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An Account of a Workshop on Research Approaches to Predation/Competition Questions in River Fish Communities

C. D. Levings and G. A. Hunter

Biological Sciences Branch
Department of Fisheries and Oceans
West Vancouver Laboratory
4160 Marine Drive
West Vancouver, British Columbia V7V 1N6

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AN ACCOUNT OF A WORKSHOP ON RESEARCH APPROACHES TO PREDATION/COMPETITION QUESTIONS IN RIVER FISH COMMUNITIES

by

C. D. Levings and G. A. Hunter[1]

Biological Sciences Branch

Department of Fisheries and Oceans

West Vancouver Laboratory

4160 Marine Drive

West Vancouver, British Columbia V7V 1N6

[1] Pegasus Consulting Group
2874 Fromme Road
North Vancouver, B.C. V7K 2C5

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TABLE OF CONTENTS

ABSTRACT

Levings, C. D. and G. A. Hunter. 1992. An account of the workshop on research approaches to predation/competition questions in river fish communities. Can. Manuscr. Rep. Fish. Aquat. Sci. 2150: 66 p.

A workshop was convened to explore alternatives to research on predator-prey relationships in river fish communities. To examine the various possible methods, investigators from the Pacific Northwest presented case studies on approaches they had used to examine predation and competition. These studies were discussed in the context of the critical study components: estimation of predation/competition rates, the influence of behaviour and habitat on rate, the impact of predation/competition on fish production and modelling and statistical methods. Participants rated a number of techniques and experimental designs for research projects dealing with predation and competition. An annotated bibliography of papers dealing with predation on and competition with juvenile salmonids in rivers is included.

RÉSUMÉ

Levings, C. D. and G. A. Hunter. 1992. An account of the workshop on research approaches to predation/competition questions in river fish communities. Can. Manuscr. Rep. Fish. Aquat. Sci. 2150: 66 p.

Un atelier a été organisé au sujet des diverses voies qui s'offrent à la recherche sur les relations de prédation dans les communautés de poissons des cours d'eau. Pour examiner les diverses méthodes possibles, des chercheurs de la région nord-ouest du Pacifique ont présenté des études de cas sur des approches qu'ils avaient utilisées pour examiner la prédation et la compétition. Ces études ont été analysées en fonction des éléments critiques: estimation des taux de prédation et de compétition, influence du comportement et de l'habitat sur ces taux, effet de la prédation et de la compétition sur la production de poissons, et enfin modélisation et méthodes statistiques. Les participants ont coté un certain nombre de techniques et de méthodes expérimentales pour les projets de recherche concernant la prédation et la compétition. Une bibliographie annotée sur les publications traitant de prédation et de compétition dans le domaine des salmonidés juvéniles est jointe à l'article.

INTRODUCTION

This workshop was convened on February 28 and March 1, 1991 to provide participants with an opportunity to explore alternative approaches to research on predator-prey relationships in river fish communities. This area of research is of considerable academic and immediate practical interest. At issue are the nature and magnitude of changes in river fish communities due to predation and competition.

Evidence for predation as a force structuring fish and invertebrate communities in major rivers is growing steadily (Power 1990) but detailed knowledge in rivers lags well behind that from lakes and coastal waters. However, major rivers such as the Columbia, Fraser and Yukon are now known as more than migratory corridors for salmon. Juvenile chinook salmon, (Oncorhynchus tshawytscha) for example, are found in the mainstem Fraser almost all year round (Levings and Lauzier 1991). The young salmon are therefore interacting with predators such as squawfish (Ptychocheilus oregonensis) and competing with smaller cyprinids (e.g., redside shiner, Richardsonius balteatus) for major portions of their life history.

To make defensible decisions concerning habitat management(stream flow, pollution, logging effects) better information is required about how predation can change when habitat is altered. Interaction between habitat and predation/competition must be considered when hypotheses on these topics are being tested in rivers. Unlike the pelagic zone of lakes and coastal waters rivers are rich in structure. Features such as varying substrate sizes, velocity differences between riffles and pools and temperature differences between off-channel habitats and the mainstream and the amount and type of woody debris may provide refuges from predation. The complexities of river ecosystems require that the investigator factor these features into experimental designs and this requires considerable ingenuity.

Abstracts of presentations by workshop participants experienced in predator-prey and competition investigations are given below, to help guide future work. Changes in fish habitat and river discharge from flow manipulations and climate variation are currently a major concern for salmon habitat management in British Columbia. An annotated bibliography compiled (Bruce 1991) for a review of papers dealing with predation/ competition in rivers with flow changes was complied in a related project. The annotated bibliography is presented below as a introduction to the literature on this complex topic.

ACKNOWLEDGMENTS

Thanks are due to staff at the Cultus Lake Laboratory for providing facilities to host the Workshop. We would like to thank all participants for lively discussions on a complex topic. A major snow storm hampered travel on March 1, and special dedication was required by all participants to attend. We are grateful for the time and effort expended.

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ABSTRACTS OF PRESENTED PAPERS

Determining predation mortality rates of juvenile salmon in Alberni Inlet and Barkley Sound, B.C.

N. Brent Hargreaves
Department of Fisheries and Oceans, Pacific Biological Station
Hammond Bay Road, Nanaimo B.C.

Predation is commonly thought to be a major cause of mortality for juvenile salmon during both the fresh and salt water stages of the life history. The three main approaches used to estimate predation rates are 1) directly measuring changes in prey population size, 2) observing feeding activity of predators, and 3) using predator abundance and stomach contents data to estimate predation rates. Each of these approaches have advantages and disadvantages, and some combination of these approaches is often required.

In some situations it is practical to determine mortality rates of juvenile salmon by directly measuring changes in population size during some time interval. This method is most common in laboratory experiments, but has also been successful in field situations where the salmon prey population is small and localized (eg, a kokanee population isolated in a small stream, pond, or lake). This "full count" method is also suitable if the number of juvenile salmon can be accurately counted at both the start and end of some space or time interval. Examples include determining predation rates of smolts during their migration through a section of river or steam, or mortality during the period between when sockeye migrate into a lake in the spring and out again as smolts the following year. Mark-recapture methods can also be used if either the salmon population, or the body of water, is too large to capture and count the entire salmon population. One of the main advantages of the full count and mark-recapture methods is that direct estimates of the mortality of juvenile salmon can be obtained without requiring any information or assumptions about the predators. This is an important advantage in cases where the predators are relatively rare, highly mobile, difficult to capture, or have not been identified. The major disadvantages of the direct count and mark-recapture methods are that: 1) the source of mortality is not confirmed, and 2) the size of the prey population must remain unchanged during the measurement period, except for the losses due to predation. Otherwise any changes in the prey population that result from immigration, emigration, or other sources of mortality must also be accurately measured. With juvenile salmon these additional data are often difficult or impossible to obtain. Another limitation is that juvenile salmon populations are often large and widely dispersed. This makes it difficult and prohibitively expensive to mark and recapture a large enough proportion of the prey population to provide reliable estimates of predation rates.

Estimating predation rates by directly observing feeding activity of predators requires that the feeding behaviour be readily observable, that the prey being eaten can be identified, and that the population size of the predators can be reliably enumerated. This method has been widely used to estimate predation rates in laboratory experiments, but also has been effective in the field for birds or mammals feeding on juvenile salmon. This method typically is not suitable in field situations where the major predators of salmon are other fish species, due to the difficulty in adequately monitoring the feeding behaviour.

Predation rates can also be estimated by determining the abundance of potential predators, and examining their stomach contents to determine the incidence of predation. This method is most effective in cases where the predator population is relatively stable, or any changes can be monitored. The gastric evacuation rates of the predator may also have to be determined, if this data is not already available in the literature. A major advantage of this method is that predation mortalities can be estimated without requiring any information or assumptions about the prey population. This is most important in situations where the salmon population is changing rapidly, such as during the smolt migration period.

Barkley Sound Predation Study

During the past four years I have attempted to determine the marine survival of juvenile salmon during the early sea-life period in Alberni Inlet and Barkley Sound. The field work has included two main activities: 1) purse seine sampling to determine the abundance and distribution of juvenile salmon, and 2) estimation of the mortality of juvenile salmon due to predation.

The purse seine sampling of juvenile salmon typically commenced in early April and ended in mid-July each year. The sampling schedule has varied, but typically one set of purse seine data was collected every two to three weeks from 24 fixed locations throughout the study area. All of the purse seine samples were collected during daylight between 0600 and 2100 hours, and the juvenile salmon were immediately identified, counted, and fork lengths measured at sea.

The results from the purse seine sampling indicate that juvenile sockeye were the most abundant species of salmon every year, followed by chum, chinook, and coho salmon. The peak abundances of sockeye, chum, and coho all typically occurred between the last week of May and middle of June. The peak abundance of juvenile chinook salmon occurred about one month later. Chinook appear to utilize Barkley Sound differently, and to a much greater extent as a rearing area, than sockeye, chum, and coho salmon.

My main approach to determining predation mortality of juvenile salmon has been to sample potential predators, and determine the incidence of predation on juvenile salmon by examination of their stomach contents. A variable mesh-size floating gillnet was used to sample predators in all four years, and a balloon trawl was also used in 1989 and 1990. The gillnet was fished at night, at fixed locations, from April - July, and typically 25 to 30 gillnet sets were made every three weeks. The balloon trawl was fished simultaneously throughout the study area, and was used to sample predators between 10 and 50 meters, below the depth fished by the gillnet. In 1989 hydroacoustic surveys were also made to obtain additional data on the abundance and distribution of predators. The predator abundance data from the gillnet, balloon trawl, and hydroacoustic surveys were used, in conjunction with the stomach contents data, to estimate the total mortality of each species of salmon due to predation.

The results of the predation work indicate that Pacific hake, walleye pollock, and spiny dogfish are the most important predators of juvenile salmon in Alberni Inlet and Barkley Sound. The incidence of predation on salmon varied considerably by time and area. For example, in 1989 the percentage of hake in Alberni Inlet with salmon in their stomachs ranged from a low of 0% to a high of 75 percent for gillnet caught hake. Preliminary mortality estimates indicate that about 12 million juvenile sockeye (more than 50 percent of total production) and 7 million juvenile chinook salmon (75 percent of the total production from Robertson Creek Hatchery) may have been consumed by predators during the early sea-life period in Alberni Inlet and Barkley Sound in 1989. The predation rates appear to have been similar in 1987 and 1988, but much lower in 1990.

Problems in Estimating Rates of Predation and their Impact on Juvenile Salmon Production

M. Healey
Westwater Research Centre, University of British Columbia
1933 West Mall Annex, Vancouver B.C.

Rather than a case study, this will be a series of anecdotes about predation from my 20 years of conducting research on salmonids. I selected the anecdotes to illustrate what I consider to be some significant difficulties in quantifying losses of salmon fry to predation in natural communities (Table 1.).

Ecological theory recognizes predation as a dominant force shaping community structure and individual population dynamics. In the case of specific populations, however, it is sometimes difficult to be sure who the real predators are. While trapping for chum fry in the Nanaimo River on Vancouver Island, for example, we would frequently catch coastrange sculpins in the fry traps. Sculpins taken from the traps would almost always have chum fry in their stomachs. Yet, sculpins seined from the river never contained fry. Neither did juvenile steelhead, cutthroat, or dolly varden caught in the river at the peak of the fry run, nor staghorn sculpins, juvenile coho and chinook captured in association with dense concentrations of chum fry in the estuary. Samples of most potential predators were small, so that low incidence of predation would have gone undetected. Yet this experience does demonstrate that close association of known piscivores and salmon fry does not guarantee that predation will occur. Nor are the "obvious" candidates necessarily the most important predators. The number of potential predators in north temperate riverine ecosystems is relatively small, but still numbers several tens of species. Deciding what contribution each of these makes of predation mortality and under what circumstances is a formidable task.

Once the predators have been identified quantifying the amount of prey each consumes poses further technical difficulties. If the predators are abundant relative to prey (often the case in marine ecosystems), thousands may have to be examined to determine the rate of predation with any precision. If the predator is also a valued species, destructive forms of sampling may be unacceptable. In many circumstances, non-destructive sampling may be impossible. For example, while studying the dynamics of lake whitefish in northern lakes, I attempted to determine rates of consumption of whitefish by trout, pike, and burbot. The combined population of piscivores in these lakes was about equal to the population of lake whitefish. Whitefish occurred in about 1% of the predator stomachs examined, but the confidence interval was wide. Although the incidence of predation was "appropriate" to account for all whitefish mortality, it could also account for less than half or more than twice the estimated rate.

Table 1. Problems with estimating rate and impact of predation.

1. Who are the predators?
   - many species to choose from
   - obvious choices may be wrong
   - predation may be in artificial context
   - abundant predators and rare prey
   - predation may be localized in time and space

2. What is the predation rate per predator?
   - accuracy and precision are difficult at low predation rates
   - sampling of rare or valuable predators may not be possible
   - biased predator behaviour(some do, some don't)
   - parameterization of feeding rate models

3. What is overall predation rate?
   - problems of population estimation
   - scaling up from observations that are restricted in space and time (interpolation, extrapolation, prediction)

4. What are the alternatives?
   - analysis of conditions that encourage or discourage predation
   - non-destructive manipulations

To get these confidence limits down to something like +/- 15% would have required that I sample most of the predators. Gillnetting was the only effective capture technique in these lakes, so that non-destructive sampling was not an option. I had the authority to kill as many fish as I wanted, but I am not sure what I would have learned from such an investigation.

The estimation of predation rate, of course, involves more than just measuring consumption rates per predator. To estimate predation rate in a single instance and relate it to mortality rate of the prey, the abundance of predators and the mortality rate of the prey must also be measured. To assess predation rates over time many other measures are also required, including numerical or functional response by the predators to changing abundance of prey, prey switching by the predator, and learning by the prey. My own attempts to estimate consumption rates by juvenile salmon preying on zooplankton have been dissatisfying in the sense that different models of consumption gave widely different results. In work that I did on the Nanaimo estuary some years ago, I was able to show that chum fry were either starving to death or obtaining maximum rations depending on the consumption model that I applied to my data. Similar imprecision must plague estimates of consumption by predators of salmon.

These and similar experiences have led me to doubt the practicality of attempting to quantify the contribution of predation to total mortality. They have also led me to question the importance of such quantification. I now feel that it is more important to understand the conditions that promote or discourage predation than it is to quantify precisely the rate.

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Habitat heterogeneity, prey exploitation and competitive interactions in pelagic, littoral and benthic fish communities

Kim D. Hyatt
Department of Fisheries and Oceans, Pacific Biological Station
Hammond Bay Road, Nanaimo B.C.

Pelagic communities (PC's) and littoral and benthic communities (LBC's) of fishes are generally well represented within the continuum that defines riverine ecosystems. Consideration of some fundamental principles as well as results from a variety of empirical studies suggest that physical and biological heterogeneity are much greater in littoral-benthic than in pelagic fish communities. For example, physical heterogeneity in PC's is defined principally by vertical gradients involving changes in features such as light, temperature, water velocity or in some cases salinity. By contrast, physical heterogeneity in LBC's is commonly defined not only by vertical and horizontal changes in light, temperature and oxygen, but also by factors such as substrate composition (e.g. type, size, texture, degree of compaction etc...) and quantitative plus qualitative aspects of vegetative cover. Differences in habitat heterogeneity in PC's versus LBC's are reflected in the fish communities they support and in the mechanisms which mediate prey exploitation, prey community structure and competition among fishes. Relatively low levels of habitat heterogeneity in pelagic communities reduce the scope for the evolution of diverse antipredator responses by invertebrates. The consequences are that: (i) invertebrate prey are generally exploited more intensely by fish in PC's than in LBC's, (ii) invertebrate community structure is frequently subject to top down control by vertebrate predators, (iii) both inter and intraspecific competitive interactions among fish are most commonly mediated by prey exploitation and (iv) competitive interactions among planktivorous fish are intense and persistent. In LBC's higher levels of habitat heterogeneity have promoted a diversity of morphological and behavioural antipredator adaptations such that: (i) vertebrate predators seldom, if ever, exert the degree of control commonly observed in PC's over invertebrate community structure, (ii) competitive interactions among fish are mediated not only by direct exploitation of prey but also by indirect effects on prey behaviour such that dramatic changes occur in either their short or long term availability to fish and consequently (iii) the intensity of competition among fishes will generally exhibit greater variability in LBC's than in PC's.

Behavioural mechanisms that mediate the effects of predation in fish communities

Mark R. S. Johannes
Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C. and
Natural Resource Management, Simon Fraser University, Burnaby, B.C.

Ecologists have traditionally been concerned with examining patterns of species abundance and composition, predation and competition and with using these observations to predict the mechanisms involved in structuring animals at the population and community level(top-down approach). Behavioural ecologists have been primarily interested in functional components of individual animal behaviour and from this more detailed view have attempted to gain insight into broader processes determining population and community structure(bottom-up approach). Use of either top-down or bottom-up approaches to research has an influence on: the manner in which questions are asked and, what type of experimental approach is adopted to answer these questions. The approach I have taken here has proceeded from population and community levels processes and has led to a more detailed population level examination of factors which determine patterns of behaviour observed in nature. This top-down approach has provided an alternate mechanism to investigate questions of behaviour and their role in population and community level processes.

Aquatic ecosystems represent environments where fish behaviour is primarily characterized by options in behaviour which have fitness consequences, such as feeding and avoiding predators. Numerous studies have shown that the behaviour of fish is responsive to variations in food availability and predation risks.Although behaviour is responsive to many environmental stimuli, few behavioural responses are ultimately as important as predator-avoidance.

I have used a set of field observations and manipulations to look at questions about behavioural mechanisms mediating the effects of predation in fish populations. Fish behaviour was observed in nature in the context of three field studies. The first study provided observations of behaviour in in situ enclosures manipulated to produce both low and high predation pressure. The second study provided observations of behaviour in a system with high predation pressure. The third study provided observations of behaviour in a system with low predation pressure.

Fish observed in these studies showed considerable behavioural flexibility in response to changing predation pressure. Results indicated that differences in body-size had considerable effect on the range of behavioural responses used to avoid predators. Higher levels of predation pressure led to a more limited range of behaviour in smaller sized fish relative to larger sized fish. Consequently, as fish grew in size they showed an improved ability to modify behaviour. At the population level, size related responses in behaviour to changes in predation pressure accounted for changes in natural patterns of survival and led to improved fish abundance.

These results suggest that population structure and abundance is more strongly influenced at higher levels of predation pressure by changes in behaviour and survival of smaller sized fish than by changes in larger sized fish. Factors which alter the vulnerability of smaller sized fish to predators, including altered habitat complexity and growth patterns, have consequences on total population abundance and ultimately fish community structure. Understanding how behaviour can mediate the effects of predation can lead to predictions about factors and mechanisms which control population abundance and success in physically (habitat) and biologically (predator and prey communities) different environments over both ecological and evolutionary time periods.

Effects of predators on salmon production: lessons from Cultus Lake and implications for salmon in rivers

David A. Levy
Levy Research Services Ltd.,
Suite 102-2221 Folkstone Way, West Vancouver, B.C.

The Cultus Lake predator removal experiment conducted by Ricker and Foerster in the 1930's had the following effects on sockeye salmon: 1) an increase in within-lake survival rates, 2) an increase in sockeye production rate, 3) a small (statistically non-significant) increase in sockeye smolt size, and 4) an increase in sockeye marine survival rate. These trends can be explained by a reduction in predator-induced mortality rate, coupled with behavioural shifts by sockeye juveniles in the absence of predators. A shift in sockeye vertical migration behaviour is hypothesized to account for the increase in sockeye production and absence of density-dependent feedbacks on sockeye growth. Currently, the Biological Sciences Branch (DFO) is repeating the Cultus Lake experiment by undertaking selective squawfish (Ptychocheilus oregonensis) removal with the assistance of volunteer seine fishermen from the Fishing Vessel Owners Association.

For those salmonids which rear in rivers as juveniles (e.g. coho, chinook) there may be opportunities to enhance production by undertaking predator removal. This possibility should be evaluated experimentally in future, either via field experiments, or else via manipulations in artificial stream troughs.

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Approaches to estimating predation losses in a large river system: consumption of juvenile salmonids by northern squawfish in the Columbia River

James H. Petersen and Thomas P. Poe
U.S.Fish and Wildlife Service
National Fishery Research Center, Seattle
Columbia River Field Station
Cook, Washington, USA

Studies conducted during 1983-86 showed that 9-19% of the juvenile salmonid run was lost to predation within John Day Reservoir, with northern squawfish (Ptychocheilus oregonensis) accounting for about 78% of this loss (Poe and Rieman 1988). Management of predation has since become a high priority in the lower Columbia and Snake Rivers. Since relatively little is known about predation losses outside John Day Reservoir, the U.S. Fish and Wildlife Service (USFWS) and the Oregon Department of Fish and Wildlife (ODFW) are estimating relative predation intensity in other reservoirs to guide management efforts.

Two indices of northern squawfish consumption upon juvenile salmonids were developed for use throughout the Columbia River Basin. Description and first-year results are described here for a direct Consumption Index (CI). A Bioenergetics Index (BI), which is also being developed, models growth, consumption, excretion/evacuation and respiration processes, and predicts the consumption required to produce an observed growth increment (e.g., Rice and Cochran, 1984: Stewart and Binkowski, 1986). Sensitivity study of the preliminary bioenergetics model has directed research toward refinement of respiration parameters for northern squawfish.

Consumption Index (CI)

The Consumption Index (CI) is based upon the concept of meal turnover time and takes into account the number of salmonids, temperature, total gut content weight and predator weight. The estimated number of salmonids consumed per day by an individual predator, p, can be expressed as:

$$C_p = \sum_{i=1}^{n} 1 / (\text{Evacuation time for prey item i})$$

or,

$$C_p = \sum_{i=1}^{n} 1 / D90_i \qquad (1)$$

where C_p is consumption rate (number of salmonids•individual northern squawfish^{-1} day^{-1}),

$D90_i$ is number of days to 90% digestion for salmonid prey item i, and n is total number of salmonids found in the gut. Using 90% digestion time, rather than 100%, avoids the problem of non-digestible prey parts that may remain in the gut for extended periods.

Beyer et al. (1988) developed an equation for 90% evacuation time (hours) in northern squawfish:

$$D90_i = 1147 \cdot M_i^{0.61} \cdot T^{-1.60} \cdot W_p^{-0.27} \qquad (2).$$

where M_i is meal size (g) at time of ingestion of salmonid prey item i, T is water temperature (°C), and W_p is predator weight (g). Equation 2 was substituted into equation 1, and the meal size term was simplified, to produce a Consumption Index equation:

$$CI = 0.0209 \cdot T^{1.60} \cdot MW^{0.27} \cdot [MTsal \cdot MGutwgt^{-0.61}] \qquad (3).$$

where T is water temperature (°C), MW is mean predator weight (9), MTsal is mean number of salmonids per predator, and MGutwgt is mean gut weight (9) per predator. All variables in CI are averaged over all predators in a sample; CI is the consumption index for a collection (sample) of predators. Variance of a CI was computed by a bootstrap resampling technique (Efron and Tibshirani 1986; Petersen et al. 1990).

CI was well correlated with independent estimates of consumption for the John Day reservoir (r=0.89; P <.001: n=Sl) and the McNary Boat Restricted Zone (r=0.95; P <.001: n=Sl). Calculation of actual consumption (prey • $predator^{-1}$ • day^{-1}), rather than index units, is possible by using the regression equation shown in Figure 1.

1990 Consumption indexing results

During the spring and summer of 1990, the consumption rates of northern squawfish preying upon juvenile salmonids were indexed in four reservoirs of the lower Columbia River (Bonneville, The Dalles, John Day and MCNary Reservoirs). Boat electroshocking was used to collect predators. Data were stratified into those areas close to dams (BRZ's, Boat Restricted Zones) versus reservoir-wide samples (outside the BRZ's).

The overall diet of squawfish was dominated by fish and crustaceans (45% and 37%, respectively: N=1,598). Fish were the most important prey item for northern squawfish from the BRZ areas. In contrast, crustaceans were the dominant prey item of northern squawfish in reservoir-wide areas, except in the John Day reservoir. Crayfish made up the greatest portion of crustacean weight.

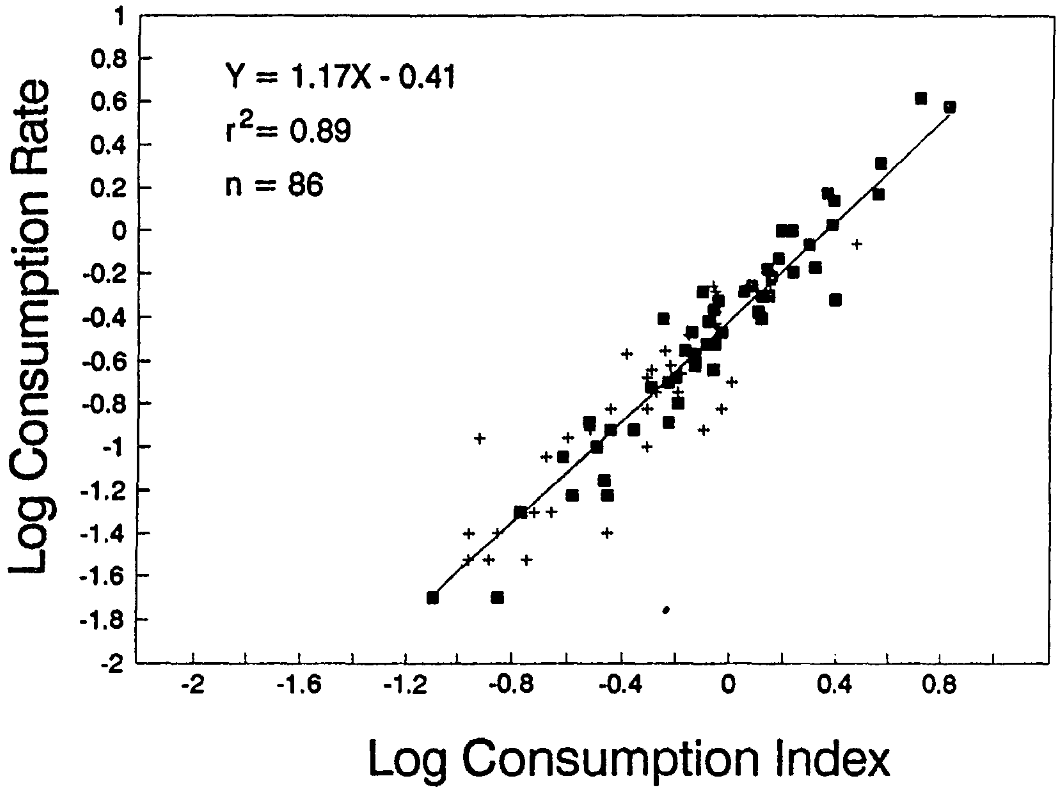

Figure 1. Regression of actual consumption estimates predicted by Consumption Index for McNary BRZ and John Day pool (1983-86). Only days with 15 or more northern squawfish, greater than 250 mm, were used. Squares represent the McNary BRZ (n=5l) and crosses represent the John Day pool (n=35; days with a consumption rate of zero were excluded from the regression.

Using diagnostic bones (Hansel et al. 1988), 939 juvenile salmonids were found in 435 northern squawfish that contained food. The highest number of salmonids per gut were generally found in dam tailrace areas. Squawfish at mid-reservoir sites had the lowest number of salmonids • gut^{-1}, except at the upper McNary location. Northern squawfish within BRZ areas contained much higher numbers of juvenile salmonids (0.9 salmonids • gut^{-1}) than predators collected in the reservoir-wide areas (0.2 salmonids • gut^{-1}). Guts from northern squawfish collected in the spring period contained more juvenile salmonids than sguawfish sampled in the summer.

Other species of prey fish comprised only 7% of the total number of fish ingested by northern sguawfish. In reservoir wide areas, 26% of the prey fish consumed were non-salmonids, while only 4% of the prey fish consumed were non-salmonids in the BRZ zones. Sculpins made up 63% of the other prey fish category and were mostly found in predators collected around Bonneville Dam and at Bonneville mid-reservoir area.

During the spring, northern squawfish CI's were particularly high at the BRZ's of Bonneville Dam tailrace, McNary Dam tailrace and forebay, and the Ice Harbour Dam tailrace, although sample size was fairly small in the BRZ's of Ice Harbour Dam tailrace and the McNary Dam forebay (Figure 2). During the summer, the northern squawfish collected from the BRZ's of tailraces of Bonneville, John Day and McNary dams had high CI's (4.6-11.2): in contrast, The Dalles and Ice Harbour tailrace BRZ's had summer CI's near zero (Figure 2).

Northern squawfish reservoir-wide CI's were quite low (< 1.0) in spring and summer (Figure 2). In the spring period, the rank order of northern squawfish CI's, from lowest to highest, was Bonneville, The Dalles, MCNary and John Day reservoirs. The inter-quartile ranges of the four reservoirs did not overlap, suggesting northern squawfish consumption rates may differ among some reservoirs. In the summer, mean CI's of northern squawfish in Bonneville and The Dalles reservoirs were near zero. Out of 229 gut samples examined from these reservoirs in the summer, only 2 salmonids were recovered. The CI's for northern squawfish from John Day and MCNary reservoirs were higher than CI's of northern squawfish in Bonneville and The Dalles reservoirs (Figure 2).

Ongoing studies

In future studies, northern squawfish consumption and predation indices from the lower Columbia River (Petersen et at. 1991), the lower Snake River (scheduled 1991) and the mid-Columbia River (planned 1992) will be compared to provide a relative ranking of juvenile salmonid losses to predators in different reservoirs. Since sampling in the lower Columbia River, the lower Snake River and the mid-Columbia River will be conducted in separate years (1990-92), direct comparisons of regional data will not be possible.

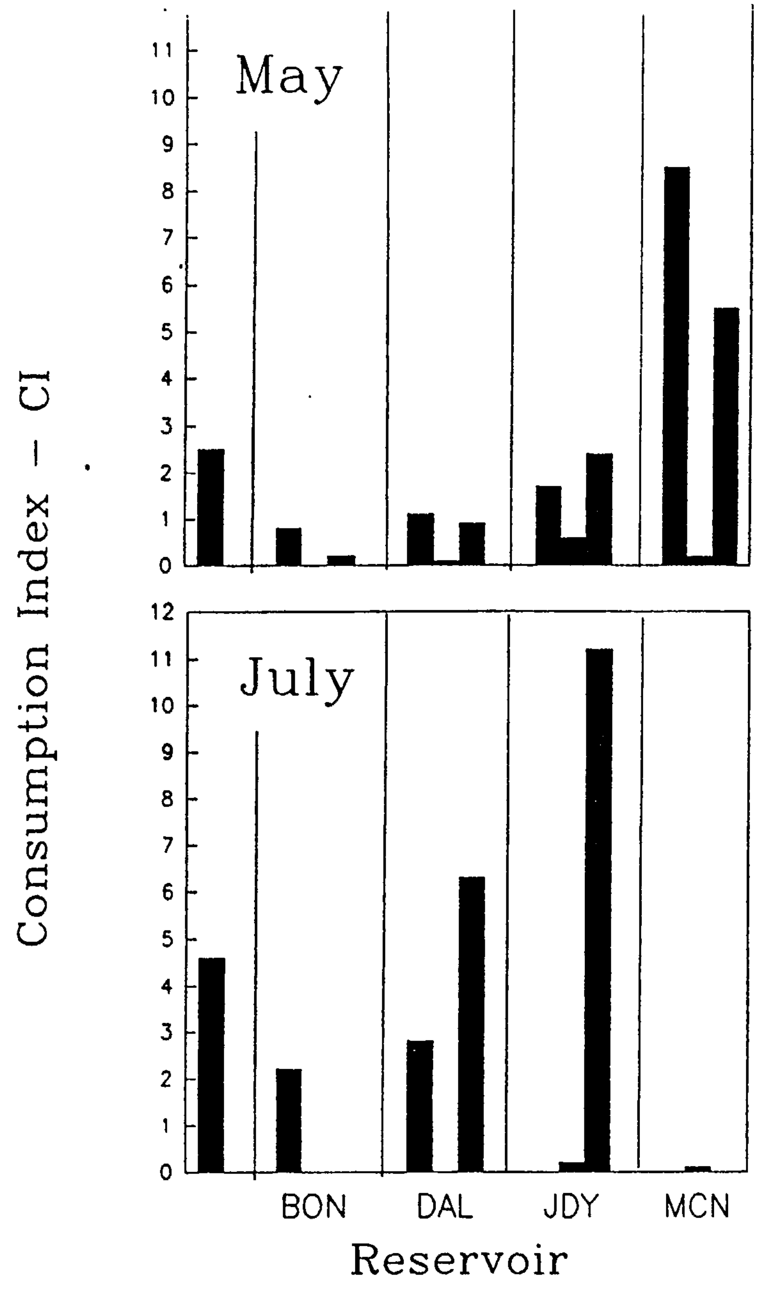

Figure 2. Consumption indices during 1990 for four reservoirs on the lower Columbia River (Bonneville BON, The Dalles DAL, John Day JDY, McNary MCN). Three estimates were made within a reservoir: the forebay of the downstream dam (leftmost vertical bar in a group of three bars), mid-reservoir (middle bar), and the tailrace of the upstream dam (right bar in group). The bar at the far left represents the Bonneville Dam tailrace.

The study design calls for John Day Reservoir to be sampled each year (1990-92), providing a reference point for assessing inter-annual effects. Predation in John Day Reservoir was also studied in 1983-86 and 1988 (Poe et al, 1988: Petersen et al. 1990), supplying additional data for comparisons. Future work will integrate consumption index results (USFWS) with predator abundance data (ODFW) to allow a ranking of sampled areas according to estimated loss of juvenile salmonids to northern squawfish, and other predators if warranted.

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Influence of habitat on the structure and composition of communities of juvenile anadromous salmonids in coastal Oregon streams

Gordon H. Reeves
Forestry Sciences Laboratory, Pacific Northwest Research Station,
3200 Jefferson Way, Corvallis, Oregon

We have examined the structure and composition of communities of juvenile anadromous salmonids (coho salmon, Oncorhynchus kisutch; steelhead trout, O. mykiss; and cutthroat trout, O. clarki) in coastal Oregon streams at different spatial and temporal scales. At the scale of the habitat unit (e.g. pools), salmonid abundance and diversity is positively associated with physical complexity of the habitat. This relationship at the fine spatial scale of the habitat unit appears to underlie diversity patterns at large higher spatial and temporal scales. At the watershed scale, the diversity of the community varies with both land-management history and geomorphic structure. There is a strong negative correlation between the amount of a basin area subjected to timber harvest and salmonid biodiversity. We believe this relationship is due to reduce habitat complexity in stream systems that have been subjected to timber harvest activities. Large-scale geomorphic features (>1 km in length) also influence community structure. Diversity is greater in unconstrained areas (valley width:active channel width ratio ≥3) than in constrained areas (valley width: active channel width ratio ≤3). Habitat complexity in unconstrained areas is generally more complex than in constrained areas. Over large time scales (200+ years), community structure and composition vary naturally in stream systems. Community characteristics appear to be related to the time interval since the systems were subjected to major catastrophic disturbance. Diversity is low in the period following disturbance (<120-150 years), high in at 150-200 years after disturbance, and then declines after 200 years. This pattern appears to be related to the complexity and variety of habitat conditions present at during these time intervals. At present, it is unclear whether the patterns observed are due to interactive or selective segregation.

Predation on sockeye salmon by fish and wildlife in Alaska

Gregory T. Ruggerone
Fisheries Research Institute, University of Washington WH-10,
Seattle, Washington

Predation appears to be an important factor in the survival of sockeye salmon in several, but not all major salmon producing systems in western Alaska. Predation may be especially great in "bottleneck" areas where predators aggregate in response to high prey densities. Bottleneck areas may occur in creeks, rivers, littoral areas of lakes and in estuaries as smolts enter the ocean. In these areas, avoidance of predation by sockeye is constrained by emergence, migration and spawning activities. Prey (salmon) availability in bottleneck areas tends to be predictable in time and space and often leads to an aggregated response by the predator. Potential effects of predation on adult salmon production increase when "bottlenecks" occur later in the life of salmon. Three case histories are presented which describe predator-prey interactions during sockeye emergence and lake residence, smoltification and spawning,

In Chignik Lake, on the Alaska Peninsula, juvenile coho salmon are abundant and primarily consume sockeye fry as they emerge from the shoreline spawning grounds. Coho selectively consume smaller fry and may have influenced the large size of these fry at emergence. Sockeye fry also immediately migrate offshore where coho are less abundant, then return to the shoreline after reaching sizes that are less vulnerable to predation. Relatively little predation occurs after sockeye reach ~35 mm. In contrast, predation in nearby Black Lake is low, apparently because sockeye are not predictably concentrated in one area of the lake and sockeye outgrow the size of vulnerability. Adult production of Chignik Lake sockeye adults (return per spawner) during the past 14 years was inversely related to Chignik coho abundance and sockeye production in Black Lake, western and central Alaska. Plans are being developed to control juvenile coho abundance by harvesting the underutilized adult coho salmon.

In the Wood River lakes, near Bristol Bay, Arctic char congregate each spring at the mouths of rivers that connect the lakes and feed on migrating sockeye smolts. Char are abundant (~4,000 to 12,000 fish per river), large (~450 mm) and consume sockeye smolts as the major component of their diet during spring and early summer. Daily char predation increases with smolt abundance, but at a decreasing rate (type two functional response). Larger than average smolts are consumed by char, but this is related to time of feeding rather than selective feeding. During the late 197O's, the Alaska Department of Fish and Game controlled char predation by capturing char in purse seines and holding them in net pens until the smolt migration subsided. In 1977, approximately 900,000 smolts were estimated to be saved after enclosing about 50% of the char population at one large river. The program was terminated in the early 1980's because funding declined and sportfishermen were concerned.

Presently, we are examining the effect of brown bear predation on spawning sockeye salmon in the Wood River lakes. Anecdotal information indicates that bear abundance has sharply increased since 1979 relative to the previous 30 years and that bears could kill many salmon before spawning. Numbers, sizes, sex and maturity stage of sockeye killed by bears in relation to those available were examined in a small creek (historically 200-14,000 spawners) during 1990. Next summer, we plan to test the hypotheses that bear predation rates are dependent on stream size and that behaviour and morphology of spawning sockeye is modified by bear predation rates.

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Predation in Riverine Habitats of Juvenile Salmon

Robert C. Wissmar
Fisheries Research Institute, University of Washington,
WH-10 Seattle, Washington

Minimal information is available about predator-prey interactions during juvenile salmon residence and migration between rearing habitats. Different age classes ("sizes") of juvenile salmon require rearing habitats that are distributed throughout river basins. Habitat preferences of specific size classes are influenced by numerous biotic and physical factors that change seasonally and over longer periods of time. Degradation and loss of any of these habitats implies that the ultimate smolt production can be limited by the least number of a fish size class surviving limited habitats. These habitats may be "predation bottlenecks" during the late summer and fall because limited carrying capacity (e.g., less forage, de-watering and crowding of fish) increases fish susceptibility to predation. Both carrying capacity and mortality constraints in late summer-fall can force the juveniles to shift to downstream-winter habitats where spatial conditions, food availability and warmer temperatures may improve fish growth. Fish moving between summer and winter habitats may also encounter additional "predation bottlenecks" in shallow side-channels (e.g., birds) and deep pools (e.g., large trout). For example, Alexander (1979) noted that Great Blue Herons and large Brown trout were the major predators on Brook trout in a stream. Herons took the large size classes of brook trout prey in shallow waters while Brown trout (>30 cm) took large numbers of small brook trout at varying depths.

A desirable approach to examining predator-prey interactions in different salmonid rearing habitats would be to assess changes in fish fitness ("mortality and growth") for different size class of fish. However, this information can be difficult to obtain in the simplest cases because size-specific mortality rates can vary widely with different habitats and predators. A more realistic approach would be to define juvenile fish avoidance of predators by fish size and depth distributions in different habitats and during fish movements between habitats. These studies, while providing information about prey susceptibilities to different predators, could also reveal seasonal uses of habitats by predators. Burgess (1985) provides an excellent example of how mink took more prey in streams during summer months than in riparian habitats. Mink predation on fish and crayfish was attributed to mink denning and rearing of young and availability of prey. In the fall, mink predation shifted to riparian habitats because of the apparent low water levels and lack of forage in streams. The use of riparian habitats was also related to dispersal by young mink and prey availability and ease of capture (e.g., mice, voles and shrews).

The evaluation of juvenile fish avoidance of predators by fish size and depth distributions in different habitats and during shifts between habitats could involve simple manipulation experiments. Stream depth would be the easiest factor to manipulate. "Controlled" depths along with fish sizes (net enclosures of specific reaches containing select size classes of fish with and without predators) could be used to determine depth-specific foraging frequency and size selectivities by predators as well as a predator's seasonal use of a habitat. Additional habitat manipulations might consider substrate and streamflow conditions. Such experiments should try and simulate stream-riparian habitats with different fluvial and geomorphic constraints. The most difficult component of these studies would be assessing predator-prey interactions during prey movements between habitats, specifically, time of prey movement and migration rates. All these studies have both basic and applied interest in understanding the functioning of natural and altered salmonid rearing habitats and their predator-prey interactions.

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Problems with modelling numerical responses of predators of juvenile salmonids

Chris C. Wood
Fisheries and Oceans, Pacific Biological Station
Hammond Bay Road, Nanaimo B.C.

Mortality caused by predators is typically estimated as the product of the rate of predation by individual predators and the numbers of predators foraging. Both variables are influenced by the density of prey available to predators. The functional relationship between rate of predation (per predator) and prey density is termed the "functional response", and that between the number of predators and prey density, the "numerical response". The numerical response will be of greater importance than the functional response in determining overall prey mortality where (1) the number of predators is potentially very high, or (2) the predators feed almost exclusively on the prey in question. The numerical response has two components: rapid, localized changes in predator density resulting from food-searching behaviour (the "aggregative response"), and the longer-term changes in overall abundance resulting from increased reproduction or decreased survival (the "reproductive response").

It is useful to model numerical responses by predators in situations where predator abundance cannot be estimated directly, or where the impact of predators must be predicted, perhaps under a variety of different conditions. Because of the complexity of behaviour and reproductive biology producing numerical responses, it is usually necessary to deduce numerical responses by incorporating simple, synoptic relationships governing a predator's probability of arrival (or birth) and probability of departure (or death). Often, particular aspects of the situation being studied permit much greater simplification.

Three types of studies of predation on juvenile salmonids are discussed to illustrate the potential range in complexity that might be considered; they include studies to determine the impact of (1) hatchery-reared steelhead trout and coho salmon feeding on seaward-migrating sockeye and chinook smolts; (2) avian predators feeding on hatchery-reared salmonids during their seaward migration; and (3) lake-resident arctic charr and northern squawfish feeding on underyearling sockeye during lake residence. The first example involves predetermined numbers of predators and prey mixing during downstream migration; however, changes in the duration of stream residence of hatchery steelhead and coho may produce an aggregative response. The second example involves complicated aggregative responses driven by relative availability of prey in neighbouring streams, and constraints on aggregation imposed by the seasonal migratory and breeding habits of the avian predators. The last example involves both an aggregative response in that arctic charr and squawfish sometimes congregate where sockeye are most vulnerable (e.g. near the lake outlet during the smolt migration) and a reproductive response because rates of reproduction and growth are determined by food supply and thus, in part, by the availability of sockeye fry.

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DISCUSSION SUMMARIES

Estimation of Rates of Predation

Discussion Leader : Mike Henderson

Discussion centred on the difficulties inherent in obtaining accurate estimates of predation. Estimating rates of predation involves answering the following questions:

Who are the predators?

In most cases there are several potential predators to choose from and those considered the most obvious may not in fact be causing the major portion of impact.

What is the predation rate per predator?

Accurate and precise estimates are very difficult to obtain where predation rates are very low. Where sampling rates are necessarily very high the process can be extremely expensive. In cases where the predator is rare or valuable it may not be possible to sample them in large enough numbers to obtain an estimate. Some predators exhibit biased and variable feeding behaviour.

What is the overall predation rate?

The estimate of overall predation rate is dependent on both an accurate estimate of the predation rate per predator and an accurate estimate of total population of predators, both of which are difficult to obtain. The estimate necessarily involves scaling up ie. interpolation or extrapolation, from observations which are restricted in time and space.

There was general agreement that it was possible to obtain predation rate estimates but this quantitative approach was likely to be difficult, expensive, time consuming and likely to yield only gross estimates. Further, because of the many assumptions required and the numerous sources of error additional hypothesis testing is usually required.

Two alternatives to predation rate estimation were briefly discussed. These were analysis of conditions that encourage or discourage predation and the use of system perturbations to understand the predation response of the entire system.

While much of the discussion centred on predation rate estimation in the marine environment there was general consensus that a similar level of difficulty would be encountered in rivers.

Influence of Habitat and Behaviour on Rates of Predation/Competition

Discussion Leader: Tom G. Brown

Research approaches to document the effects of reduced flow on predation on juvenile chinook salmon in the Nechako River in British Columbia were solicited after a proposed flow control project was described. The complexity of effects was recognized but no clear suggestions developed from discussions.

Impact of Predation/Competition on Fish Production

Discussion Leader: Pat Slaney

Possible approaches to mitigate reduced flow in the Nechako River were described by the Discussion Leader. Some of the techniques included provision of refuges for juvenile chinook salmon using debris structures. The effectiveness of the refuges with respect to predation needs to be confirmed with experiments, possibly using enclosures/exclosures.

Modelling, Statistical Methods and Monitoring
Discussion Leader : Steve Macdonald

Statistical methods required to analyze predator-prey relationships are similar or the same as those required to analyze almost any biological data. As with most biological data, data from predator-prey studies rarely follow parametric assumptions and are often multivariate and multifactorial in nature.

Analysis of predator-prey data begins with a concise statement of the hypothesis (es); a hypothesis that may develop from a period of preliminary sampling. Preliminary samples provide the researcher with a number of advantages beyond the clarification of the hypothesis. They allow the evaluation of the efficiency with which sampling devices sample a range of sampling conditions and allow the selection of sample unit size. Preliminary samples also provide an estimate of the number of samples required to describe the organisms present in the community and an estimate of variation within the area proposed for sampling. The estimated variation will permit a calculation of the number of replicate samples required to obtain the precision required by solving for n in the equation used to calculate confidence limits on the mean (Green, 1979).

$$\overline{x} \pm t_{(.05)}\ S/\sqrt{n}\ 0.5$$

Once the data have been collected a number of analysis methods are available to the researcher to determine if the predators' diets differ from the potential prey abundance available in the environment (i.e., selective feeding). The simplest method is based on Ivlev's (1961) electivity index.

$$E = \frac{r_i - p_i}{r_i + p_i}$$

Where: r_i = % item i in the stomach
p_i = % item i in the environment

If the experiment involves competition between two species "p" could be a second species and E is an estimate of the degree of competition for prey item "i". However, as the number of items in the diets and the number of predators increases the size of the matrix of E values becomes increasingly large and uninterpretable. Niche overlap indices have been developed to avoid this problem by comparing prey species common in two predators' diets (competition estimates) or between a predator's diet and the available food in the environment (Levins 1968). The result is also a matrix of pairwise comparisons of all predator species and the available food in the environment in which they live. However, because this method doesn't compare each prey species separately, the matrix is smaller than generated by electivity indices.

Both of these methods ignore the multivariate and multifactorial nature of data generated from predator-prey studies. When data collected fit into an n by p matrix with group structure (where a group is a predator species, or the environment in which the predator species lives, from which n samples are taken and p prey or potential prey species are identified) one should suspect multivariate methods provide the best analysis techniques. Whether it be cluster or discriminant analysis or a multivariate analysis of variance, multivariate techniques allow the analysis of all groups in the data set at once, provide an efficient means to isolate the prey species that differ significantly among groups (particularly when there are many prey species) and most importantly, take into consideration the variation within each group. Differences among diets of different species of predators (or among predators species and prey environmental availability) can only be demonstrated by comparison to differences within.

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RECOMMENDATIONS

Participants were asked to provide a qualitative estimate of the potential success of a variety of field and laboratory approaches to predation and competition questions. They were asked to rate the potential of the various approaches as "poor" or "good". The responses are summarized below in Table 1. The results demonstrate divergent opinions among the workshop participants. One participant pointed out that the usefulness of particular techniques was dependent on whether a "bottom-up"(emphasis on individual species behaviour patterns) or "top-down"(emphasis on patterns of species abundance and composition) was being used to predict the mechanisms involved in structuring animal populations and communities. Other factors affecting the utility of various research approaches included the characteristics of the study area and the quality of available data.

Table 1. Subjective estimate of the potential of various research approaches to predation/competition, as rated by seven Workshop participants.

	Rate Estimates	Habitat Influences	Influence on Production
Field experiment	Good (5)**	Good (6)	Good (4)
Semi-Natural	Good (6)*	Good (6)	Good (5)
Enclosures	Good (4)	Good (6)	Good (5)
Mesocosms	Poor (4)	Good (5)	Poor (4)
Models(Field Data)	Poor (4)	Poor (4)	Good (5)
Models(Lab Data)	Good (4)	Poor (4)	Poor (5)
Inferences from Behaviour	Poor (5)	Good (7)	Poor (6)

* If top-down perspective is used.

**Indicates number of respondents in agreement.

PARTICIPANT CONTACT LIST

Participant	Phone/ FAX	Address
Tom G. Brown	604-756-7091 604-756-7053	Fisheries and Oceans Pacific Biological Station Hammond Bay Road Nanaimo B.C., V9R 5K6
James Bruce	604-324-4522 604-322-0128	Aquatic Resources Ltd. Suite 40, 942 S.W. Marine Drive Vancouver, B.C., V6P 5Z2
Brent Hargreaves	604-756-7035 604-756-7053	Fisheries and Oceans Pacific Biological Station Hammond Bay Road Nanaimo B.C., V9R 5K6
Mike Henderson	604-666-6746 604-666-3540	Fisheries and Oceans 555 West Hastings Vancouver B.C., V6B 5G3
Mike Healey	604-228-4956 604-228-5357	Westwater Research Centre University of British Columbia 1933 West Mall Annex Vancouver B.C., V6T 1W5
Jeremy Hume	604-858-7117 604-858-3757	Fisheries and Oceans Cultus Lake Laboratory, 4222 Columbia Valley Highway Cultus Lake, V0X 1H0
George Hunter	604-985-4220 604-985-4220	Pegasus Consulting Group 2874 Fromme Road North Vancouver, B.C., V7K 2C5
Kim Hyatt	604-756-7217 604-756-7053	Fisheries and Oceans Pacific Biological Station Hammond Bay Road Nanaimo B.C., V9R 5K6

Mark Johannes	604-756-7217 604-756-7053	Fisheries and Oceans Pacific Biological Station Hammond Bay Road Nanaimo B.C., V9R 5K6
Colin Levings Chairperson	604-666-7915 604-666-3497	Fisheries and Oceans West Vancouver Laboratory 4160 Marine Drive West Vancouver, B.C., V7V 1N6
Dave Levy	604-926-4431 604-926-4338	Levy Research Services Ltd. Suite 102-2221 Folkstone Way West Vancouver, B.C., V7S 2Y6
Steve Macdonald	604-666-7910 604-666-3497	Fisheries and Oceans West Vancouver Laboratory 4160 Marine Drive West Vancouver, B.C., V7V 1N6
Eric Parkinson	604-664-1812 604-660-1849	B.C. Ministry of Environment 2204 Main Mall, University of British Columbia Vancouver, B.C., V6T 1W5
Jim Petersen	509-538-2299 509-538-2843	US Fish and Wildlife Service National Fisheries Research Centre, Columbia River Field Station, MP 5.48 Cook Underwood Road, Cook, WA 98605-9701
Gordon Reeves	503-750-7314 503-750-7329	Forestry Sciences Laboratory Pacific Northwest Research Station, 3200 Jefferson Way, Corvalis, Oregon, 97331
Bill Ruble	604-279-2093 604-279-2047	Triton Environmental Consultants #120-13511 Commerce Parkway Richmond B.C., V6V 2L1
Greg Ruggerone	206-543-7546 206-543-4650	Fisheries Research Institute University of Washington Seattle, Washington, 98195

Pat Slaney	604-660-1812 604-660-1849	B.C. Ministry of Environment 2204 Main Mall, University of British Columbia Vancouver, B.C., V6T 1W5
Kim West	604-666-0179 604-666-3540	Fisheries and Oceans 555 West Hastings Vancouver B.C., V6B 5G3
Robert Wissmar	206-543-7467 206-543-4650	Fisheries Research Institute University of Washington, WH-10 Seattle, Washington, 98195
Chris Wood	604-756-7140 604-756-7053	Fisheries and Oceans Pacific Biological Station Hammond Bay Road Nanaimo B.C., V9R 5K6

APPENDIX-ANNOTATED BIBLIOGRAPHY

Competitive and predator-prey interactions with juvenile salmonids in the context of reduced stream flows

Prepared by

J.A. Bruce
Aquatic Resources Limited
Vancouver, B.C.

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An example of how temperature, through its effects on prey survival and abundance, can affect the structure of predator populations.

Allee, B.A. 1981. The role of interspecific competition in the distribution of salmonids in streams, p.111-122. In E.L. Brannon and E.O. Salo [eds.] Proceedings of the salmon and trout migratory behaviour symposium. School of Fisheries, University of Washington.

Prior residence did not appear to provide a competitive advantage to fish in an artificial stream environment. Although previous studies have suggested that size may be an important factor in intraspecific interactions, this does not appear to be the case for interspecific interactions. Regardless of size, juvenile coho were able to out compete steelhead trout for stream positions. Agnostic tendencies appear to be a more important factor since coho were more aggressive than steelhead in all experimental conditions. Although a certain degree of interspecific competition was observed, it was minimal. Habitat preferences were sufficiently different between the two species to allow for coexistence. Intraspecific interactions were found to be more important in the distribution of salmonids in streams than interspecific competition.

Andrusak, H. and T.G. Northcote. 1971. Segregation between adult cutthroat trout (Salmo clarki) and Dolly Varden (Salvelinus malma) in small coastal British Columbia Lakes. J. Fish. Res. Bd. Can. 28: 1259-1268.

A description of the life history and ecology of cutthroat trout and Dolly Varden and mechanisms leading to their segregation, and consequently their coexistence, in lake systems. Dolly Varden are principally bottom feeders while trout feed in more pelagic waters.

Arthur, W. 1987. The niche in competition and evolution. John Wiley and Sons, Toronto.

Presents current theories on competition, niche breadth, predation, and stability of ecosystems.

Backiel, T. and E.D. LeCren. 1978. Some density relationships for fish population parameters, p.279-302. In S.D. Gerking [ed.] Ecology of Freshwater Fish Production. Blackwell Scientific Publications, Oxford.

Describes some of the consequences of crowding. These include emigration and reductions in growth.

Baltz, D.M. and P.B. Moyle. 1984. Segregation by species and size class of rainbow trout, Salmo gairdneri, and Sacramento sucker, Catostomus occidentalis, in three California streams. Environ. Biol. Fishes. 10: 101-110.

A comparison of microhabitat preferences of rainbow trout and suckers at different sucker densities showed that competition between the two species is minimal. Although both species preferred similar maximum water depths, mean velocities, focal point velocities, surface velocities and substrate types, there was a strong vertical segregation which minimized interspecific interactions; trout occupying positions in the water column and suckers remaining in contact with the bottom. These responses were independent of sucker density. Focal point depths however overlapped considerably when young of the year of each species were compared. Thus the potential for competition appears to be greatest in young fish and lessens as both species grow.

Baltz, D.M., P.B. Moyle and N.J. Knight. 1982. Competitive interactions between benthic stream fishes, riffle sculpin Cottus gulosus, and speckled dace Rhinichthys osculus. Can. J. Fish. Aquat. Sci. 39: 1502-1511.

Field and laboratory experiments showed that water temperature was the primary factor leading to the segregation and habitat utilization of specked dace and riffle sculpins. Both occupy similar riffle habitat when in allopatry. In the coolest reach of the experimental stream (21-29°C), sculpins dominated the riffle habitat while dace were restricted to deeper and slower waters. In the warmest reach (21-32°C) sculpins were largely absent, allowing the dace to predominate the riffle habitat. In the intermediate reaches, the abundance of dace and sculpins in riffle habitats were negatively correlated. Within these latter reaches, dace occupation of riffle habitat appears to be a function of sculpin density. Lab studies showed a progressive displacement of dace from cover positions as sculpin density increased. Sculpin density in turn appears to be mediated by temperature, their numbers decreasing as temperature increases. Whether dace at warmer temperatures are able to actively exclude sculpins from the area is not known. It could be that sculpins were expressing avoidance behaviour.

Baltz, D.M., B. Vondracek, L.R. Brown and P.B. Moyle. 1987. Influence of temperature on microhabitat choice by fishes in a California stream. Trans. Amer. Fish. Soc. 116: 12-20.

Eight microhabitat variables were recorded for each of four California stream fishes. Discriminant function analysis revealed that temperature was one of the more important factors governing the distribution of fish. These findings are related to selective segregation.

Bams, R. 1967. Differences in performance of naturally and artificially propagated sockeye salmon migrant fry as measured with swimming and predation tests. J. Fish. Res. Bd. Can. 24: 1117-1153.

Relates size and condition factor to swimming performance: the larger the fry, the more effective the performance. This in turn was found to be highly correlated with the fry's ability to avoid predation by juvenile cutthroat trout. The relationship is causal. No direct test of the hypothesis was made. Differences in vulnerability between artificially and naturally propagated sockeye fry appears to be explained by this relationship.

Beamesderfer, R.C. and B.E. Rieman. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River reservoir: III Abundance and distribution of northern squawfish, walleye, and smallmouth bass, p.211-248. In: T.P. Poe and B.E. Rieman [eds.] Predation by Resident Fish on Juvenile Salmonids in John Day Reservoir. Bonneville Power Administration, Portland, Oregon.

Examines the abundance and distribution of squawfish in the John Day Reservoir. Squawfish generally prefer low velocity waters. Consequently, they tend to remain in near shore areas. During the summer when flows are considerably reduced, squawfish may be found in the mainstem where they may prey on out-migrating salmonids.

Beamesderfer, R.C., B.E. Rieman, L.J. Bledsoe and S. Vigg. 1990. Management implications of a Model of predation by a resident fish on juvenile salmonids migrating through a Columbia River reservoir. N. Amer. J. Fish. Manag. 10: 290-304.

A model of squawfish predation was developed to evaluate the effects of water temperature, streamflow, predator and prey abundance on the survival of migrating juvenile salmonids in the John Day Reservoir in the Columbia River basin. Sensitivity analysis showed that the number of predators was the most influential variable affecting salmonid predation. Temperature was also in important factor. The consumption rate of squawfish as temperatures increased. Streamflow however had only a limited effect. It is hypothesized that streamflow effects occur through changes in water temperature. Prey abundance also had a significant effect, the greater the number, the better the survival rate. Since streamflow reductions would also increase the density of prey, streamflow effects could also have been mediated through this variable. The water temperature - maximum food consumption rate curve showed a peak between 20 and 25 °C, thus FTP is likely in that range. This appears to be the only study which has intensively investigated the effects of various stream parameters on predatory interactions.

Begon, M. and M. Mortimer. 1981. Population ecology: a unified study of animals and plants. Blackwell Scientific Publications, Oxford. 342pp.

Includes a brief discussion on the functional responses of predators and provides an explanation for each of the four types.

Beitinger, P.L. and L.C. Fitzpatrick. 1979. Physiological and ecological correlates of preferred temperature in fish. Amer. Zool. 19: 319-329.

The thermal preference patterns of fish are related to the temperatures at which physiological activities collectively operate with maximum efficiency. Thermal preferenda are also correlated with the temperatures to which these fish are normally subjected in nature.

Belford, D.L. 1978. Simulation of coho smolt predation on pink and chum fry: the importance of relative size and growth rate. M.Sc. Thesis, University of British Columbia. 167pp.

Competition for food between juvenile pink and chum in an estuary habitat was examined by simulation models to determine how it would affect predation by coho smolts. The results suggest that intense competition would reduce growth and in turn prolong the period of time pink and/or chum fry are susceptible to coho predation.

Bjornn, T.C. 1971. Trout and salmon movements in two Idaho streams as related to temperature, food, streamflow, cover, and population density. Trans. Amer. Fish. Soc. 100: 423-438.

The objective of the study was to examine the adaptive significance of and mechanisms which trigger the migratory behaviour of non-smolt trout and salmon in streams during late fall and winter. Streamflow and food abundance were found not to be a significant factor. Stream temperatures below 4-6oC were found to trigger a hiding response in both salmonid species but was apparently not a direct factor inducing migration. The level of cover provided by large rubble substrate appeared to the factor of greatest importance. Large substrate provides cover for hiding fish. The lack of it apparently forces these fish to move out in search of it. Population density apparently modified this migratory behaviour. The numbers emigrating from the system increased with population density. The data also suggest that emigration timing may also be affected. Thus, it appears that salmonids may compete for limited hiding spaces.

Bjornn, T.C. 1978. Survival, production and yield of trout and chinook salmon in the Lemhi River, Idaho. University of Idaho, College of Forestry, Wildlife and Range Sciences Bull. No. 27, Moscow, Idaho. 57pp.

A 14 year study on the effects of steelhead trout and chinook salmon stocking programs in the Lemhi River, Idaho. Explores competitive interactions between steelhead, chinook, resident rainbow and brook trout and other fishes. Mortality rates, population fluctuations, stocking density, yield, and migration are only some of the parameters explored. In general, the stocking of steelhead and chinook did not affect the resident population of brook trout but caused a reduction in the numbers of resident rainbow trout.

Chinook appeared to out compete steelhead fry for food and space since chinook faired better than steelhead when stocked jointly. Total stream production was considerably higher when steelhead trout and chinook salmon were stocked jointly than when steelhead alone was stocked at very high numbers. Suggest that these species show a certain degree of segregation allowing for their coexistence. Effects on other species are rater inconclusive.

Brannon, E., A. Setter, J. Altick and M. Miller. 1987. Columbia River white sturgeon genetics and early life history: population segregation and juvenile feeding behaviour. Final Report (1987) to the Bonneville Power Administration. School of Fisheries WH-10, University of Washington, Seattle, Washington. 48pp.

Includes an experiment which explores the ability of white sturgeon juveniles and subadults to capture salmonid fry. Turbidity and light intensity were examined as modifying factors. The latter apparently impair the ability of fry to detect and avoid predation.

Breeser, S.W., F.D. Stearns, M.W. Smith, R.L. West and J.B. Reynolds. 1988. Observations of movements and habitat preferences of burbot in an Alaskan glacial river system. Trans. Amer. Fish. Soc. 117: 506-509.

The migratory patterns of burbot, a potential predator on juvenile salmon, were followed by radio telemetry. Observations were related to what is known of the general biology. Contains some life history information.

Brown, L.R. and P.B. Moyle. 1981. The impact of squawfish on salmonid populations: a review. N. Amer. J. Fish. Manag. 1: 104-111.

Squawfish appear not to be major competitors of salmonids, although food habits, particularly of younger members, may overlap. There appears to be major differences in microhabitat preferences between the two species which may minimize competitive interactions. Studies which employ squawfish removal programs generally show increases in trout populations, but too many confounding variables exist (e.g. fishing and predation) to attribute this increase to competitive interactions. Squawfish do not appear to be major predators of salmonids in streams under natural conditions. Predation may be high however when local concentrations may be high, such as during seaward migration, hatchery releases, and below dams and diversions where conditions are unusually favourable for predation (e.g. greater number of confused and injured fish, slower moving waters, high concentrations of squawfish competing for food). Evidence of all this however is not conclusive.

Buchanan, D.V., R.M. Hooton and J.R. Moring. 1981. Northern squawfish (Ptychocheilus oregonensis) predation on juvenile salmonids in sections of the Willamette River basin, Oregon. Can. J. Fish. Aquat. Sci. 38: 360-364.

Little salmonid predation was observed in the squawfish population of Willamette River basin, an unregulated stream. The fish most commonly eaten appear to be sculpins. Suggests that previous reports of squawfish predation may have been misleading since the observations were made principally below dams and after hatchery releases.

Campbell, K.P. 1979. Predation principles in large rivers: a review, p.181-190. In H. Clepper [ed.] Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, DC.

Outlines some general principles of predation in rivers and streams based on a review of literature

Chapman, D.W. 1962. Aggressive behaviour in juvenile coho salmon as a cause of emigration. J. Fish. Res. Bd. Can. 19: 1047-1080.

In a natural stream systems, the author found that coho fry emigrated due to dominance of larger coho fry. When the emigrants were placed in an uninhabited stream, migratory behaviours ceased.

Chapman, D.W. 1966. Food and space as regulators of salmonid populations in streams. Amer. Nat. 100: 345-358.

A review of literature which explores the hypothesis that competition between salmonids in streams may lead to emigration, reductions in growth and reduced survival. It is thought that these latter attributes regulate salmonid populations.

Chapman, D.W. and T.C. Bjornn. 1969. Distribution of salmonids in streams with special reference to food and feeding, p.388. In: T.G. Northcote [ed.] Symposium on salmon and trout in streams. Institute of Fisheries, University of British Columbia.

Discusses the biology of chinook and steelhead in allopatry and in sympatry. Includes a review of a few other salmonid interaction studies and puts the winter hiding behaviour observed in both species into perspective.

Clothier, D.W. 1953. Fish loss and movements in irrigation diversions from the west Gallatin River, Montana. J. Wildlife Manage. 17: 144-158.

Relates movements of fish in an irrigation canal to reductions in flow (water level). Observed both upstream and downstream movements among the fish population. Assumes that this is due to increased competition for remaining available habitat.

Clothier, W.D. 1954. Effect of water reductions on fish movement in irrigation diversions. J. Wildlife Manage. 18: 150-160.

The author observed increased upstream as well as some downstream movements in fish when streamflow was reduced. The author attributes this migration to increased intraspecific competition for remaining habitat.

Cohen, Y. 1987. A review of harvest theory and applications of the optimal control theory in fisheries management. Can. J. Fish. Aquat. Sci. 44 (No. 2): 75-83.

Applies optimal control theory to multispecies interactions, ecosystem stability and vulnerability.

Colby, P.J., P.A. Ryan, D.H. Schupp and S.L. Serns. 1987. Interactions in north temperate lake fish communities. Can. J. Fish. Aquat. Sci. 44 (Suppl. No. 2): 104-128.

Relates predation and competition to community structure. Stresses that removal and stocking programs as well as man-made changes to the habitat may not necessarily yield desired results. A better understanding of species interactions is imperative in order to predict the outcome of environmental perturbations.

Congleton, J.L., T.C. Bjornn, B.H. Burton, B.D. Watson, J.I. Irving and R.R. Ringe. 1985. Effects of handling and crowding on the stress response and viability of chinook salmon parr and smolts. Completion Report to Bonneville Power Administration, Portland, Oregon.

Overcrowding causes stress in young chinook salmon which could increase their susceptibility to predation.

Coutant, C.C. 1973. Effect of thermal shock on juvenile salmonids to predation. J. Fish. Res. Bd. Can. 30: 965-973.

Thermally shocked rainbow trout and chinook salmon were selectively preyed upon by larger trout in the laboratory. The minimum exposure time to lethal temperatures which increased predation was 10% of the median time to equilibrium loss for chinook salmon and 20% for rainbow trout. Apparently, thermal shock increases the rate of discovery and reduces the effectiveness with which predator avoidance behaviours are elicited. Abnormal swimming behaviours appear to be the primary means by which predators are able to discern disabled prey.

Coutant, C.C., R.B. Mclean and D.L. DeAngelis. 1979. Influences of physical and chemical alterations on predatory-prey interactions, p.57-68. In: H. Clepper [ed.] Predator-prey systems in fisheries management. Sport Fish. Inst., Washington, DC.

Includes a general discussion on how temperature may influence predator-prey interactions.

Cowx, I.G. and R.A. Gould. 1985. The effects of short-term regulation releases from an impoundment on downstream fish fauna. Aquacult. Fish. Manage. 1: 257-264.

Short-term releases of water from an impoundment apparently displaced fish from the

upper sections of a regulated stream. This caused a transitory increase in fish density further downstream. It is presumed that these fish migrate upstream to regain station once there is an abatement in flows.

Cramer, S.P. 1986. Lost Creek Dam fisheries evaluation: the influence of river temperature and flow on the production and harvest of summer steelhead in the Rogue River. Oregon Department of Fish and Wildlife, Portland, Oregon. 64pp.

A model is presented to help predict the effects of various temperature and flow regimes on the productivity and harvest of steelhead trout. These predictions are interpreted with respect to the chinook salmon fishery. River warming and increased flows during summer are recommended to improve the steelhead fishery. However, temperatures should be less than 13oC since warmer temperatures would increase the mortality of spawning chinook and river warming should be delayed as much as possible to prevent the early emergence of chinook fry during Spring.

Cramer, S.P., T.D. Satterwaite, R.R. Boyce and B.P. McPherson. 1985. Lost Creek Dam fisheries evaluation phase I completion report. Summary and recommendations. Oregon Department of Fish and Wildlife, Portland. 21pp.

A summary of the research done on Rogue River at the Lost Creek Dam. The warmer temperatures created by the dam during winter caused fry to emerge much earlier than normal. As a result, mass losses due to starvation occurred. However, the warmer temperatures during the remaining part of the freshwater phase increased growth and in turn, adult survival. Coho and steelhead do not appear to be affected in the same way. Both species spawn and rear in the tributaries which remain relatively unaffected by the dam.

Dettman, D.H. 1976. Distribution, abundance, and microhabitat segregation of rainbow trout and Sacramento squawfish in Deer Creek, California. M.Sc. Thesis, University of California, Davis.

Squawfish and rainbow trout segregate along a stream velocity axis: squawfish tend to occupy areas of low velocity while trout occupy much faster waters. This reduces the extent with which the two species interact. Apparently, squawfish are unable to hold the position in fast waters, particularly at cold temperatures.

Dill, L.M. and A.H.G. Fraser. 1985. Risk of predation and the feeding behaviour of juvenile coho salmon (Oncorhynchus kisutch). Behav. Ecol. Sociobiol. 16: 65-72.

Coho salmon reduced foraging distances and apparently became more vigilant when exposed to a predator. Similar responses may be expected among other stream dwelling salmonids.

Dill, L.M., R.C. Ydenberg and A.G.H. Fraser. 1981. Food abundance and territory size in juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Zool. 59: 1801-1809.

High intruder pressure resulted in a reduction in the territory size defended by coho salmon in a natural stream.

Dolloff, C.A. and G.H. Reeves. 1990. Microhabitat partitioning among stream-dwelling juvenile coho salmon, *Oncorhynchus kisutch* and Dolly Varden, *Salvelinus malma*. Can. J. Fish. Aquat. Sci. 47: 2297-2306.

Microhabitat preferences of juvenile coho salmon and Dolly Varden were examined under field and laboratory conditions. Coho preferred midwater positions and were territorial. Dolly Varden were more closely associated with the stream bottom and were generally closer to cover. In both species, depth of water, depth of focal point and distance from nearest fish increased with size. In a laboratory stream channel, habitat use did not differ between sympatric and allopatric conditions, indicating that segregation is achieved through innate behavioral differences and is not due to interspecific interactions.

Edmundson, E., F.E. Everest and D.W. Chapman. 1968. Permanence of station in juvenile chinook salmon and steelhead trout. J. Fish. Res. Bd. Can. 25: 1453-1464.

Juvenile chinook and steelhead remained within a confined area during most of their freshwater residence. Individuals spent most of their time at a particular station. Diel inshore/offshore movements were evident in both species. At night the steelhead were found at the bottom in areas of low velocity and were inactive. Chinook were found principally in still waters at night add occupied positions through out the water column. Chinook tended to be closer to shore at night than steelhead. Both species were active in faster waters during the day.

Eggers, D.M., N.W. Bartoo, N.A. Richard, R.E.E. Nelson, R.C. Wissmar, R.L. Burgner and A.H. Devol. 1978. The Lake Washington ecosystem: the perspective from the fish community and forage base. J. Fish. Res. Bd. Can. 35: 1553-1571.

Includes a discussion of squawfish predation in the lake system. The prey consumed by squawfish appeared to reflect it's availability in the system. Prey switching responses are implicated.

Elliott, J.M. 1984. Numerical changes and population regulation in young migratory trout *Salmo trutta* in a Lake District stream, 1966-83. J. Anim. Ecol. 53: 327-350.

Mortality was found to be density dependent: increasing with population density. Although emigration may be possible, it was not measured. Comparisons are based on the density of brown trout collected over a period of several years.

Elliott, J.M. 1984. Growth, size, biomass and production of young migratory trout Salmo trutta in a Lake District stream, 1966-83. J. Anim. Ecol. 53: 979-994.

No significant changes in growth were found as a function of population size. Comparisons are based on the density of brown trout collected over a period of several years.

Elliott, J.M. 1987. Population regulation in contrasting populations of trout Salmo trutta in two Lake District streams. J. Anim. Ecol. 56: 83-98.

Elliott, J.M. 1988. Growth, size, biomass and production in contrasting populations of trout Salmo trutta in two Lake District streams. J. Anim. Ecol. 57: 49-60.

Elson, P.F. 1962. Predator-prey relationships between fish eating birds and Atlantic salmon. Fisheries Research Board of Canada, Ottawa, Ontario. 87pp.

Predation of Atlantic salmon at various stocking densities by mergansers and kingfishers was examined. Numerical and functional relationships were observed. Kingfishers selectively preyed on non-salmonids while mergansers were found to be a limiting factor of smolt production. Merganser control measures are discussed.

Erman, D.C. and G.R. Leidy. 1975. Downstream movement of rainbow trout fry in a tributary of Sagehen Creek, under permanent and intermittent flows. Trans. Amer. Fish. Soc. 104: 467-473.

Under intermittent flows which followed a diel pattern, downstream movements peak when flows reached their daily maximum. Although correlated with streamflow, temperature was apparently not a factor since, during short periods of continuous flow where daily fluctuations in temperature were maintained, downstream migration ceased. Under permanent flows, downstream movements were correlated with light intensity; migration rate peaked at night. Although not tested, it was hypothesized that intraspecific competition for space increased during periods of low flow, forcing fish to emigrate out of the system when flows where high enough to permit passage over riffles. Under conditions of permanent flow, fewer fish emigrated, presumably because of the increased usable habitat. It was suggested that those migrating out of the system were surplus production and that this migration, in absence of more dramatic cues, was related to light intensity.

Evans, D.O., B.A. Henderson, N.J. Bax, T.R. Marshall, R.T. Oglesby and W.J. Christie. 1987. Concepts and methods of community ecology applied to freshwater fisheries management. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 448-470.

Reviews general theory, hypotheses, and methods of community ecology with reference to freshwater fisheries management. Describes the importance of interspecific interactions as a mechanism defining the structure of a fish community and how this may change with manmade perturbations in the environment.

Everest, F.R. and D.W. Chapman. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. J. Fish. Res. Bd. Can. 29: 91-100.

Both chinook salmon and steelhead trout move into deeper and faster waters as the grow in size. Juvenile chinook and steelhead of the same size occupy similar microhabitats. However, social interactions between the two species are minimized through temporal segregation; chinook spawn in the fall and therefore the young of the year are larger at any given time during the summer than steelhead, which spawn in the spring.

Faler, M.P., L.M. Miller and K.I. Welke. 1988. Effects of variation in flow on distributions of northern squawfish in the Columbia River below McNary Dam, p.72-89. In: T.P. Poe and B.E. Rieman [eds.] Predation by Resident Fish on Juvenile Salmonids in John Day Reservoir. Bonneville Power Administration, Portland, Oregon.

The distribution of squawfish was followed at different flows below the McNary Dam. They hug the shore at high velocities and move into the mainstem at low velocities. Squawfish are of greatest predatory threat to juvenile salmonids in the latter case.

Fausch, K.D. 1984. Profitable stream positions for salmonids relating specific growth rate to net energy gain. Can. J. Zool. 62: 441-451.

A model was developed which demonstrates the trade-off between quantity of drift at high water velocities and the energy expenditure required to remain at feeding stations. Salmonids appear to select stream positions which maximize the former and minimize the latter, thus maximizing net energy gain. These positions in the stream are competed for intraspecifically. The model can be used to make *a priori* predictions with respect to growth on the outcome of interspecific competitive interactions.

Fausch, K.D. and R.J. White. 1981. Competition between brook trout (Salvelinus frontinalis) and brown trout (Salmo trutta) for position in a Michigan stream. Can. J. Fish. Aquat. Sci. 38: 1220-1227.

Brown trout apparently compete with brook trout for resting positions, but not feeding station, when in sympatry. Removal of brown trout from the experimental stream allowed brook trout to occupy these resting stations which, presumably increased survival. Thus it appears that brown trout were excluding brook trout from these positions.

Fenderson, O.C. and M.R. Carpenter. 1971. Effects of crowding on the behaviour of juvenile hatchery and wild landlocked Atlantic Salmon (Salmo salar L.). Anim. Behav. 19: 439-442.

At low densities, aggression in wild Atlantic salmon is initially high and as density increases, aggression gradually declines. For hatchery reared salmon, aggression was initially low and increases gradually as density increases. Differences may be due to early life history. It may be that wild fish are able to recognize dominants more readily than hatchery reared fish. In both populations, increases in density resulted in a reduction in consumption rate due to social interaction.

Flick, W.A. and D.A. Webster. 1975. Movement, growth, and survival in a stream population of wild brook trout (Salvelinus frontinalis) during a period of removal of non-trout species. J. Fish. Res. Bd. Can. 32: 1359-1367.

No changes in growth or survival were observed following the removal of all non-trout species from a small Adirondack Mountain stream of low productivity. However, there was a cessation of movement of both trout and non-trout species over time. Abundance estimates were not available to determine whether the number of resident trout increased as a consequence. The experiment was carried out over a 13 year period.

Foerster, R.E. and W.E. Ricker. 1941. The effect of the reduction of predacious fish on survival of young salmon at Cultus Lake. J. Fish. Res. Bd. Can. 5: 315-336.

Describes the outcome of predator control measures on the population of juvenile salmonids in Cultus Lake, British Columbia. Predators, which included squawfish, were removed by continuous gillnetting. Resulted in increased survival of sockeye juveniles.

Fraser, D.F. and R.D. Cerri. 1982. Experimental evaluation of predator-prey relationships in a patchy environment: consequences for habitat use patterns in minnows. Ecology. 63: 307-313.

Both the creek chub and the blacknose dace avoided areas which contained predators in a structurally simple stream. As habitat complexity increases, this avoidance behaviour is less intense, i.e. in structurally complex habitats, more prey fish are likely to be found coexisting with predators than in less structurally complex habitats.

Fraser, F.J. 1968. The effect of population densities on survival, growth, and behaviour of coho salmon and steelhead trout fry. M.Sc Thesis, University of British Columbia.

Survival was found to be dependent on intraspecific factors. Low density population survived well even in the presence of high densities of a competing species. Growth was inversely related to density. Considerable emigration was observed at high densities.

Fresh, K.L. and S.L. Schroder. 1987. Influence of the abundance, size, and yolk reserves of juvenile chum salmon (Oncorhynchus keta) on predation by freshwater fishes in a small coastal stream. Can. J. Fish. Aquat. Sci. 44: 236-243.

Large rainbow trout and coho salmon were found to be the principle predators of juvenile chum salmon. Other fishes which preyed on chum included cutthroat trout and sculpins, but level of predation was comparatively small. Predation on chum salmon appeared to follow a Type II response curve. Body size did not affect the chum's susceptibility to predation, however there was an apparent selectivity among predators for chum still retaining much of their yolk reserves. Presumably, the latter are easier to catch.

Gee, A.S., N.J. Milner and R.J. Hemsworth. 1978. The effect of density on mortality in juvenile Atlantic salmon (Salmo salar). J. Anim. Ecol. 47: 497-505.

Mortality of rearing Atlantic salmon was found to increase with population density when different sections of a coastal stream were compared. Emigration was not examined. Relates findings to species interactions although direct tests were not made.

Gibson, R.J. 1978. The behaviour of juvenile Atlantic salmon (Salmo salar) and brook trout (Salvelinus frontinalis) with regard to temperature and to water velocity. Trans. Amer. Fish. Soc. 107: 703-712.

Habitat selection and interactive behaviours of brook trout and Atlantic salmon were studied in two experimental stream channels. At low temperatures (9-10°C), both the trout and the salmon sheltered in rubble. The author notes that these fish may compete with longnose suckers for hiding places in the rubble. At warmer temperatures, the salmon preferred the faster waters of riffles. As water velocity increases, territoriality increases as with aggressive acts. Low velocities may initiate the hiding response of salmon regardless of water temperature. The author notes that in low velocity environments (pools), an active foraging strategy is usually adopted. The author also cites evidence for interactive segregation. In sympatry, Atlantic salmon occupy riffle habitat while the brook trout occupy the pool habitats. In allopatry, both species occupy riffle habitat. It would appear that brook trout also increase aggression towards conspecifics with velocity. When given a choice of shade or deeper waters, both the trout and the salmon tend to prefer the deeper waters. The author notes that turbulent water surfaces may also provide cover, particularly from avian predators.

Gibson, R.J. 1981. Behavioural interactions between coho salmon (Oncorhynchus kisutch), Atlantic salmon (Salmo salar), brook trout (Salvelinus frontinalis) and steelhead trout (Salmo gairdneri), at the juvenile fluviatile stages. Can. Tech. Rept. Fish. Aquat. Sci No. 1029. Department of Fisheries and Oceans, St. John's, Newfoundland. 116pp.

Steelhead trout were the most aggressive of all the species tested. Brook trout and Atlantic salmon were the least aggressive, forming loose schools in pool habitat with the dominant fish in the lead. Dominance was largely based on size - those growing the best being dominant in all cases. Severe competition would most likely occur between Atlantic salmon and steelhead trout (both being found predominantly in riffle habitat) and between coho and brook (both being primarily pool dwellers).

Ginetz, R.M.J. and P.A. Larkin. 1976. Factors affecting rainbow trout (Salmo gairdneri) predation on migrant fry of sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Bd. Can. 33: 19-24.

Experience proved to be a major factor in reducing the vulnerability of sockeye fry to rainbow trout predation. Light intensity also appeared to be a major factor, mortality due to predation increasing with light intensity. At low light intensities however, the relationship between both variables was reversed, predation increasing as light levels decreased. Stream turbidity and velocity also affected the survival of fry, both contributing to greater mortality when at low levels.

Glova, G.J. 1978. Pattern and mechanism of resource partitioning between stream populations of juvenile coho salmon (Oncorhynchus kisutch) and coastal cutthroat trout. Ph.D Thesis, University of British Columbia. 170pp.

During the late summer low flow, coho and cutthroat trout are partially segregated, the former found mainly in low velocity habitats and the latter in faster waters. In addition, coho prey selectively on adult insects while cutthroat consumed mainly insect larvae. This pattern of segregation was also observed in an artificial stream. Coho numerically dominated pools and the trout dominated riffles. When in allopatry however, both appeared to prefer pools. Under winter conditions, both species occupied the pool habitat.

Both species increased levels of aggression when food was present. At cool temperatures, aggression was low. Based on the evidence above, it is concluded that coho and cutthroat segregate interactively. The author also stresses the importance of behavioral flexibility in increasing survival.

Glova, G.J. and J.C. Mason. 1977. Comparison of coastal cutthroat trout populations in allopatry and those sympatric with coho salmon and sculpins in several small coastal streams on Vancouver Island, B.C. Fish. Mar. Serv. MS Rep. 36pp.

Includes observations on the interactions between the salmonids and sculpins.

Grant, J.W. and D.L.G. Noakes. 1988. Aggressiveness and foraging mode of young of the year brook char, Salvelinus fontinalis (Pisces, Salmonidae). Behav. Ecol. Sociobiol. 22: 435-445.

Brook char in streams adopt either an active or a sit-and-wait strategy for foraging and express a range of resource defence from territoriality to conspecific tolerance. In quiet waters, these trout adopt an active foraging strategy, express greater mobility and show little aggression towards conspecifics. As current velocities increase, aggression initially increases but drops at higher velocities. Also in response to increased current velocity, mobility decreases and a sit-and-wait foraging strategy is adopted. These behavioral changes are hypothesized to be related to maximum net energy returns. A literature review suggests that these behavioral changes may apply to other salmonids.

Grant, J.W.A. and D.L. Kramer. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. Can. J. Fish. Aquat. Sci. 47: 1724-1737.

Territory size in relation to fork length of salmonids was found to be a good predictor of carrying capacity of streams. Density dependent growth, mortality and emigration were all significantly correlated to a habitat saturation index derived from the territory-size regression.

Grant, J.W.A., D.L.G. Noakes and K.M. Jonas. 1989. Spatial distribution of defence and foraging in young-of-the-year brook charr (Salvelinus frontinalis). J. Anim. Ecol. 58: 773-784.

Relates the territory size of brook trout to their body size and energy requirements.

Gray, G.A., D.E. Palmer, B.L. Hilton, P.T. Lofy, S.D. Duke, P.J. Connolly, H.C. Hansel, J.M. Beyer, M.J. Parsley, M.G. Mesa, G.M. Sonnevil, L.A. Prendergast. 1986. Feeding activity, rate of consumption, daily ration and prey selection of major predators in the John Day Pool. Annual Report (1984) to the Bonneville Power Administration. National Fishery Research Center, Cook, Washington. 163pp.

Describes the food habits of major predators in the John Day Reservoir which includes northern squawfish. Includes an extensive literature review on predation control measures. Discusses the pros and cons of each method along with its applicability to large riverine systems.

Hall, F.A. 1979. An evaluation of downstream migrant chinook salmon (Oncorhynchus tshawytscha) losses at Hallwood-Cordua fish screen. California Department of Fish and Game, Anadromous Fisheries Branch Administrative Report No. 79-5. 19pp.

Sacramento squawfish were found to be the most important predator of chinook fry at the Hallwood-Cordua fish screen. Observed schooling responses appeared to reduce the rate of predation. Chinook released in "dribble" format suffered greater losses than those which were released as a "mass". The latter appeared to maintain their loose school. Predation was much greater at the fish screen than in the diversion channel.

Hall, F.A. 1980. Evaluation of downstream migrant chinook salmon, Oncorhynchus tshawytscha, losses in Clifton Court Forebay, Contra Costa County, California. California Department of Fish and Game, Anadromous Fisheries Branch Administrative Report No. 80-4. 15pp.

Chinook salmon losses attributed to predation ranged from 15% to 88% depending on the study site. The study however does not attempt to quantify the extent to which each predatory species contributes to these losses.

Hartman, G.F. 1965. The role of behaviour in the ecology and interaction of underyearling coho salmon (Oncorhynchus kisutch) and steelhead trout (Salmo gairdneri). J. Fish. Res. Bd. Can. 22: 1035-1081.

During spring and summer, coho and rainbow trout have similar microhabitat preferences and exert these preferences when in allopatry. But when in sympatry, interactive segregation is involved - coho displacing trout from the preferred pool habitats into riffle habitat. High densities and higher aggression levels at this time of the year appear to accentuate the interactions. In fall and winter, microhabitat preferences are different, coho defending pools and trout defending riffles.

Heggberget, T.G. and T.M. Heggberget. 1986. Behaviour of juvenile Atlantic salmon, Salmo salar L., in rapid and slow flowing sections of a small Norwegian stream. Aquacult. Fish. Manage. 17: 191-194.

The density of Atlantic salmon was observed to be much lower in slow waters than in fast waters. In fast waters, the salmon maintained a territory and feed on drift. In slower waters, the salmon expressed much greater movements and showed no evidence of territoriality. The authors suggest that the salmon switch foraging strategies in slower water from drift feeding to active foraging and that this may account for the reduced densities.

Heggenes, J. 1988. Effect of experimentally increased intraspecific competition on sedentary adult brown trout (Salmo trutta) movement and stream habitat choice. Can. J. Fish. Aquat. Sci. 45: 1163-1172.

Habitat selection of brown trout was examined at high and low densities. Resident brown trout appeared to have a competitive advantage over non-resident trout. The former occupied all favoured habitats and grew at a faster rate than the latter which occupied less favoured habitats. No emigration was observed due to overcrowding. Demonstrates the importance of prior residence in establishing dominance over other conspecifics.

Hillman, T.W. and J.S. Griffith. 1987. Summer and winter habitat selection by juvenile chinook salmon in a highly sedimented Idaho stream. Trans. Amer. Fish. Soc. 116: 185-195.

As chinook increase in size, they occupy progressively deeper and faster waters. During winter, 80% of the chinook emigrated from the system. Addition of large rubble substrate reduced emigration considerably, providing added cover for hiding chinook. Because of sedimentation, much of the added substrate was covered with silt and sand. Chinook emigration returned to pre-treatment levels.

Holey, M., B. Holender, M. Imhof, R. Jesien, R. Konopacky, M. Toneys and D. Coble. 1979. Never give a sucker an even break. Fisheries. 4: 2-6.

Little evidence that competitive interactions between suckers and salmonids result in dramatic reductions in the density of salmonids. Differences in microhabitat use appears to minimize interactions between the two species.

Holling, C.S. 1966. The functional response of invertebrate predators to prey density. Mem. Entomol. Soc. Can. 48: 1-86.

Describes the response of predators to prey density in the form of functional response curve. Includes a discussion of their biological significance.

Howland, H.C. 1974. Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. J. Theor. Biol. 47: 333-350.

Discusses the importance of swimming performance in a prey ability to avoid predation. Cites several examples obtained through the literature.

Hume, J.M.B. and E.A. Parkinson. 1987. Effects of stocking density on the survival, growth and dispersal of steelhead trout fry (Salmo gairdneri). Can. J. Fish. Aquat. Sci. 44: 271-281.

Little dispersal was observed among the trout fry regardless of the stocking density. Growth was inversely related to density. Mortality increased with stocking density. Density dependent growth and mortality was attributed to the higher levels of intraspecific competition for food.

Hunter, J.G. 1959. Survival and production of pink and chum salmon in a coastal stream. J. Fish. Res. Bd. Can. 16: 835-886.

Hunter refers to sculpins as major predators of pink and chum salmonid fry. Mortality due to this predation can be very high (average of 14%). Swamping predators with salmonid prey improved the numbers that survived (percentage lost decreased).

Jenkins, T.M. 1971. The role of social behaviour in the dispersal of introduced rainbow trout (Salmo gairdneri). J. Fish. Res. Bd. Can. 28: 1019-1027.

Hatchery reared rainbow trout failed to show any socially mediated density regulation responses (i.e emigration) when stocked in an empty stream. Aggression increased with density, but the level of aggression was not proportional to level of emigration. Although dispersal occurred, it was primarily through individual differences in habitat preference. Fish in large aggregates moved more extensively than fish in smaller groups or individually.

Jeppson, P.W. and W.S. Platts. 1959. Ecology and control of the Columbia squawfish in Northern Idaho lakes. Trans. Amer. Fish. Soc. 88: 197-202.

Gillnetting, explosives, reservoir level manipulations, and rotenone were employed over a 6 year period to reduce the numbers of squawfish in lake environments. The removal resulted in improved fishing for salmonids. The catch of predators declined by 90% over the length of the experiment.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (Salmo salar L. and S. trutta). Rep. Inst. Freshwat. Res., Drottningholm. 39: 55-98.

Explores the interactions between two salmonid species at different water velocities. At low velocities, aggression declined, and both species appear to form loose schools. At higher velocities, aggression was high and territories were actively defended.

Kennedy, G.J.A. and J.E. Greer. 1988. Predation by cormorants, Phalacrocorax carbo (L.), on salmonid populations of an Irish river. Aquacult. Fish. Manage. 19: 159-170.

Cormorants were found to fed heavily on salmonid smolts during spring. Mortality rates ranged from 51-66% for wild smolts and 13-28% for hatchery smolts. The difference in mortality is likely due to differences in population density, the latter being much larger than the former. Mortality is likely to be depensatory.

Kirn, R.A., R.D. Ledgerweed and R.A. Nelson. 1986. Increased abundance and the food consumption of northern squawfish (Ptychocheilus oregonesis) at river kilometer 75 in the Columbia River. North. Sci. 60: 197-200.

Discusses the food habits of squawfish and their abundance in the lower sections of the Columbia River. Predation on salmonids does not appear to be as intense (considered not to be significant) in the area when compared to the John Day Reservoir.

Kraft, M.E. 1972. Effects of controlled flow reduction on a trout stream. J. Fish. Res. Bd. Can. 29: 1405-1411.

Examines the effects of reduced streamflow on a brook trout population in a Montana stream. Streamflow was reduced by 67% and 90% in successive years. Significant changes in standing crop of trout only occurred with the highest reduction in streamflow. Emigration caused most of the changes in standing crop. There was also a tendency for fish to migrate from riffle areas into pools. Presumably, the higher densities in pools increased intraspecific competition, which in turn caused the observed emigration.

Larkin, P.A. 1956. Interspecific competition and population control in fresh water fish. J. Fish. Res. Bd. Can. 13: 327-342.

Discusses the role of competition in the population control of freshwater fish in streams and lakes.

Lister, D.B. and C.E. Walker. 1966. The effect of flow control on freshwater survival of juvenile chum, coho and chinook salmon in Big Qualicum River. Can. Fish Cult. 37: 3-25.

Stabilized flows and temperature regulation resulted in a substantial increase in the survival rate of chinook, chum and coho salmon. For chinook salmon, the increase in numbers was accompanied with a reduction in size and an earlier emigration time.

Lister, R.R. and D.D. Genoe. 1970. Stream habitat utilization by cohabitating underyearlings of chinook (Oncorhynchus tshawytscha) and coho salmon (Oncorhynchus kisutch) in the Big Qualicum River, British Columbia. J. Fish. Res. Bd. Can. 27: 1215-1224.

Juvenile chinook and coho salmon of the same size occupy similar microhabitats. Both species occupy stream margins soon after emergence. As they increase in size, they move away from the stream margins into progressively faster waters. However, because chinook fry emerge one month earlier than the coho fry and grow at a faster rate, they are larger than the coho at any given time. The size difference results in a high degree of spatial segregation. Discharge rates were held constant throughout most of the study.

Mace, P.M. 1983. Predatory-prey functional responses and predation by staghorn sculpins (Leptocottus artmatus) on chum salmon fry (Oncorhynchus kisutch). Ph. D Thesis, University of British Columbia.

The functional response of sculpins to various densities of coho fry was examined. Includes an extensive mathematical analysis of the four types functional response curves. Also includes an analysis of gull predation on fry in the Big Qualicum River.

Mace, P.M. 1983. Bird Predation on Juvenile salmonids in the Big Qualicum Estuary, Vancouver Island. Can. Tech. Rept. Fish. Aquat. Sci No. 1176. Department of Fisheries and Oceans, Vancouver, BC. 79pp.

Discusses bird predation on juvenile coho and chinook salmon rearing in an estuary. Includes recommendations to minimize salmonid losses and a preliminary study which examines the success of some of the recommendations that were implemented.

Martin, R.M. and A. Wertheimer. 1989. Adult production of chinook salmon at different densities and released as two smolt sizes. Prog. Fish-Cult. 51: 194-200.

Chinook salmon were reared at densities ranging from 6.6 to 24.3 kg/m^3. Growth was found to be inversely related to rearing density despite efforts to maintain high growth. In addition, food conversion efficiency decreased at high densities. This may be due to stress resulting from intraspecific competition. The reduced size of smolts at the higher rearing densities had a negative effect on adult return rate.

McCart, P. 1967. Behaviour and ecology of sockeye salmon fry in the Babine River. J. Fish. Res. Bd. Can. 24: 375-428.

Provides a list of predators which have been shown to prey of juvenile sockeye salmon in a river system. Includes both piscine and avian predators.

McFadden, J.T. 1969. Dynamics and regulation of salmonid populations in streams, p.313 329. In: T.G. Northcote [ed.] Symposium on salmon and trout in streams. Institute of Fisheries, University of British Columbia, Vancouver.

A few generalizations are presented which relate intra- and interspecific competition and population regulation to life history events. With respect to stream resident fry, territoriality causes dispersal (or emigration), therefore reducing the intensity of intraspecific competition. The level of emigration is roughly proportional to population density. Mortality of fry during the first few months can be very high (commonly > 90%). Intra and interspecific predation, starvation and exhaustion due to competitive interactions and physical factors can account for much of these losses. Temperature and food supply, by affecting growth, can influence the length of time a cohort is exposed to these hazards. When emigration is prevented, survival decreases as density increases. Apparently, fish density decreases rather than growth rate when food abundance decreases and this is generally accompanied by an increase in territory size. Predation appears to account for most of the mortality among juveniles and adults aside from environmental extremes.

Metcalfe, N.B., F.A. Huntingford and J.E. Thorpe. 1987. The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. Anim. Behav. 35: 901-911.

Exposure to predation causes a significant change in the foraging tactics of Atlantic salmon. They are less likely to orient to food particles and attack only those food items that come into close proximity. This trade-off between foraging and predator avoidance decreases over time after predator exposure.

Miller, R.B. 1958. The role of competition in the mortality of hatchery trout. J. Fish. Res. Bd. Can. 15: 27-45.

Demonstrates the mortality of hatchery reared catchable sized trout (2-3 years old) due to competition with wild trout of the same species. Concentrates on cutthroat trout. Conclusions are drawn from field experiments done on Gorge Creek, Alberta. The excessive build up of lactic acid in those fish introduced in sympatry with resident fish is interpreted as being the result of the physical activity generally associated with competitive interactions.

Mittelbach, G. 1986. Predator-mediated habitat use: some consequences for species interactions. Environ. Biol. Fishes. 16: 159-169.

A general discussion on the indirect effects of predation on habitat use and competitive interactions. Although the discussion concentrates on centrarchidae fishes, the principles are applicable to other fish.

Moore, S.E., B. Ridley and G.L. Larson. 1983. Standing crops of brook trout concurrent with removal of rainbow trout from selected streams in Great Smoky Mountains National Park. N. Amer. J. Fish. Manag. 3: 72-80.

Removal of rainbow trout resulted in an increase in the standing crop of brook trout. Evidently, competitive and/or predatory interactions are involved between the two species and these interactions can severely affect the growth of the subordinate species.

Mortensen, E. 1977. Density-dependent mortality of trout fry (Salmo trutta) and it's relationship to the management of small streams. J. Fish Biol. 11: 613-617.

Observed density dependent mortality when different stream sections were compared. Did not investigate the extent with which emigration may be involved. Put these findings into a management perspective.

Moyle, P.B. 1977. In defense of sculpins. Fisheries. 2: 20-23.

Presents the argument that sculpins in undisturbed streams do not pose a significant predatory or competitive threat to salmonids. Of the 7785 stomachs examined in 15 studies done in undisturbed streams, only 0.6% contained salmonid eggs or fry. However, the author does not state that sculpins will consume salmonid eggs and fry if they are presented to them. Chum and pink salmon appear to be the most vulnerable to sculpin predation. Chinook and coho fry on the other hand appear to effectively avoid sculpin predation. Although there may be some overlap in the food consumed by salmonids and sculpins, the vertical segregation between the two fishes minimizes competition. Thus competition does not appear to be significant.

Murphy, M.L. and J.D. Hall. 1981. Varied effects of clear cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Can. J. Fish. Aquat. Sci. 38: 137-145.

Clear-cut logging was found to increase the level of primary production by increasing the stream's exposure to sunlight. This greater level if productivity resulted in increases in fish and invertebrate biomass and a greater level of species richness. This relationship was mediated by stream gradient. The steeper the gradient the greater the level of productivity. It is believed that sedimentation may be responsible, being less of a problem in steep streams than in lower gradient streams.

Nilsson, N.A. 1967. Interactive segregation between fish species, p.295-313. In: S.D. Gerking [ed.]. The Biological Basis of Freshwater Fish Production. Blackwell Scientific Publications, Oxford.

Discusses the difference between interactive and selective segregation in fish communities and provides several examples from the literature.

Nilsson, N.A. 1978. The role of size biased predation in competition and interactive segregation in fish, p.303-325. In: S.D. Gerking [ed.]. Ecology of freshwater fish production. Blackwell Scientific Publications, Oxford.

Noakes, D.L.G. 1978. Social behaviour as it influences fish production, p.360-382. In: S.D. Gerking [ed.] Ecology of Freshwater Fish Production. Blackwell Scientific Publications, Oxford.

A general discussion of the relationship between social behaviour (territoriality and social hierarchies) and fish production. Provides several examples from the literature.

Oaten, A. and W.W. Murdoch. 1975. Switching, functional response and stability in predator prey systems. Amer. Nat. 109: 299-318.

A theoretical paper examining the role of prey switching in the functional responses of predator-prey systems and the concept of stability.

Olla, B.L. and M.W. Davis. 1989. The role of learning and stress in predator avoidance of hatchery-reared coho salmon (Oncorhynchus kisutch) juveniles. Aquaculture. 76: 209-214.

Stress due to handling may increase the predator detection and avoidance ability of hatchery reared salmonids. Coho that were "handled" prior to release appeared to survive better in the presence of predators than coho which were not similarly treated.

Partridge, B.L. 1982. The structure and function of schools. Sci. Amer. 246: 114-123.

Discusses the role of schooling behaviours as a predator avoidance strategy. Relates findings to functional response curves.

Patten, B.G. 1971. Predation on fall chinook salmon (Oncorhynchus tshawytscha) fry of hatchery origin. U.S. Nat. Mar. Fish. Serv. Special Scientific Report-Fisheries. No. 621. 14pp.

Sculpin predation on migrating chinook salmon fry can be a significant source of mortality. Of the species investigated, prickly sculpins, because of their larger size, appear to be the most voracious. Smaller chinook were preyed upon more often than larger individuals. Predation rates may be quite high. Also includes a brief discussion of the predation rates of large rainbow trout.

Patten, B.G. 1977. Body size and learned avoidance as factors affecting predation on coho salmon (Oncorhynchus kisutch), fry by torrent sculpin (Cottus rhotheus). NOAA Fishery Bulletin. 75: 457-459.

Sculpins appear to prey selectively on smaller fry. This may be related to the mouth gape of the sculpins or the ability of larger fry to avoided predation.

Peterman, R.M. 1977. A simple mechanism that causes collapsing stability regions in exploited salmonid populations. J. Fish. Res. Bd. Can. 34: 1130-1142.

Introduces the modified type II response curve and discusses it's biological significance.

Peterman, R.M. and M. Gatto. 1978. Estimation of functional responses of predators on juvenile salmon. Can. J. Fish. Aquat. Sci. 35: 797-808.

A general discussion on the function responses of predators in aquatic habitats. Includes a discussion on methods of estimating these functional responses and the difficulty of differentiating between a type II and type III response curve.

Peterson, J.H., M.G. Mesa, J. Hall-Griswold, W.C. Schrader, G.W. Short and T.P. Poe. 1990. Magnitude and dynamics of predation on juvenile salmonids in Columbia and Snake Rivers reservoirs. Bonneville Power Administration, Division of Fish and Wildlife. Annual Report of Research, 1989-1990, Portland, Oregon. 82p.

Squawfish predation of chinook salmon appeared to follow a type III functional response curve. The curve was derived from the variable densities of chinook passing through the McNary Dam over time. Predation was greatest during peak migration. Dead and injured prey were consumed more readily than live and healthy fish. The response of squawfish to chinook stressed by handling of perturbations in their environment did not differ significantly from controlled fish. A noteworthy observation: when under predatory pressure, the chinook salmon in the test chamber displayed a loose schooling response. Presumably, this is a adaptation to reduce the risk of predation.

Poe, T.P., H.C. Hansel, S. Vigg, D.E. Palmer and L.A. Prendergast. 1988. Predation by northern squawfish, walleye, smallmouth bass and channel catfish in a mainstem Columbia River reservoir: feeding ecology during the salmonid smolt out-migration, p.13-55. In: T.P. Poe and B.E. Rieman [eds.]. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-1986. Bonneville Power Administration, Portland, Oregon.

Through stomach content analysis, the extent with which squawfish prey on juvenile chinook salmon is followed over time and length of the reservoir. These data are related to the outward migration of chinook salmon.

Poe, T.P., P.T. Lofy and S.D. Duke. 1988. Feasibility of reducing or controlling predation induced mortality of juvenile salmonids in Columbia River reservoirs, p.153-173. In: T.P. Poe and B.E. Rieman [eds.]. Predation by Resident Fish on Juvenile Salmonids in John Day Reservoir. Bonneville Power Administration, Portland, Oregon.

A discussion paper on various predator control and prey protection measures and their applicability to large river systems. Includes a brief review of these techniques.

Pritchard, A.L. 1936. Stomach content analysis of fishes preying upon the young of Pacific salmon during the fry migration at McClinton Creek, Masset Inlet, British Columbia. Can. Field Nat. 1: 104-405.

Through stomach content analysis, Dolly Varden were found to be one of the major predators of Pacific salmon during the outward migration.

Reeves, G.H., F.H. Everest and J.D. Hall. 1987. Interactions between the redside shiner (Richardsonius balteatus) and the steelhead trout (Salmo gairdneri) in western Oregon: the influence of water temperature. Can. J. Fish. Aquat. Sci. 44: 1603-1613.

This study demonstrates the influence of temperature on the competitive interactions between redside shiner and rainbow trout. In cool waters (12-15°C), trout prevailed. They were strongly territorial and severely limited access of shiners to food. In addition, shiners were restricted to deeper and slower waters than when alone. The energetic cost of maintaining territories in the presence of shiners appeared to be negligible. In warmer waters (19-22°C), the shiners prevailed. They were more active and responded more quickly to food. Trout abandoned attempts to establish territories and migrated out of the channel. Production of trout in the presence of shiners was 54% less than in the absence of shiners. The authors also stress the importance of disease susceptibility in competitive interactions. At warmer temperatures, disease susceptibility increases and may therefore modify interactions between species.

Reimers, P.E. 1968. Social behaviour among juvenile fall chinook salmon. J. Fish. Res. Bd. Can. 25: 2005-2008.

The social behaviour of chinook was found to be similar to that of coho. Through agnostic behaviour, territories were established in riffle habitats and a social hierarchy in pool habitats. Agnostic vs aggregative behaviour appears to be a function of current, the former more prominent in faster waters and the latter in slower water.

Rensel, J., K.L. Fresh, J.J. Ames, R.L. Emmett, J.H. Meyer, T. Scribner, S. Schroder and C. Willis. 1984. Evaluation of potential species interaction effects in the planning and selection of salmonid enhancement projects. Species Interaction Work Group of the Enhancement Planning team, Washington. 80pp.

A review of salmonid interactions within the context of salmonid enhancement projects. An evaluation method is presented which categorizes the level of intensity of competitive and predatory interactions between salmonid species as well as with other species. Both marine and freshwater environments are examined.

Ricker, W.E. 1941. The consumption of young sockeye salmon by predaceous fish. J. Fish. Res. Bd. Can. 5: 293-313.

Predation by resident fish, particularly squawfish, on sockeye fry residing in a British Columbia lake. Squawfish had a significant impact on the numbers of fry in the system.

Rieman, B.E. and R.C. Beamesderfer. 1990. Dynamics of a northern squawfish population and the potential to reduce predation on juvenile salmonids in a Columbia River reservoir. N. Amer. J. Fish. Manag. 10: 228-241.

Eradication programs were evaluated in a simulation model to determine their effectiveness in reducing losses through predation. Northern squawfish, particularly larger members, prey heavily on juvenile salmonids and a reduction in their numbers by 10-20% annually would reduce salmonid predation by more than 50%.

Rieman, B.E., R.C. Beamesderfer, A.A. Nigro, S. Vigg, H.C. Hansel and D.E. Palmer. 1986. Preliminary estimates of loss of juvenile anadromous salmonids to predators in John Day Reservoir and development of a predation model. Bonneville Power Administration, Division of Fish and Wildlife 1986 Interim Report., Portland, Oregon. 53pp.

Of the salmonid losses not accounted for by the direct effects of dam passage, most is due to squawfish predation. Predation rate directly below the McNary Dam was the most intense, due in part to the large aggregation of squawfish in the area. Overall however, predation losses were greatest in the mid-reservoir area. Estimated mortality from predation during spring was 7-9% for chinook salmon (age I) and 10-15% for steelhead. During late summer, predation losses of chinook (age 0) ranged from 26-55%.

Rieman, B.E., R.C. Beamesderfer, S. Vigg and T.P. Poe. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River reservoir: IV Estimated total loss and mortality of juvenile salmonids to northern squawfish, walleye, and smallmouth bass, p.249-273. In: T.P. Poe and B.E. Rieman [eds.]. Predation by Resident Fish on Juvenile Salmonids in John Day Reservoir. Bonneville Power Administration, Portland, Oregon.

Mortality rates are reported for chinook salmon and steelhead trout as a result of the predatory activities of northern squawfish. Of all the predators in the system, squawfish cause the most mortality. Estimates range from 7 to 61 percent.

Ringstad, N.R. 1974. Food competition between freshwater sculpins (genus Cottus) and juvenile coho salmon (Oncorhynchus kisutch): an experimental and ecological study in a British Columbia coastal stream. Fish. Mar. Ser. Tech. Rept No. 457. 71pp.

Sculpins at natural densities did not affect the growth of coho salmon. However, at high densities, sculpins were able to crop down the benthos to such an extent that drift densities dropped. In turn, a corresponding drop in coho growth was observed.

Rondorf, D.W., G.A. Gray and R.B. Fairley. 1990. Feeding ecology of subyearling chinook salmon in riverine and reservoir habitats of the Columbia River. Trans. Amer. Fish. Soc. 119: 16-24.

Demonstrates the opportunistic nature of feeding in chinook salmon. Whether in riverine or reservoir habitats, the food organisms consumed most often were those which were available at the greatest density. Within each habitat however, a certain degree of selectivity was observed.

Rose, G.A. 1986. Growth decline in subyearling brook trout (Salvelinus frontinalis) after emergence of rainbow trout (Salmo gairdneri). Can. J. Fish. Aquat. Sci. 43: 187-193.

Prior to rainbow trout emergence, newly emerged brook trout grow at a fairly fast rate. After rainbow trout emergence, growth in brook trout declined dramatically and remained suppressed until rainbow trout shifted habitat preferences later in the summer. Evidence of the effect of competition on growth.

Ruggerone, G.T. 1986. Consumption of migrating juvenile salmonids by gulls foraging below a Columbia River dam. Trans. Amer. Fish. Soc. 115: 736-742.

Schlosser, I.J. 1985. Flow regime, juvenile abundance, and the assemblage structure of stream fishes. Ecology. 66: 1484-1490.

Examines community structure of stream fishes at different flow regimes. During low flow, juvenile abundance increased dramatically and three species emigrated from the system.

Schutz, D.C. and T.G. Northcote. 1972. An experimental study of the feeding behaviour and interaction of coastal cutthroat (Salmo clarki) and Dolly Varden (Salvelinus malma). J. Fish. Res. Bd. Can. 29: 555-565.

Feeding behaviour of cutthroat trout and Dolly Varden was examined in sympatry and allopatry. Although both populations expressed considerable plasticity in feeding strategy, Dolly Varden fed more successfully on benthic organisms and cutthroat on surface prey. These differences were not modified by interaction. Therefore, segregation between the two species appears to be of the "selective" type.

Shaffter, R.G. 1978. An evaluation of juvenile king salmon (Oncorhynchus tshawytscha) loss in Clifton Court Forebay. California Department of Fish and Game, Anadromous Fisheries Branch Administrative Report No. 78-21. 12pp.

Considerable losses were observed when chinook salmon of hatchery origin were released into the system. Mortality appeared to be size selective since the majority of the losses were fish if smaller sizes. This change in size distribution could not be attributed to growth since the post-release census started the following day after release. Predation losses appeared to be both of piscine and avian origin.

Simms, C.W., W.W. Bentley and R.C. Johnsen. 1977. Effects of power peaking operations on juvenile salmon and steelhead trout migrations-progress report 1976. National Marine Fisheries Service, Northwest Fisheries Center, Seattle, Washington. 77pp.

Fluctuating flows related to power peaking events can delay the seaward migration of young salmonids and thus prolong their exposure to potential predators.

Slaney, P.A. and T.G. Northcote. 1974. Effects of prey abundance on density and territory behaviour of young rainbow trout (Salmo gairdneri) in laboratory stream channels. J. Fish. Res. Bd. Can. 31: 1201-1209.

The density of rainbow trout in an artificial stream which permitted emigration was found to vary as a function of food abundance, the greatest density occurring at the highest level of prey availability. Density was apparently a function of territory size, which decreased as food abundance increased. Emigration was related to the level of aggression, both of which increased as prey availability decreased. Evidence of intraspecific competition.

Slaney, T.L., J.D. McPhail, D. Radford and G.J. Birch. 1985. Review of the effects of enhancement strategies on interactions between juvenile salmonids. Can. Ms. Rep. Fish. Aquat. Sci No. 1852. 72pp.

Review of the competitive and predatory interactions between stocked and wild salmonids in freshwater and marine habitats.

Solazzi, M.F., S.L. Johnson and T.E. Nickelson. 1983. The effectiveness of stocking hatchery coho presmolts to increase the rearing density of Juvenile coho salmon in Oregon coastal streams. Oregon Dept. Fish and Wildlife, Fish Division. Information Report No. 83-1. 14pp.

Although stocking programs successfully increased rearing densities, it resulted in a decrease in wild stocks. The decrease was attributed to the size advantage of hatchery reared coho which allowed them to out compete wild coho for food and space.

Stein, R.A., P.E. Reimers and J.D. Hall. 1972. Social interactions between juvenile coho (Oncorhynchus kisutch) and fall chinook salmon (O. tshawytscha) in Sixes River, Oregon. J. Fish. Res. Bd. Can. 29: 1737-1748.

The emergence of juvenile chinook and coho salmon was found to overlap in the Sixes River of Oregon. Initially, they occupy similar habitats and are distributed throughout the system. As temperatures increase through time, chinook remain in the warmer tributaries and mainstem. Coho are found primarily in the cooler tributaries. Temperature is thought to play a role in the segregation of the two species. In laboratory troughs, coho consistently out competed chinook for prime stream positions, allowing them to grow at a faster rate. In allopatry, chinook grew at a faster rate but not as fast as coho. This however may be a temperature related issue. The authors note that, at warmer temperatures, chinook are able to grow more effectively than coho (18 vs 13 °C respectively. Taking into consideration the observations of Lister and Genoe (1970), the growth advantage of chinook at these warmer temperatures may allow them to out compete coho for these profitable stream positions. Nevertheless, temperature appears to be a major factor mediating the interactions between these two species. Of note is the observation that coho defend larger territories than chinook whether in allopatry or sympatry.

Swales, S., R.B. Lauzier and C.D. Levings. 1986. Winter habitat preferences of juvenile salmonids in two interior streams of British Columbia. Can. J. Fish. Aquat. Sci. 64: 1506-1514.

Overwintering juvenile salmonids showed considerable habitat segregation. Coho salmon primarily occupied off channel ponds while chinook made use of riprap and deep pools containing log debris and steelhead trout shelter in crevices and beneath larger boulders. It is argued that the majority of chinook migrate out of the system to deeper and warmer habitats downstream. Dolly Varden were found in all habitats surveyed and showed no clear preference for on type over another. Although much of the segregation observed between the salmonids species of the system appeared to due attributed to selective forces, it is still possible that coho may out compete other species which may find the pond habitats attractive (e.g. rainbow and steelhead). The latter would be an example of interactive segregation.

Sylvester, J.R. 1972. Effect of thermal stress on predator avoidance in sockeye salmon. J. Fish. Res. Bd. Can. 29: 601-603.

The survival of sockeye salmon fry (prey) in the presence of coho salmon (predator) were examined under various thermal regimes. Both acclimation temperature and rapid temperature changes were found to severely affect the survival rate of sockeye fry in the presence of coho salmon. It would appear that temperature can have a great impact on predator avoidance by sockeye salmon fry.

Symons, P.E.K. 1971. Behavioral adjustments of population density to available food by juvenile Atlantic salmon. J. Anim. Ecol. 40: 569-587.

When food abundance is low, population densities decline - apparently due to increases in territory size.

Symons, P.E.K. 1974. Territorial behaviour of juvenile Atlantic salmon reduces predation by brook trout. Can. J. Zool. 52: 677-679.

Atlantic salmon which were given the opportunity to establish territories were less vulnerable to brook trout predation than Atlantic salmon not given the opportunity. Suggests that territoriality may offer a certain degree of protection from predators.

Taylor, E.B. 1988. Water temperature and velocity as determinants of microhabitats of juvenile chinook and coho salmon. Trans. Amer. Fish. Soc. 117: 22-28.

Water temperature and to a smaller extent, water velocity, had a significant effect on the microhabitat use of juvenile coho and chinook salmon. The juveniles of both species were more closely associated with cover and occupied areas of lower water velocity at 2°C than at 12°C. Large differences were observed in the response of both species to water temperature and velocity. Coho were more closely associated with cover, occupied mainstem areas more frequently and became more aggregated than chinook. Chinook salmon preferred faster waters than coho. Water velocity preferences appeared to drop at cooler temperatures for both species when in low-velocity waters but remained unchanged at higher water velocities. Microhabitat use was similar when each species was tested in allopatry and in sympatry, indicating that selective segregation allows for their coexistence in streams. Of note, hatchery reared fish behaved differently than wild-reared fish. Use of cover and pond areas was considerably lower in year 2 (Hatchery reared fish) than in year 1 (wild fish). In addition, pond habitat use as a function of temperature differed between populations. This may also be a size related effect.

Taylor, E.B. and P.A. Larkin. 1986. Current response and agnostic behaviour in newly emerged fry of chinook salmon, Oncorhynchus tshawytscha, from ocean- and stream-type populations. Can. J. Fish. Aquat. Sci. 43: 565-573.

Stream-type chinook showed a stronger positive current response and were more aggressive in both interspecific and intraspecific competitive interactions (with coho fry) than ocean-type chinook. These differences in behaviour are consistent with their length of freshwater residence. Coho fry clearly dominated chinook of both populations.

Taylor, E.B. and J.D. McPhail. 1985. Burst swimming and size related predation of newly emerged coho salmon Oncorhynchus kisutch. Trans. Amer. Fish. Soc. 114: 546-551.

Argues that burst swimming performance is the basis for the size related differences commonly observed in susceptibility to predation. Small fish were generally slower than larger fish during the initial 0.03 s of acceleration, the critical period of predator avoidance. In addition, maximum swimming speed was faster in large fish than in small fish, also contributing to the successful escape from predators.

Thompson, R.B. 1959. Food of the squawfish (Ptychocheilus oregonesis Richardson) of the lower Columbia River. U.S. Fish Wild. Ser. Fish. Bull. 158: 43-58.

Describes the food types consumed by squawfish. Considers predation on juvenile salmonids to be significant.

Thompson, R.B. and D.F. Tufts. 1967. Predation by Dolly Varden and northern squawfish on hatchery-reared sockeye salmon in Lake Wenatchee, Washington. Trans. Amer. Fish. Soc. 96: 424-427.

Examines the predaceous activities of Dolly Varden and northern squawfish towards sockeye fry in a lake system. Both appear to be major predators of sockeye salmon fry.

Tripp, D. and P. McCart. 1983. Effects of different stocking strategies on coho and cutthroat trout production in isolated headwater streams. Can. Tech. Rep. Fish. Aquat. Sci. No. 1212. 176pp.

Examines the effects of various stocking densities and release times of coho salmon on the production and mortality of coho and cutthroat trout populations in headwater streams. As stocking density increased, mortality increased. The authors presume that this is due to increased intraspecific and interspecific competition. The extent with which competitive interactions contribute to the overall mortality rate is unknown since only qualitative observations were made. Other sources of mortality such predation and malnutrition were not factored out.

Vigg, S. 1988. Functional response of northern squawfish predation to salmonid prey density in McNary tailrace, Columbia River, p.174-207. In: T.P. Poe and B.E. Rieman [eds.]. Predation by Resident Fish on Juvenile Salmonids in John Day Reservoir. Bonneville Power Administration, Portland, Oregon.

A study of the functional response of squawfish to different prey densities at the tailrace of the McNary dam. A type III response curve was observed.

Vigg, S., T.P. Poe, L.A. Prendergast and H.C. Hansel. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River reservoir: II. Consumption rates of

northern squawfish, walleye, smallmouth bass and channel catfish, p.59-115. In: T.P. Poe and B.E. Rieman [eds.]. Predation by Resident Fish on Juvenile Salmonids in John Day Reservoir. Bonneville Power Administration, Portland, Oregon.

Examines the food consumption rate of squawfish at different ages. The proportion of chinook fry and smolts which comprises the diet of squawfish is compared for each age group. Diel feeding chronology of squawfish is also explored.

Vondracek, B. and P.B. Moyle. 1983. Squawfish predation at Red Bluff Diversion Dam. Contract Report for Cal. Dept. Water Res. 34pp.

Studies were carried out to examine squawfish predation on migrating chinook salmon fry. Predation estimates ranged from 1.72% to 2.54% and were considered to be a bit high. The congregation of squawfish below the Red Bluff Diversion Dam was due to their spawning migration, which generally peaked in June. Wild chinook migration generally peaks much earlier in spring. Therefore the potential for squawfish predation on wild chinook may be minimal. Hatchery releases later in the season however may be more prone to predation.

Ware, D.M. 1971. Predation by Rainbow trout (Salmo gairdneri): the effect of experience. J. Fish. Res. Bd. Can. 28: 1847-1852.

Explores the role of experience in the predatory behaviour of rainbow trout towards novel prey. Relates findings to functional response curves and selectivity.

Wilzbach, M.A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream dwelling cutthroat trout (Salmo clarki). Can. J. Fish. Aquat. Sci. 42: 1668-1672.

Cutthroat trout in laboratory streams emigrated at a higher rate when food abundance was low (5% vs 15% total trout biomass). Cover did not significantly affect this response. However, cover use declined substantially when food abundance was low.

Withler, F.C. 1948. Fish predation on the young sockeye (Oncorhynchus nerka) in certain lakes of the Skeena River drainage as evaluated by study of the catches and stomach contents of predators obtained by gillnetting. M.Sc. Thesis, University of British Columbia. 52pp.

Evidence of burbot predation on juvenile salmonids based on stomach content analysis.

Wood, C.C. 1987. Predation of juvenile Pacific salmon by the common merganser (Mergus merganser) on Eastern Vancouver Island. I: Predation during seaward migration. Can. J. Fish. Aquat. Sci. 44: 941-949.

Mergansers fed almost exclusively on salmon smolts migrating seaward. Mortality rate attributed to merganser predation did not exceed 8% of any particular stock. Although this may represent a substantial number of fish, it is recommended that these losses be accepted. Because mortality appears to be depensatory, it is further recommended that smolt releases be increased to minimize losses.

Wood, C.C. 1987. Predation of juvenile Pacific salmon by the common merganser (Mergus merganser) on Eastern Vancouver Island. II: Predation of stream resident juvenile salmon by merganser broods. Can. J. Fish. Aquat. Sci. 44: 950-959.

Merganser ducklings, which forage in freshwater while young, were found consume large numbers of stream resident salmon fry and smolts. Mortality attributed to this predation was estimated to range between 24-65%. As the ducklings grew, they spent progressively more time in tidal waters and reduced their predation on juvenile salmonids.

Wood, C.C. and C.M. Hand. 1985. Food searching behaviour of the common merganser (Mergus merganser) I: Functional responses to prey and predator density. Can. J. Zool. 63: 1260-1270.

Mergansers were less successful at capturing young coho in the stream enclosure with cover than that without cover. Coho previously exposed to merganser predation where less vulnerable than those with no previous exposure. This response was only observed for smolts. Feeding success of mergansers was independent of flock size when they numbered less than 25 birds. An asymptotic (Type II) functional response curve was observed, i.e. attack rate increases asymptotically with prey density. Smolt where preferred over fry.

Woodsworth, B.L. 1982. The predatory functional responses of the prickly sculpin (Cottus asper) to density of sockeye salmon (Oncorhynchus nerka) fry. M.Sc. Thesis, University of British Columbia.

Includes a description of functional responses and attempts are made to distinguish between a type II and type III response curve in the predation of sockeye fry by sculpins. Based on mortality curves, it appears to that a type II response is involved.

Yocum, T.G. and T.A. Edsall. 1974. Effects of acclimation temperature and heat shock on the vulnerability of fry of lake whitefish (Coregonus clupeaformis) to predation. J. Fish. Res. Bd. Can. 31: 1503-1506.

Acclimation temperature was found to increase the effectiveness with which the predator was able to capture and handle the whitefish fry (prey). Acclimation temperature did not apparently alter the predator avoidance behaviour of the fry. Brief exposure to lethal temperatures however did increase the vulnerability of fry to predation. Optimum temperature for swimming performance and other physiological variables related to predator avoidance was not taken into consideration in the discussion.