying degrees of piscivory, with molluscs, crustaceans and insects forming the remainder of the diet.

The potential for fish to aggregate appears to play a major role governing the extent of predation and in turn, mortality rate (C. Wood, Pers. comm.). Birds that are non-territorial and migratory such as Bonaparte's gulls and common mergansers can congregate into large numbers and consequently feed heavily on juvenile salmonids when abundant (i.e. they express a numerical response) (Elson 1962; Mace 1983; Wood 1987a,b). In contrast, territorial birds like the kingfisher appear to have less impact on salmonid survival (Elson 1962; C. Wood, pers. comm.). Territorial birds patrol and actively defend a single section of stream, therefore preventing a numerical response. Because a single pair of foraging birds can be quickly swamped with prey, their impact on emerging, rearing and migrating salmonids is minimal. However, Elson (1962) noted when the number of breeding pairs/km of stream is high, there can be a significant impact.

The extent that a given species preys on fish may shift with age. In a series of three coastal streams in the Big Qualicum River region of B.C., Wood (1987a,b) noted that the estimated mortality rate of juvenile chinook salmon due to common merganser predation did not exceed 8% for adults but was up to 39% for ducklings. Elson (1962) noted similar age differences in predation intensity for a population of common mergansers in New Brunswick. Whether other species express similar shifts is unknown.

BIRDS OF THE NECHAKO RIVER AND CHESLATTA SYSTEM

A census of the bird species found in and around the Nechako River and Cheslatta System was carried out by Envirocon Ltd (1984) over a five year period (1978 to 1982). Results of this census are summarized in Table 2. Of the 49 species observed during the survey, nine are considered to be moderately to highly piscivorous. An additional 12 species may consume fish on occasion. The remaining species pose no apparent predatory threat towards juvenile salmonids rearing in the Nechako River.

Based on their relative abundances and their tendency for piscivory, those species which appear to pose the greatest threat to rearing or migrating chinook salmon are the common mergansers and herring gulls. The fact that both species are able to aggregate into relatively large numbers accentuates their predatory threat. Of the two species, mergansers probably pose the greatest threat since they have been found to breed in the region (Envirocon Ltd. 1984). As noted earlier, merganser broods are voracious predators of juvenile salmonids. Herring gulls are only present in the region while passing through during their migration to and from northern breeding sites (Envirocon Ltd. 1984). As pointed out by Mace (1983), when the migration of gulls coincide with the outward migrations of salmonid juveniles, a numerical response is possible which can have a significant impact on the out-migrants. The remaining piscivorous species are too few in number to cause significant depredation (in particular the belted kingfisher, loons, and other gull species). Ospreys, although a largely piscivorous bird, poses little threat to juvenile salmonids as they generally prey on much larger fish.

Although on an individual basis, few species appear to pose a predatory threat to rearing and migrating salmonids, collectively they may have a considerable impact. However, without specific food habit information of the species in the region, their relative consumption rates, and population size, the extent of depredation cannot be determined.

Table 2
Bird species of the Nechako River and Cheslatta system.

Common name	Status/ Abundance	Piscivory[3]
Common loon	SR(R)	H
Red-throated loon	T(R)	H
Red necked Grebe	T(U)	H
Canada goose	SR(FC);T(A)	L
Mallard	SR(FC);T(A)	L
Pintail	T(FC)	L
Green-winged teal	T(FC)	L
Blue-winged teal	T(FC)	L
American wigeon	T(C)	L
Ring-necked duck	T(U)	L
Scaup sp.	SR(R)	L
Goldeneye sp.	SR(FC)	L
Bufflehead	T(U)	L
Scoter sp.	T(U)	L[1]
Common merganser	SR(C)	H
Hooded merganser	T(U)	H
Red-tailed hawk	SR(U)	N
Marsh hawk	SR(R);T(R)	N
Bald eagle	SR(C)	N
Osprey	SR(U)	L[2]
Falcon sp.	T(R)	N
Merlin	T(R)	N
American kestrel	SR(U)	N
Ruffed grouse	PR(U)	N
Spruce grouse	PR(FC)	N
Sandhill crane	T(U)	N
American coot	T(C)	N
Killdeer	T(FC)	N
Common snipe	T(U)	N
Spotted sandpiper	SR(U)	N
Greater yellowlegs	T(U)	N
Lesser yellowlegs	T(U)	N
Mew gull	T(U)	H
Herring gull	T(FC)	H
Black tern	SR(R)	H
Common nighthawk	SR(R)	N
Belted kingfisher	SR(U)	H
Pileated woodpecker	PR(R)	N
Bank swallow	SR(U)	N
Gray jay	PR(U)	N
Black-billed magpie	T(R)	N
American crow	SR(C)	N
Common raven	PR(FC)	N
Black-capped chickadee	PR(U)	N

Table 2 (Continued)
Bird species of the Nechako River and Cheslatta system.

Common name	Status/ Abundance	Piscivory[3]
Water pipit	T(FC)	N
Cedar waxwing	SR(U)	N
Yellow-rumped warbler	T(U)	N
Rusty blackbird	T(U)	N
Dark-eyed junco	T(U)	N

Status is indicated by the first set of letters and abundance estimates are indicated with brackets. The status coding is as follows: PR = permanent resident; SR = summer resident; T = transient (i.e. passe through area during migration). The abundance coding is as follows: A = abundant (> 100 birds/date); C = common (>5-10 birds/date); FC = fairly common (<5-10 birds/date); U = Uncommon (>2 birds/date); R = rare (1 bird/date). Where seasonal shifts in abundance occur, two listings are given. (After Envirocon Ltd., 1984). The degree of piscivory is was determined from the data reported by Elson (1962), Godfrey (1966), Mace (1983), Rensel et al. 1985, and Wood (1987a,b).

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[1] Although not considered piscivorous, it is capable of consuming large numbers of migrating fry when available in large numbers (Mace 1983).

[2] Only preys on larger individuals

[3] H = moderate to high incidence; L = low incidence; N = not piscivorous.

EFFECTS OF REDUCED STREAM FLOWS

No studies were uncovered during the literature search which examined directly the effects of reduced flows on bird predation. However, based on the discussion above on bird and fish predation, some effects can be hypothesized. Following a sudden drop in flows, overcrowding conditions can occur. As with piscine predators, floe reduction has the potential to elicit prey switching responses in birds. In the Big Qualicum River, Mace (1983) noted that scoters, which are not generally considered to be piscivorous, switched to a diet largely composed of hatchery reared chinook salmon following an unusually large release from a point upstream of the study area. Dense concentrations of fish are also known to promote a numerical response among some fish eating birds, particularly mergansers and gulls (Mace 1983; Wood 1987a,b). Reductions in stream flow are generally accompanied by a reduction in the system's wetted width. Consequently, the water's edge moves away from the overhanging vegetation which provides a valuable source of cover for young salmonids. With less overhanging vegetation, greater numbers of fish can potentially fall prey to birds. Without specific studies, the extent with which these or other flow related factors influence bird predation can not be determined.

SUMMARY AND CONCLUSIONS

a) Competitive interactions have been shown to reduce the survival and productivity of juvenile salmonids and appears to depend largely on the extent of niche overlap between the competing species. Mortality due to competition is primarily a function of predation, although mortality can occur directly (e.g. starvation). Stress, malnutrition and injury arising from competitive interactions can increase the susceptibility of juvenile chinook and other stream dwelling salmonids to predation.

b) Predation can potentially reduce the survival and productivity of juvenile salmonids in riverine systems. Much of this predation occurs during out-migration. Squawfish, cottids and other salmonids pose the greatest predatory threat to juvenile salmonids. Avian predators can also have a significant impact. The extent of this predation depends largely on the number of predators and prey in the system.

c) Reductions in stream flow can alter predator-prey and competitive interactions by:

   1) concentrating species in a smaller area.

   2) changing the competitive, predatory or predator avoidance abilities of fish through shifts in temperature away from their optimum.

   3) changing the patterns of spatial and temporal segregation through shifts in temperature and stream velocity.

   4) changing the social behavior/structure of salmonids through shifts in stream velocity.

d) There are a total of 20 fish species that reside in the Nechako River system. Of these, 6 were identified as potential predators of juvenile chinook salmon and an other 6 species as potential competitors (Table 3). Competition for space during the winter may also occur between chinook salmon and bottom dwelling species. Chinook salmon apparently hide among the interstices of large substrate during winter (Bjornn 1971; Emmet 1989; Emmet and Convey 1990).

It is apparent from this review that the effects of reduced stream flows on the behavioral interactions between and among juvenile chinook salmon and other Nechako River fishes are likely to be varied and complex. The diversity of the Nechako River fish community and the fact that little is known of the population characteristics and distribution of each species under pre and post flow conditions makes it difficult to assess how these interactions will change. As the study of Schlosser (1985) clearly demonstrates, dramatic changes in species composition can occur following stream flow reductions. In addition, the population size of some or all species in the community are also subject to change. At this stage, attempts to predict the out come of flow reductions on the species interactions of the Nechako River fish community would be highly speculative and of little practical value. Clearly, further research is required.

Table 3
Potential interactions between chinook salmon and other Nechako River fishes.

Species	Predation	Competition
Chinook salmon	L	H
Sockeye salmon	L	L
Coho salmon	H	H
Rainbow trout	H	H
Dolly Varden	H	L
Rocky Mountain whitefish	L	H
Largescale sucker	L	L
Longnose sucker	L	L
White sucker	L	L
Bridgelip sucker	L	L
Redside shiner	L	H
Longnose dace	L	W
Leopard dace	L	W
Northern squawfish	H	H
Peamouth chub	L	H
Brassy minnow	L	L
Prickly sculpin	H	W
Burbot (ling)	H	U
White sturgeon	H	L
Pacific Lamprey	L	L

L = Low; H = High; W = Winter only

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